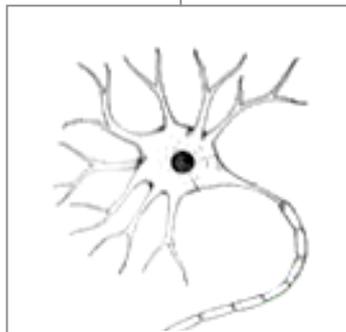


# Wisdom through reflection

The mirror neuron system and its role in learning

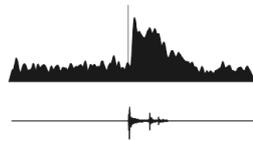


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## \* | SUMMARY

Since their discovery in monkeys some seventeen years ago, mirror neurons have been the focus of an extensive debate. These neurons are active both when a monkey observes an action and when it executes the same action. Clustered in the ventral premotor cortex and inferior parietal lobule, these areas form the so-called mirror neuron system. Multiple brain imaging studies have shown activity in human brain areas homologous to mirror neuron areas in monkeys while watching and executing actions. It is therefore likely that humans also possess a mirror neuron system. This system has many connections to other brain areas and is thought to be involved in action understanding and empathy. Another possibility, which is the main topic of this thesis, is that it is also involved in certain types of learning.

Mirror neurons mainly seem to code for the goals of observed actions and through connections with the limbic system they are also able to couple emotions to certain facial expressions. Indeed in both monkeys and humans they seem to be important for understanding others actions and could play a role in learning of appropriate social interactions. In humans, mirror areas show more activity than in monkeys during observation of movements themselves, next to their goals. Humans also show the ability to imitate observed actions exactly and also imitate to a much greater extent than monkeys do. Also new actions can be imitated and become integrated into the motor repertoire. The human mirror system therefore also seems to be involved in imitation learning. Finally the discovery of audiovisual mirror neurons, which respond to both vision and sound of certain actions in monkeys, also indicates this system could be involved in coupling words to certain actions. Especially in humans it probably plays a role in language learning and comprehension of language.

In contrast to the direct evidence of mirror neurons in monkeys, hardly any direct evidence exists for mirror neurons in humans. In imaging studies it is not correct to simply ascribe mirror neuron activity to those brain areas that are both activated during observation and execution of action. At this moment only one preliminary study using depth electrodes shows that humans indeed possess neurons with mirror properties. Future research should shed more light on this issue and show which neurons exactly are active in humans in conditions studied so far using brain imaging techniques.

The mirror neuron system indeed seems to play an important role in several types of learning. It is probably essential for imitation learning in humans. Furthermore it reduces time and costs for learning actions and goals from others by direct and automatic linking of observed actions and corresponding motor areas. In humans this is also true for action related language. However one needs to keep in mind that this system is not responsible for any type of learning on its own. It integrates information from other brain areas and in turn it is also regulated by other brain areas. It mainly is an important link in the whole process of action and goal learning.

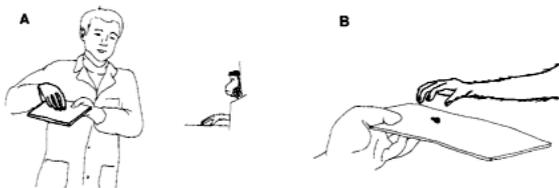
# 1 | INTRODUCTION

In the early 1990's a monkey (*Macaca nemestrina*) was sitting in a laboratory, an electrode connected to a single neuron in its premotor cortex. The aim of the experimenters, who put the monkey in this position, was to study activity patterns of neurons in area F5 during certain behavioural situations. What actually was discovered was something completely different. When an experimenter picked something up from a table using his hand the neuron to which the electrode was connected would fire. This happened even though the monkey did not move; it merely observed the experimenter picking up the item from the table. What made this neuron even more interesting was that it also fired when the monkey itself performed the same action (grasping the item (a bit of food) from the table; figure 1). More neurons in the same brain area (F5) were tested and it seemed that the first neuron was not an exception. A relatively large proportion of neurons in F5 seemed to have the same properties (di Pellegrino et al., 1992). Since this study an ever growing body of work has been done on investigating the exact properties and activity patterns of these neurons, which became known as “mirror neurons” a few years later (Gallese et al., 1996).

Until now, no detailed single-cell recordings have been done to show the presence of mirror neurons in humans (Rizzolatti & Craighero, 2004; Dinstein, 2008), simply because it is much harder and can often only be done in patients giving consent. There is, however, an increasing amount of evidence that, like monkeys, humans also possess brain areas with mirror properties. Due to the expanding area of non-invasive techniques to measure brain activity, more light is shed on brain areas involved in both action observation and action execution and connections between these and other areas. Such techniques include functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS), positron emission tomography (PET), electroencephalography (EEG), magnetoencephalography (MEG).

By discovering ever more properties of mirror neuron systems in both humans and monkeys, also more questions arise. Is the mirror neuron system (MNS) involved in understanding others? How did it change from monkey to human? Are there many brain areas in humans evolutionary homologous to those in monkeys and could the evolution of the MNS have led to the development of speech in humans? What, for example is the effect of a dysfunctional MNS? Is this really responsible for symptoms seen in patients with autism spectrum disorder (ASD) as currently hypothesized?

A question that incorporates a bit of each of these questions is what the role of the MNS might be in learning. It seems likely that at least in some ways the MNS is involved in aspects of learning, because it couples observation and execution of actions. Nevertheless, not much research addressing this possibility has been carried out. Although some work has been done showing a possible role of the MNS in the forming of motor memories (Stefan et al., 2005; 2008). Whether the MNS really plays



**Fig 1.** Neurons in area F5 of the monkey fire both when an experimenter grabs an item while the monkey watches passively (A), and when the monkey itself grabs the item in the way the experimenter did (B). From di Pellegrino et al., 1992

a role here, how important it is and whether it could play a role in other types of learning will be the scope of this thesis. First I will discuss differences between the monkey and human MNS and how this might lead to differences in importance for learning. Next I will investigate different types of learning and what could be possible roles of the MNS, with special focus on imitation and the acquired function of speech in humans. Finally I will have a look at some research and theories about the implications of a dysfunctional MNS and if this indeed affects the learning abilities.

## 2| DIFFERENT MIRROR NEURON SYSTEMS

**A**s described earlier, the first mirror neurons were discovered in area F5 of the macaque brain (di Pellegrino et al., 1992; Figure 2). Since then a lot of research has been done on mirror neurons, and more areas have been discovered that contain neurons with mirror properties. First by using more single cell recordings in monkeys, but later also through the use of non-invasive brain imaging techniques. Especially when research started with the aim to find a similar mechanism in the human brain. Soon after the discovery of mirror neurons in the monkey brain it was already suggested that humans might possess a similar system (Gallese et al., 1996). Earlier experiments had already shown higher activation levels in arm muscles and in the inferior frontal gyrus (IFG) homologue to area F5 in the monkey brain, during observation of grasping actions (Fadiga et al., 1995; Rizzolatti et al., 1996). Therefore after the discovery of mirror neurons in the monkey brain, it seemed very plausible that these earlier findings hinted at a similar system in the human brain. Indeed, since the late 1990's the evidence for a human MNS has become ever more substantial. With different techniques, ranging from looking at activity patterns using fMRI to inducing artificial lesions using TMS, also different aspects of this system have been discovered.

In this chapter I will discuss similarities and differences between the monkey and the human MNS. Most likely monkeys and humans are not the only living beings having neurons with mirror like properties. Other social mammals might possess a similar system too (Arbib, 2002). This could be an interesting field of research in the near future, but because not much is known about the existence of such systems at present, I will focus on the monkey and human MNS. These are by far the most extensively studied examples to date and therefore can provide most information on the role the MNS might play in learning.

### THE MONKEY MIRROR NEURON SYSTEM

#### *Area F5 (frontal MNS)*

It is probably clear by now that area F5 in the monkey brain is an important area in the monkey MNS (Figure 2). Area F5 is located in the rostral part of the monkey ventral premotor cortex (vPMC) and mirror neurons only account for part of all neurons present in this area (Fogassi et al. 1998, cited in Dinstein, 2008). The earliest studies mainly found mirror neurons responding to observation/execution of hand and arm movements (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996; see also figure 1). Later on also “mouth” mirror neurons were found, that responded either to ingestive or communicative mouth action observation/execution (Ferrari et

al., 2003). The only difference here is that mirror neurons responding to the observation of communicative mouth actions also responded to ingestive mouth actions made by the monkey itself. This could indicate a link from the use of mouth actions only for ingestion to its more symbolic use in the form of communication signals (Ferrari et al., 2003; Rizzolatti & Craighero, 2004).

It was also discovered that a small proportion of mirror neurons in area F5 do not just respond to the observation of an action, but also to just the sound of that action. This is especially true for actions that occur more frequently in the monkeys' natural repertoire such as breaking a peanut (Kohler et al., 2002). These neurons were dubbed 'audiovisual mirror neurons'. A more detailed study even showed subclasses of audiovisual mirror neurons (Keysers et al., 2003). Some respond to the vision and the sound of an action together as well as the vision and the sound separately. Others have a response to vision and sound together that is as large as the sum of responses to vision and sound separately. A last class of audiovisual mirror neurons responded most strongly to the perception of an actions sound alone. Only a relatively small proportion of mirror neurons in area F5 has been tested in this experiment. It is therefore possible that more audiovisual mirror neurons responding to sounds and vision of other actions exist, which could enable a more detailed perception and understanding of actions performed by others.

#### *Area 7b or PF (parietal MNS)*

Next to area F5, mirror neurons have also been discovered more posterior in the monkey brain, in area 7b or PF (Rizzolatti & Craighero, 2004; Figure 2). This area is located in the rostral part of the inferior parietal lobule (IPL) itself located in the parietal lobe. The percentage of neurons with mirror properties in the IPL discovered so far is only about three percent (Gallese et al., 2002, cited in Rizzolatti & Craighero, 2004), but they nevertheless contribute to the MNS as a whole. Mirror neurons in PF are mostly involved in motor aspects of actions (Iacoboni et al., 1999). Output from this area is sent to the vPMC and area F5 within it, which makes for a direct link between these two mirror neuron areas (Rizzolatti & Craighero, 2004).

#### *STS*

The superior temporal sulcus (STS) is a sulcus in the temporal lobe, containing neurons that respond to observed actions performed by others, much like the mirror neurons in area F5 (Buccino et al., 2006). These neurons, however, do not have motor properties and therefore cannot be classified as mirror neurons. The reason for mentioning the STS here anyway, is that the neurons in this area do send output directly to PF and the other way around. This could play a role in imitation, discussed in chapter 4.

### THE HUMAN MIRROR SYSTEM

Even though in the course of recent years an ever-growing body of non-invasive brain imaging studies has shown an MNS very much like that of monkeys in humans, it remains important to keep on being critical about findings. One should not project too much of what is known about the monkey MNS directly onto humans under the assumption that the monkey and human brain work in the same way. As already mentioned, up to now only non-invasive techniques have been used to study MNS responses and functions in humans and many studies mainly focussed on brain areas analogue to those in the monkey brain. The disadvantage of the non-invasive studies

mainly is the resolution. Activity in certain brain areas can be measured, but only up to a level of neuron populations, not to single neurons. This makes it harder to know whether for example the same neurons are firing in response to both observation and execution of an action, or if there are different neurons present in a same small area only firing in response to observation or execution of an action (Dinstein, 2008; Dinstein et al., 2008). The areas discovered in the human brain showing mirror properties, however, do show great correspondence to those in the monkey brain. Also one of the first few studies carried out recently, using an adaptation paradigm, showed adaptation of neurons in the inferior parietal cortex during execution of an action after the observation of that same action in humans (Chong et al., 2008).

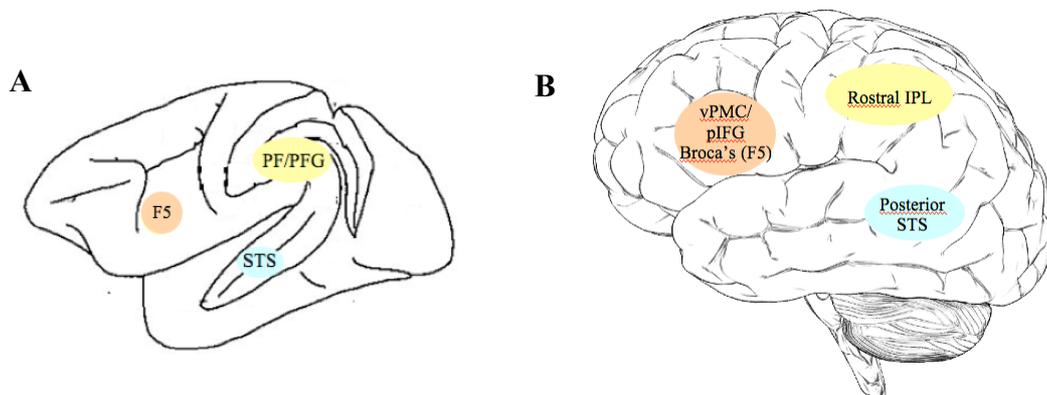
All those many studies strongly suggest that mirror neurons should be present in the human brain as well. But as long as there are no studies directly measuring single cells with mirror properties in the human brain, I prefer to use mirror areas when referring to humans. These areas certainly have mirror properties, but whether it is about single cells or closely connected cells has yet to be proven.

### *Mirror areas*

Up to now, the areas in the human brain showing mirror properties found and most studied, closely resemble those found in the monkey brain (summarized in Rizzolatti & Craighero, 2004; Iacoboni & Dapretto, 2006; Figure 2). The frontal MNS seems to be a little more developed, encompassing a part of the vPMC homolog to the monkey area F4, the posterior part of the IFG and Broca's area, both homolog to the monkey area F5. The parietal MNS, as in the monkey, mainly consists of the rostral part of the IPL and also in humans, the STS seems to be an important MNS supporting area.

### *Differences and similarities*

The main differences between the monkey and human MNS is in their functioning.

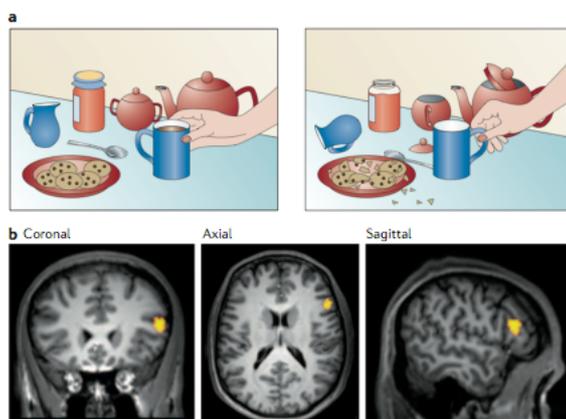


**Fig. 2.** Lateral view of the left side of the monkey brain (A) and the human brain (B). Areas known to contain neurons with mirror like properties are shown in the colours rose (frontal MNS) and yellow (parietal MNS). In the monkey, the frontal MNS of consists of area F5 in the premotor cortex and the parietal MNS consists of the inferior parietal lobule (PF/PFG). In humans, the frontal MNS consists of the posterior inferior frontal gyrus (pIFG) together with the ventral premotor cortex (vPMC) and Broca's area (homolog to the monkey area F5). The parietal MNS in humans consists of the rostral part of the inferior parietal lobule (IPL), homolog to the PF/PFG in the monkey brain. In both monkeys and humans, the MNS is thought to be supported by activity from the superior temporal sulcus (STS, indicated in blue) with which it forms a circuit.

Whereas mirror areas in humans respond both to actions where there is interaction with an object (transitive actions) and to the same actions when they are mimed and to so-called intransitive actions (actions not involving an object) (Buccino et al., 2001; 2006; Umiltà et al., 2001), mirror neurons in monkeys only seem to respond to observed transitive actions (e.g. Gallese et al., 1996; Lepage & Théoret, 2007) and not to the other two action types (Buccino et al., 2001; 2006; Rizzolatti & Craighero, 2004).

A special thing about mirror neurons both in monkeys and in humans is that they do not just seem to code for the exact motor properties of an observed action, as coded for in the parietal MNS, but also for the goal meant to achieve with the action (Buccino et al., 2006). Action goals are coded for in the frontal MNS (Iacoboni et al., 1999; Iacoboni & Dapretto, 2006). For example Iacoboni et al. (2005) discovered that mirror neuron activity in the IFG differs when two observed actions are visually the same (e.g. grasping a mug), but have different goals that can be inferred from the surroundings (e.g. grasping a mug to drink, or to clean it; figure 3). Next to this, some mirror neurons in area F5 in the monkey brain respond during observation of ingestive mouth actions, while others respond stronger to communicative than to ingestive mouth gestures. Although both mouth movements are alike, different mirror neurons respond to them, suggesting that a monkey can distinguish the two mouth gesture types (Ferrari et al., 2003). More evidence of mirror neurons coding for the goal of an action comes from a study by Umiltà et al. (2001). They performed an experiment in which a, for the monkey initially visible, object was hidden behind a screen. When a human experimenter subsequently grabbed the object with one hand, the action thereby partly obscured by the screen, the same mirror neurons responded that also respond to grabbing an object with the hand in full view. However when a screen was placed in the same position, but without an object behind it as the monkey could see before the screen was placed, no mirror neurons responded to the same grabbing action by the experimenter. It thus seems that the mirror neurons ‘know’ whether the experimenter is actually trying to grab an object or not, thereby inferring the goal of the action rather than just react to the movement itself.

Looking at the different locations and properties of mirror neurons in monkeys and mirror areas in humans, it might very well be possible that they play a role in certain forms of learning. They form a link between context and goals and seem to distinguish between self and other. The only question now is exactly in what types of learning mirror neurons could be involved. In the next chapter different types of learning will be discussed as well as the possibility for mirror neurons to play a role in these types of learning.



**Fig. 3.** (a) Different intentions/goals (drinking on the left and cleaning up on the right) with a visually comparable action, elicits different mirror neuron activity in the IFG in humans (b). From Iacoboni & Dapretto, 2006

### 3 | LEARNING AND THE MIRROR SYSTEM

**L**earning comes in many different forms. One can learn from single events, but sometimes repetition is necessary to remember something. We can learn by ourselves or from others and about facts or events. But most importantly during our lifetime we learn how to behave in our environment, how to cope in certain situations, how to reach a goal, avoid danger and how to communicate with others. Learning is an important part of survival. When looking at the properties of the mirror neuron system, it is certainly possible that it plays a role in certain learning moments in our lives and those of other animals possessing mirror neurons. It has to be said, however, that the mirror system is not enough by far to be responsible for any type of learning on its own.

But let us first have a look at the variety of ways through which can be learnt about the outside world and in which ways the MNS could be connected to these processes. For learning not only associations need to be made, but plasticity is also needed to form new networks in the brain. This aspect will also be looked at in the MNS.

#### SELF-LEARNING

Logically it is to be expected that the MNS does not play a role in learning in which no other animals are involved next to the learner himself. An example of such a type of learning is through trial-and-error. Here the learner tries out different means to reach a certain goal until he or she has found a suitable way to do so. Through this mechanism the learner teaches himself. This type of learning, however, requires only motor action and matching of action results and the imagined goal. No action observation is needed and therefore mirror neurons are unlikely to be necessary here, because half their function is about registering observed actions.

During trial-and-error learning in humans it seems that the important MNS supporting Brodmann's area 46 becomes active (Jueptner et al., 1997), which could indicate an important indirect effect of this type of learning on the functioning of the MNS. The function of area 46 in relation to the MNS will be discussed later in this chapter.

Associative and non-associative learning are also two types of learning in which one does not learn from others. Associative learning encompasses both classical and operant conditioning, while non-associative learning involves habituation and sensitization. Although learning through these ways could involve other individuals, it is not the case that one also learns from those individuals, but rather about them. Associative and non-associative learning are essentially about learning stimuli and their consequences, mostly unconsciously, and it is hard to imagine mirror neurons playing a role in these types of learning. Here, only associations involving the learner himself directly play a role, so there seems to be no need for neurons responding to both action observation and execution of those same actions.

Overall it seems unlikely that the MNS is playing any role of importance in types of learning in which no other individuals than the learner himself are actively involved or 'used'. Also in other studies of the MNS, these types of learning are never mentioned. This does not mean, however that learning by oneself and the MNS are completely unrelated to each other, only is it not the MNS which is needed for learning on ones own, but rather the other way around; the MNS often uses experience obtained through self-learning (Calvo-Merino et al., 2005; 2006).

## LEARNING FROM OTHERS

Indications that the MNS is involved in learning processes in which one learns something from others, whether by means of active teaching or through mere observation, are much stronger. This does not come as a surprise, because most often learning from others involves observation and, simultaneously or after a certain delay, execution of a certain action. These are actions in which both on the observation and execution side the MNS can be active and could form a link between the two stages of these types of learning. Being able to directly match what you observe with activation of your own motor system can enable you to understand observed actions (Rizzolatti et al., 2001; Heiser et al., 2003; Iacoboni & Dapretto, 2006) and thereby to learn from them.

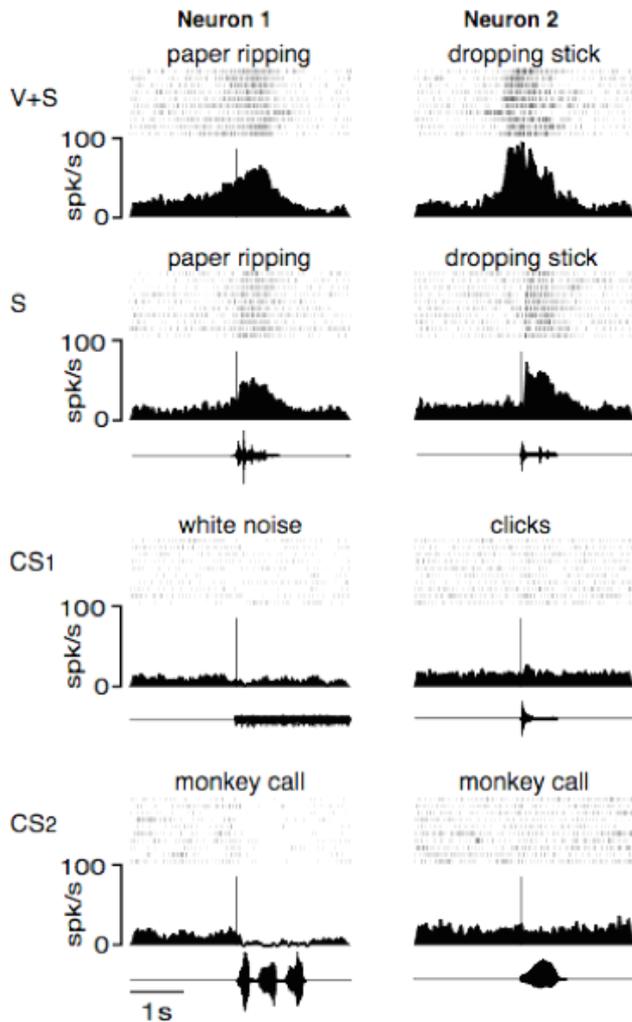
### *Prerequisites for learning from others*

To be able to learn from actions we observe in the outside world, we need to understand what we see first. If we see actions performed by others, but do not understand how they are executed, it will be hard to replicate those actions ourselves. A hypothesis dealing with this issue of action understanding is the ‘direct-matching hypothesis’ (Rizzolatti et al., 2001). This hypothesis holds that action understanding is done by matching an observed action directly with one’s own motor representation of that action when one would execute it. The MNS could well be a good explanation for the direct-matching hypothesis, and play an important role in action understanding. It is able to couple action observation and execution (Buccino et al., 2006). This system alone though is not enough to account for the whole process of action understanding (Arbib, 2002; Iacoboni & Dapretto, 2006).

Depending on the kind of learning it can be more important to understand the goal of an action or the kinematic properties, the exact movements executed, of an action. The MNS, at least in humans, seems capable of coding for both these possibilities. As described earlier, the frontal MNS is mainly concerned with coding the goals of actions. In humans the inferior parietal lobule (parietal MNS) has been found to respond to motor aspects of observed actions (Buccino et al., 2004; Chaminade et al., 2005). The robust connection between these two regions can make for a good integration of both kinematics and goals of observed actions (Iacoboni et al., 1999; Iacoboni & Dapretto, 2006; Iacoboni & Mazziotta, 2007). Therefore humans might be able to understand more actions than monkeys do. Since monkeys seem to lack the capabilities to understand the motor components of an action separately from the action goal (Rizzolatti & Craighero, 2004), they could be less capable of understanding actions without a visible goal. Indeed, as mentioned in the previous chapter, the monkey MNS does not respond to intransitive and mimed actions. The only exception is the set of mouth mirror neurons, which seem to respond specifically to intransitive (communicative) mouth actions (Ferrari et al., 2003) mentioned before. This, of course, does not mean that monkeys do not understand any actions they observe, in fact they might recognize actions and intentions of others (Iacoboni, 2005; Rizzolatti, 2005), but it does confine the types of actions they can understand and possibly learn.

One way through which monkeys might recognize actions is through their audio-visual mirror neurons. Those neurons do respond to sounds of specific actions naturally performed by monkeys, but not to other sounds (Kohler et al., 2002; Keyser et al., 2003; see figure 4). This implies that the monkeys at least distinguish known action sounds from other sounds. Thus whether it is through sound or vision, the

MNS both in monkeys and in humans seems to match observed actions with own motor activity and thus provides a mechanism through which understanding of observed actions becomes possible (Rizzolatti et al., 1996; Rizzolatti & Craighero, 2004; Montgomery et al., 2007).



**Fig. 4.** Activity (spikes per second) of two monkey audio-visual mirror neurons while seeing and hearing (V+S) or only hearing (S) actions incorporated in the monkey's natural repertoire (paper ripping or stick dropping), and while hearing non action-related sounds (white noise or a monkey call). Neuron 1 responds specifically to V+S and S of paper ripping and does not show any response to the two non action-related sounds. Neuron 2 shows the same responses, only instead of ripping paper, it responds particularly to V+S and S of dropping a stick. From Kohler et al., 2002

Next to understanding observed actions, it can also be important to understand emotions shown by others in certain situations (Hurley, 2008). Understanding emotions can give information about what emotions are appropriate in which situations and how the social relations are within the direct environment. The MNS has also been proposed to play a role in recognition of emotions, both in monkeys and in humans (Arbib, 2002; Iacoboni & Dapretto, 2006; Cheng et al., 2008; Hurley, 2008; Rizzolatti & Fabbri-Destro, 2008). Jacob & Jeannerod (2005) doubt if the MNS has any connection to emotion recognition. The examples they use, however, only involve actions from which no, or hardly any emotions can be read. Mostly facial gestures and small, strongly emotion-connected movements such as scratching are important to sense someone else's emotions. Signals also coded for by the MNS. These are also signals often unconsciously imitated during social interactions (Chartrand & Bargh, 1999). The fact that the MNS also has connections with the

limbic system (Iacoboni & Mazziotta, 2007) makes it ever more likely that it at least contributes to the recognition of emotions in others.

Understanding an action is a prerequisite for being able to learn it. By both understanding the action itself and the emotion underlying it, the observer is also able to learn in which contexts certain actions should be performed (Rizzolatti et al., 2001). Contexts themselves are not coded for by the MNS, but likely stored in the closely related pars triangularis in Brodmann area 45 (Monfardini et al., 2008). Understanding transitive actions requires merely the coding of an action's goals, which the monkey MNS seems to do (e.g. Kohler et al., 2002; Umiltà et al., 2008). Humans can even go a step further than monkeys, for they possess mirror areas coding for the exact motor properties of observed actions.

### *Memory*

Obviously, to be able to learn one needs memory. There are two broad classes of memory, each one subdivided into several components. The first class is declarative memory, also called explicit memory. Of the two types this is the memory most consciously used. It is involved in storing knowledge of facts and events from the past (Reber, 2008). Although this memory class is what most people think of when talking about memory in general, the MNS probably does not play a role in the formation of such memories. It does play a role in the second memory class called nondeclarative or implicit memory. This class mostly involves memories such as needed for priming, habit learning and skill learning, which mostly form unconsciously (Reber, 2008). But the MNS is again not the only brain system bringing about implicit memory on its own. Rather the system for nondeclarative memory is “not a memory system per se, but rather reflects a general principle of inherent plasticity in neural circuits that can support certain types of learning” (Reber, 2008, pp. 119). The MNS could well be one of these neural circuits, and it is indeed very plausible that during life it is shaped through the principle of Hebbian learning (Keyser et al., 2003; Gazzola et al., 2007; Iacoboni, 2009).

### *Experience*

Hebbian learning is based on the idea that neurons close to each other, which are also often active at the same time, tend to form strong connections for better simultaneous firing (Iacoboni, 2009). This makes for better associations in the brain and could gradually shape neural circuits through experience. Evidence is accumulating that connections in the MNS are also shaped by this or a very similar process, and that young monkeys and human children do not possess a fully functional MNS yet. Although some mirror-like functions seem already active soon after birth, these are likely due to an innate mechanism, which is therefore not learning dependent (Heyes, 2001). The MNS itself responds mostly to actions observed that are already in the motor repertoire of the observer (Buccino et al., 2004; Rizzolatti & Craighero, 2004). This has been shown nicely by Calvo-Merino et al. (2005), who used experienced dancers in ballet and capoeira and non-dancers in an fMRI experiment. It seemed that either of the two groups of dancers had higher activity in various brain areas (for an important part in the MNS) when watching performances of their own dance style, than when watching performances in the unknown dance style. For the non-dancers activity was relatively low while watching both dance styles. It seems therefore that dancers have a good feeling with their own dance style, and that stronger activation in the MNS is an important factor in this recognition. This suggests that learning a new motor act could contribute to extending the functioning of the MNS. Therefore some

coupling with this system is needed. Once new motor acts have been learnt and integrated, the MNS can subsequently cause a faster recognition of observed actions. This can be seen as one of the forms of learning the MNS contributes to; one has learnt to recognize actions and goals faster by being able to match them to one's own motor knowledge. This is one example of a way the MNS contributes to learning, which is, as mentioned earlier, often an unconscious process.

Another good example of the MNS being shaped by experience comes from a study by Catmur et al. (2007). First motor-evoked potentials (MEPs) were measured in index and little finger muscles during observation of movements of these fingers. As expected muscle MEPs were highest when observing movements also made with those muscles (i.e. index finger muscles showed the highest MEPs during observation of index finger movements, and little finger muscles during observation of little finger movements). After that some of the participants underwent 'countermirror training', during which they had to move their index finger when they observed a little finger movement and the other way around. The other half of the participants 'practiced' with congruent finger movements. After the training the countermirror group showed higher MEPs in index finger muscles when observing little finger movements and vice versa. MEPs in the congruent group showed no difference from the pre-training measurements. It seems that conscious and consequent execution of a certain movement when observing a certain (incongruent) action can reshape connections within the observation-execution matching mechanism, thought to be the MNS. This again makes a form of Hebbian learning plausible.

There is also evidence from monkeys that experience with observing certain actions can modify the MNS. Normally the monkey MNS only responds to actions observed when this contains a biologic effector (hand, mouth, leg) interacting with an object (Buccino et al., 2006). When, however, monkeys that grew up in a human environment were tested for their MNS responses, it was discovered that certain mirror neurons specifically responded to observation of actions in which tools were used. The monkeys had, in the presence of humans, seen many actions involving tools. In their MNS these tools probably have been integrated as extensions of the natural effector (the hand in this case) (Ferrari et al., 2005). These mirror neurons responded much weaker to the vision of grasping hand actions, but still responded when the monkey made a grasping hand movement itself. These tool mirror neurons therefore probably code for the goal of an action and can 'learn' to see a tool as an extension of the hand and another means to reach the same goal as with a grasping hand action (Ferrari et al., 2005; Umiltà et al., 2008). Also after explicit training to use different types of pliers did mirror neurons in monkeys fire both when observing and executing tool-grasping actions (Umiltà et al., 2008). This again shows that in monkeys, as in humans, the MNS is not an unchangeable system, but that it is plastic and complex, and can be shaped by experience with novel motor acts.

#### *Brodman area 46*

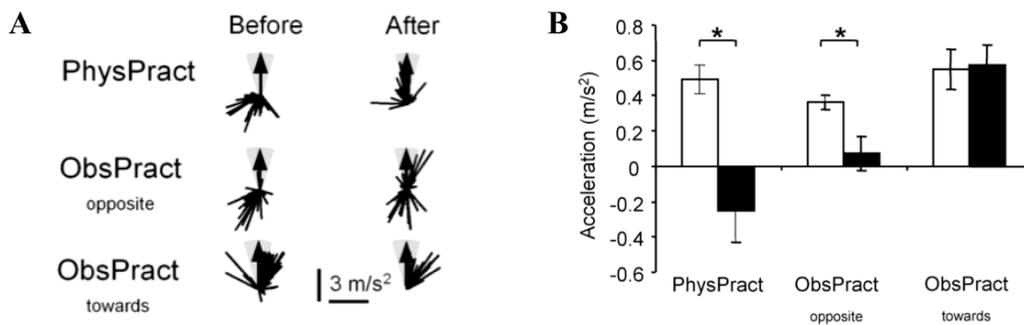
The MNS does not recombine motor acts on its own into a new form. When learning new motor actions, separate motor elements need to be recombined in order to understand and imitate those observed actions. It has been found that in humans Brodmann area 46, adjacent to the frontal MNS, probably plays an important orchestrating role in ordering and matching motor elements. This allows us to obtain a good representation of an observed new action. First an observed action is decomposed into elementary components (Buccino et al., 2004; Rizzolatti & Craighero, 2004) and after that area 46 likely recombines these elements to recreate

an action that matches the observed action. After this recombination, the new action is implemented into the MNS (Buccino et al., 2004; 2006) and the action will be easier to recognize for the observer. Now we can say the observer has learnt an action, will be able to understand and more easily execute it the next time the action is performed by another individual. This role of Brodmann area 46 has been shown nicely in an experiment by Vogt et al. (2005). In this fMRI study differences in brain activation were compared when participants were watching familiar motor actions (guitar chords), learnt the previous day, or unknown guitar chords. Both action types had to be imitated a few seconds later. Indeed activation in area 46 differed significantly, with much higher activity during the observation of unknown chords than activity during practiced chords. This shows a supporting role of area 46 in the learning of new actions comprising action components already in the observer's motor repertoire, but in a new combination or order. This is what the authors call the 'restructuring hypothesis'. Once an action has been practised a few times, it becomes more integrated into the MNS and the supporting function of area 46 is no longer needed. One has to keep in mind that the recombining action has not been shown directly, and therefore this remains a hypothesis. Nevertheless it is a very plausible assumption.

It seems likely that with the help of area 46, the MNS could well play a major role in imitation and learning through imitation. At least this seems to be the case in humans. In monkeys the function of the MNS is more limited to the recognition and understanding of observed actions and their goals (Rizzolatti & Craighero, 2004; Iacoboni, 2005) and the imitation of already familiar actions (Ferrari et al., 2006). This difference in the ability to learn new actions through imitation between monkeys and humans exists for two reasons. First, the humans MNS, as opposed to the monkey MNS, codes for both goals and means (kinematics) of actions, whereas the monkey MNS mainly codes for the goals (Rizzolatti & Craighero, 2004). This means that a monkey can use the goal of an observed action, but does not obtain a copy of the motor components of the observed action. This makes it more difficult to imitate exactly the action observed (however see the next chapter for a different view on this idea). Secondly in humans the frontal lobe, containing Brodmann area 46, has expanded significantly through evolutionary time. It could therefore be that the much smaller area 46 in monkeys does not have the orchestrating role it has in humans. The monkey MNS is therefore not able to decompose an observed action into separate motor elements and recombine these into a new form (Rizzolatti, 2005). The relation between imitation learning and the MNS will be discussed in more detail in the next chapter.

### *Observation*

Sometimes imitation is not even needed to form a memory of a new motor act. Merely observing a new action can also elicit changes in the brain and cause us to learn or at least memorize that action (Frey & Gerry, 2006; Monfardini et al., 2008). Stefan et al. (2005), amongst others, showed this principle in a TMS study. Participants watched movies of a hand making thumb movements in a certain direction opposite to or congruent with that activated by TMS. After 30 minutes the TMS signals alone evoked thumb movement potentials in the direction of the observed stimulus, whether the TMS evoked movement direction had been opposite to or congruent with these observed movements (figure 5). Although the real change seemed to have occurred in the primary motor cortex (M1), the MNS is a very likely candidate for the matching of the observed action with its motor activation in M1. The MNS is probably at the basis of the formation of this observational action memory in



**Fig. 5.** Changes in TMS evoked responses before and after physical practice (PhysPract) and observational practice (ObsPract<sub>opposite</sub>) opposite to TMS stimulated direction of thumb movement and before and after observational practice in the same direction as TMS stimulated thumb movements (ObsPract<sub>towards</sub>). **(A)** In the two opposite training types, directional responses are significantly changed towards the observed (and imitated in the PhysPract condition) movement direction. In the matching condition (ObsPract<sub>towards</sub>) there is no change in movement direction before and after training (as is to be expected). Arrow indicates movement direction of observed thumb movement, black lines indicate direction of TMS evoked responses. **(B)** The same data presented in a graph, showing that PhysPract has a somewhat stronger effect than ObsPract<sub>opposite</sub> on changing the evoked direction. ObsPract<sub>towards</sub> does not change evoked direction. Open bars: before training, filled bars: after training. From Stefan et al., 2005

the motor cortex. It has to be said that participants who simultaneously physically imitated the action they saw had a better formation of this motor memory, indicating an important role for imitation in learning (Stefan et al., 2005). Nevertheless this study showed that mere observation can also lead to memory formation and is at the basis of action learning.

While the MNS probably is at the basis of motor learning, it also makes use of actions previously learnt. Therefore it not only produces memories, but uses them as well. It has even been suggested that the MNS can use visuomotor associations recently learnt through either trial-and-error learning (first section of this chapter) or observational learning. This would need a connection between the fronto-striatal system in which trial-and-error learning is thought to take place, and the front-parietal MNS (Monfardini et al., 2008). Whether these areas really have good connections that allow for information exchange should be investigated more thoroughly.

A study investigating the connections between the MNS and surrounding areas during action observation in monkeys was carried out by Nelissen et al. (2005). An advantage of this study is that it was carried out using fMRI, which gives a better overview of active brain regions than the single cell studies often used in monkeys. The authors found that, next to the most extensively studied sub-area F5c, also sub-areas F5a and F5p and neighbouring areas 45A and B were active during grasping action observation. It was also discovered that, next to action movement, area 45B seems to play an important role in object recognition during action observation. Sub-area F5a seems to be most important for recognition of actions themselves. This distinguishes it from sub-area F5c that only responds when, next to a grasping action, also the context (the whole demonstrator, in this case the experimenter) is in full view. Taken together, all these results suggest that a set of several closely associated separate areas (mainly areas F5a and c and 45B) contribute to the understanding of observed actions. The action itself is coded for by F5a, the context by F5c and the

objects involved, which also might lead to comprehension of the action goal, by area 45B. The fact that this study used fMRI also makes it easier to compare these results to human MNS studies and get some insight on how results obtained through fMRI studies in general can be interpreted.

An interesting recent discovery suggests that the MNS could well have another function next to mirroring observed actions. While also making use of learnt motor actions, it can prepare a response action to the one observed rather than an imitative action. In their experiment Newman-Norlund et al. (2007) showed that participants had a higher MNS response when told to perform a complementary than an imitative action to an observed action. The authors ascribe this effect to the so-called 'broadly congruent mirror neurons'. These mirror neurons make up about two thirds of the total number of mirror neurons and respond when both the observed and executed actions are alike, but not necessarily exactly the same. They fire mostly based on the goal of an action, not the means to reach this goal. The last third of the mirror neurons consists of so-called 'strictly congruent mirror neurons', which respond only to observation and execution of actions which, next to the goal, are also much alike in means to reach the goal (diPelegriano et al., 1992; Rizzolatti & Craighero, 2004). The broadly congruent mirror neurons could, according to Newman-Norlund and colleagues, code for actions to be executed that logically follow an observed action. This executed action does not need to be the same as the observed action, but rather is a response and therefore often complementary to the observed action. It is an interesting theory, which certainly deserves more attention. For now there is not much other evidence supporting it and therefore more research into this area is needed. One needs also to take into account the effect shown in the study by Catmur et al. (2007), because before each trial, participants in the Newman-Norlund et al. study practiced proper responses first. This could have led to (temporary) changes in MNS response, explaining the obtained results in a different way. Nevertheless it will be good to look at the MNS from a slightly different angle.

## MOTOR IMAGERY

Next to learning an action through trial-and-error or by observing others, it is also possible to imagine an action being performed and learn it through that way (Buccino et al., 2006). This process is called motor imagery. For this, the presence of a second individual is not necessary, although the idea for a new action often comes from someone else. Motor imagery can also be done by first watching an action and subsequently rehearsing it by repeating the movements before the mind's eye. Action execution is not part of motor imagery.

Of course it is very difficult if not impossible to show this type of skill acquisition in monkeys. It is simply not possible to tell what a monkey is seeing or can see in its imagination, let alone to instruct a monkey to imagine a certain action. Therefore such studies can only be conducted in humans.

One thing that is unique to humans is their possession extensive use of language. This seems also to be the most important factor for motor imagery. Either someone can tell us directly what action to imagine, or instructions can be written down. Due to language active teaching without the use of actions themselves can take place and is a typically human characteristic. Through language people can transmit the performance of actions without the necessity of the transmitter (verbal instructor or writer) being capable of performing the actions himself. During motor imagery the MNS, among some other brain areas becomes active, suggesting that during this

process the MNS might play an important role by stimulating the appropriate motor areas. This way learning is possible in the same way as through imitation. Indeed it also has been shown that while listening to action related language, certain parts of the MNS become active. This interesting possibility for learning in which the MNS plays a role will be discussed in chapter 5.

Looking at the different aspects of learning of different motor skills, the MNS is often one of the active systems. This makes it therefore very plausible that the MNS is an important network involved in the acquisition of new motor skills. However, it is never the only system active during learning processes, which shows again the complexity of the brain; the MNS cannot be seen as the only mechanism for one type of learning. Even between people the MNS can vary while observing actions. Women seem to have higher MNS activity when observing actions performed by another human being than men do (Cheng et al., 2006; 2008). This is probably due to the difference in empathy between the sexes. Women tend to be more emotionally involved with others than men. This indicates that other brain areas, such as the limbic system for example, can also influence MNS activity. The many connections between the MNS and other areas therefore makes determining the exact function of the MNS in learning a real challenge. In the next chapters the role of the MNS in imitation learning and some connections between the MNS and language will be discussed in more detail. Dysfunction of the MNS will also be discussed to give an image of the functions of this system by looking at what goes wrong when it is (partially) shut down.

## 4| IMITATION

**P**robably the most important role in learning of the MNS in humans is during imitation learning. The direct matching between action observation and execution seems to make this system an important link in the process of imitating others. Defining imitation is important here, because this concept can be interpreted in several different ways. The most common definition is that ‘true imitation’, the form of imitation this chapter will mainly deal with, encompasses the “capacity to learn to do an action from seeing it done” (Buccino et al., 2004). This distinguishes true imitation from lower forms of imitation, such as priming and emulation or imitating. It also differs from imitating actions one recognizes because they are already incorporated in ones own motor repertoire. This type of imitation is also often referred to as copying behaviour. True imitation and learning new actions by doing so is a complex process, which combines action observation, fragmentation, recombination, imagery, and execution (Buccino et al., 2006). Indeed, true imitation is found in only very few species so far (Hurley, 2008). Because here the role of the MNS in learning is being investigated, the mentioning of imitation in this chapter will refer to true imitation.

Although imitation is not always adaptive on the short-term (think of imitating of useless actions by children), on the longer term it can be a very efficient tool for acquiring new (motor)skills (Hurley, 2008). Especially when, like in adults, the urge to imitate is more controllable. It can diminish the need for costly trial-and-error learning, which is still needed when only goal emulation takes place. This way the

spread of an efficient new method of reaching a certain goal can spread more easily through a population. Of course trial-and-error learning is still needed for new discoveries to be made, but learning through imitation certainly increases fitness.

## IMITATION IN MONKEYS

In monkeys true imitation has hardly ever been observed, and if so, learning did not seem to go as fast as in humans (e.g. Iacoboni, 2005). Mainly imitation observed by monkeys concerned movements already in their behavioural repertoire. These are movements that mainly are important social signals and since they are not new to the monkeys, no learning is involved in this type of imitation (Ferrari et al., 2006). The general idea is that true imitation had its first subtle start in monkeys, evolved somewhat further in primates (apes show more signs of imitation learning than their predecessors) and finally reached the state we currently only see in humans (Arbib, 2005; Vogt & Thomaschke, 2007). The fact that monkeys nevertheless possess a MNS indicates that imitation of novel actions is not the primary function of this system (Rizzolatti & Craighero, 2004), but rather a function acquired through evolution, making use of the initial properties of this system.

An interesting point is that monkeys do seem to recognize when they are being imitated. As Paukner et al. (2005) demonstrated, with two experimenters sitting in full view of a macaque. When one of the experimenters imitated the exact movements the monkey was making and the other experimenter also made monkey-related movements, but not connected to the movements the monkey was making at that moment, the monkey looked significantly more in the direction of the imitating experimenter. This shows that the monkey probably has some clue about a relation between its own movements and those of the imitator. Although this ability is still simpler than the actual act of imitating itself, it can well be a prerequisite for the ability to imitate. It is not sure, however whether the monkeys really attribute an intention to imitate to the imitator, or whether they merely recognize their own movements in those the imitator makes (Paukner et al., 2005).

The common idea, as mentioned in the previous chapter, is that the monkey MNS does not code for the kinematics of an action. Due to this idea, the forthcoming conclusion is that this could be one of the reasons why monkeys do not imitate. However, the fMRI study by Nelissen et al. (2005) challenges this view. This study showed that during the observation of mimicked grasping actions not involving an object/goal, sub-area F5a did become active. Activity was also higher during observation of goal directed grasping actions. The use of fMRI in this study gives a better overview of active areas in the brain during observation of different actions than single cell studies do. To discover the exact properties of the F5a neurons, single cell studies focussed on this area have to be carried out, but the Nelissen et al. study showed the interesting possibility that monkeys also possess a region coding for intransitive actions. If this is true, other theories concerning the lack of imitation in monkeys become more plausible. For example the theory of expansion of the frontal lobe in humans, which created the orchestrating role of Brodmann area 46, as mentioned in the previous chapter. The theory attributing lack of imitation learning to the inability to code for the actions themselves could seriously be challenged.

It is most likely that the primary function of the MNS is in recognizing actions and intentions of others (Iacoboni, 2005). This could also explain the finding of the coding by the MNS for actions complementary to those observed, as described in the previous chapter (Newman-Norlund et al., 2007). The MNS might have started off as

a system enabling one to observe others and respond to their actions in a proper way, rather than to learn from others by repeating what they are doing. But because the connection between the MNS and learning is the main subject here, this chapter will mainly focus on humans and their imitation learning abilities.

## IMITATION IN HUMANS

Humans, in contrast to other animals, seem perfectly able to learn new motor skills through the act of imitation. This could be due to the seemingly more advanced brain regions coding for action kinematics (e.g. the parietal MNS, Iacoboni et al., 1999). The type of learning that occurs through imitation is not a conscious process (Stefan et al., 2005) as is learning of new words for example. It rather is somewhat subtler and is best to be described as “acquiring fluency in the execution of already familiar basic movements in a certain “novel” sequence” (Vogt & Thomaschke, 2007, pp. 498). As discussed in the previous chapter even just observing actions can result in the formation of motor memories, but imitating an observed action seems to stimulate the learning process even more. Various studies have been carried out, demonstrating this principle.

### *Development of imitation*

In very young children imitation is not very controlled. Actions are often imitated when they are observed, even if imitation is not functional or relevant at that moment. In fact, a debate is still going on about whether newborn children already possess a MNS, or if their imitation mechanisms are based on an innate releasing mechanism (Iacoboni & Dapretto, 2006; Lepage & Théoret, 2007). One study showed the possibility of the presence of a (developing) MNS in 36-month old children (Fecteau et al., 2004), but since most studies on children, like this one, use only one or a few subjects, it is often hard to draw firm conclusions about the findings. For children imitation can be an important way to learn new actions and movements and to get more control over their environment, even if this happens somewhat involuntarily. Indeed, children seem to imitate many actions they observe (Lepage & Théoret, 2007). Where adults seem to be able to suppress motor stimulation generated by the MNS while observing actions, in young children the inhibitory mechanism probably has not developed far enough to affect MNS activation (Lepage & Théoret, 2007). One possible inhibitory mechanism might be located in the spinal chord, for it has been found that counter-mirror signals come from this region while observing a hand grasping action. This probably prevents unwanted imitation of the observed action by suppressing motor stimulation coming from the observation-execution matching mechanism (Baldissera et al., 2001). Another inhibitory mechanism is probably located in the inferior frontal cortex (Deiber et al., 1998).

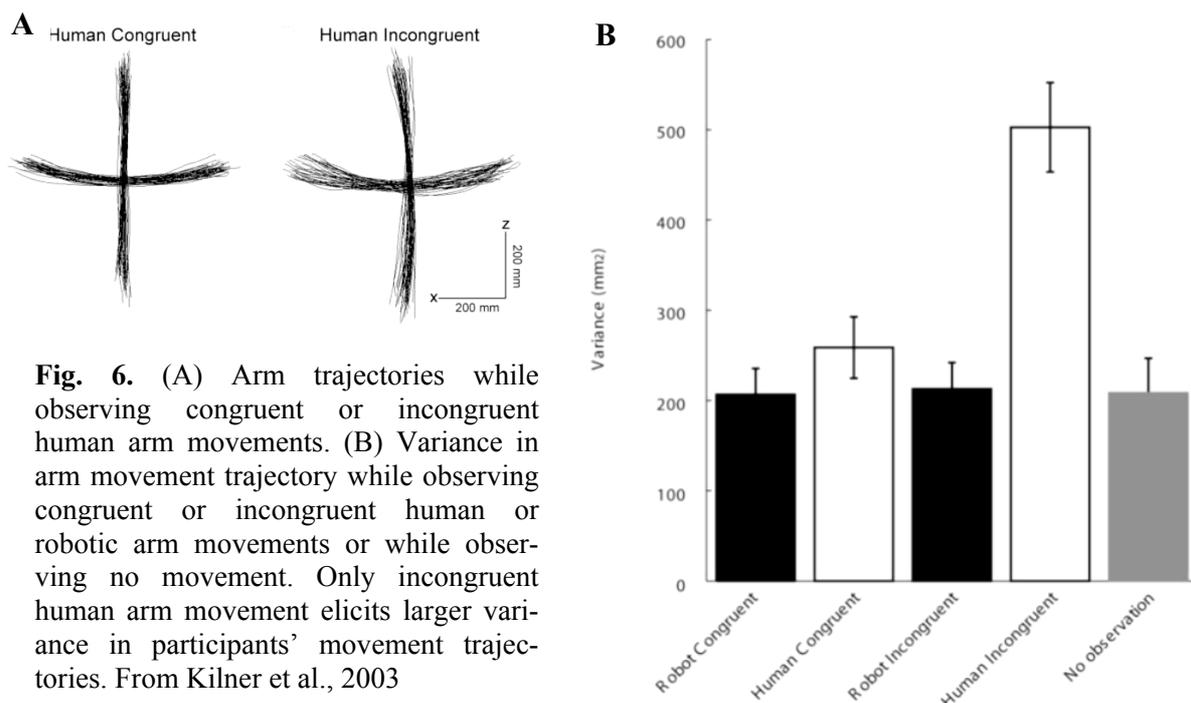
It is interesting however to see that also in adults not all observed actions are completely inhibited. Chartrand and Bargh (1999) show in their experiment that while interacting, people tend to unconsciously imitate subtle movements their partners make; the so-called ‘chameleon effect’. This is not without function, for these imitations seem to smoothen contact between people and also it could have a function in emotionally understanding others. Indeed more empathic people tend to imitate such actions more pronounced than do less empathic people (Chartrand & Bargh, 1999).

These studies show that during different stages of life imitation has different prevailing functions, from automatic action imitation during childhood to learn many motor actions, to more subtle automatic imitation during adulthood for use in social situations. Imitation learning in adults is much more controlled and not spontaneous.

### *Behavioural studies*

First several studies have been done in recent years to show the influence of observed movements on executed movements. Craighero et al. (2002) for example looked at execution of a grasping movement with a certain orientation when watching images of grasping hands in different orientations. They showed that correct grasping went faster when participants were simultaneously watching an image of a hand grasping in a matching orientation as opposed to a hand grasping in a different orientation. Kilner et al. (2003) conducted a similar experiment using movement of the whole arm while observing another human arm or a robotic arm making either congruent or incongruent movements. Observed incongruent human arm movements significantly effected executed movements of the participant (figure 6), while incongruent robotic arm movement did not. This last finding might be due to a weaker response of the MNS to non-biologic effectors, as is the case in monkeys (Buccino et al., 2006). Studies like these make, at least for biological movement, the direct-matching hypothesis very plausible and again show that a system linking observed and executed actions, like the MNS, could well play an important role in this.

In 2008 Stefan et al. carried out an experiment based on the same principles as the Stefan et al. 2005 study (figure 5). One important difference was that now the authors also looked at the influence of simultaneous action observation and execution while again stimulated with TMS. It turned out that both physical and observational practice of thumb movements in the same direction resulted in a significantly better directional response afterwards than did only physical practice or physical practice in the opposite direction of observed thumb movements.



TMS was also used in another study (Torriero et al., 2007). Only here it was applied to the dorsolateral prefrontal cortex during observation of a demonstrator solving a task. Brodmann area 46, possibly involved in MNS activity as discussed before, is part of the dorsolateral prefrontal cortex. When, by using TMS, activity of this area was inhibited while the subject was watching the demonstrator solve the task, the subject was significantly slower in imitating the observed actions. This again shows the importance of this area in supporting the MNS during imitation of actions with new motor sequences. Also it again emphasizes that the MNS cannot be responsible for imitation learning on its own. The cerebellum, for example, also seems to take part in the process of motor skill learning (Torriero et al., 2007).

A study applying TMS more directly to part of the MNS (Broca's area and its counterpart in the right hemisphere, the right pars opercularis (RPO)) also showed the importance of this area in action imitation (Heiser et al., 2003). Subjects had to imitate key presses, while either Broca's area (considered part of the MNS and homolog to the monkey area F5), RPO, or, as a control, the occipital cortex was inhibited using repeated TMS pulses (rTMS). The latter area is not considered part of the MNS and therefore not expected to impair imitation when inhibited. Indeed only during inhibition of Broca's area and the RPO subjects seemed to make significantly more errors when imitating the key presses than during occipital cortex inhibition. This also shows that in Broca's area activity probably is not due to inner speech, but really is representation of the action itself. Inner speech is not likely because inhibition of both Broca's area and the RPO thwarts imitation. Since the RPO is not involved in speech, different results would have been expected if Broca's activity was due to speech production. As this was not the case, the authors ruled out inner speech and decided Broca's area was definitely part of the MNS (Heiser et al., 2003).

The experiments discussed here clearly indicate that there must be a direct link between action observation and action execution. Associations with the MNS are easily made, but to show whether this really is a good explanation, one also has to study brain activity during action observation and imitation. Combining results from such studies with those from the behavioural studies can shed more light on the role of the MNS in imitation learning.

### *Imaging studies*

There has been some debate about the underlying mechanisms of imitation learning. Some suggested that direct matching does not take place during action observation and that the motor system only became active during physical practice afterwards, making use of observational experience. Others argued that during observation motor areas do become involved, enabling better imitation in a later stage. Over time, more studies have been carried out supporting the latter hypothesis, rather than the former (summarized in Vogt & Thomaschke, 2007). This means that during imitation learning the MNS could indeed play a supporting role through its proposed use of direct matching.

An interesting study showing the activation process in the brain during imitation learning was carried out by Buccino et al. (2004). The authors looked at activation patterns in naïve participants while observing and executing guitar chords. They found that even observing chords played by an experienced guitar player with the intention to imitate the chords afterwards, elicited higher activation of the IPL (parietal MNS) in the naïve participants than during plain observing, without the intention to imitate the chords. This gives a good indication of the role of the MNS in imitation learning. MNS activity was also high during the subsequent stages of

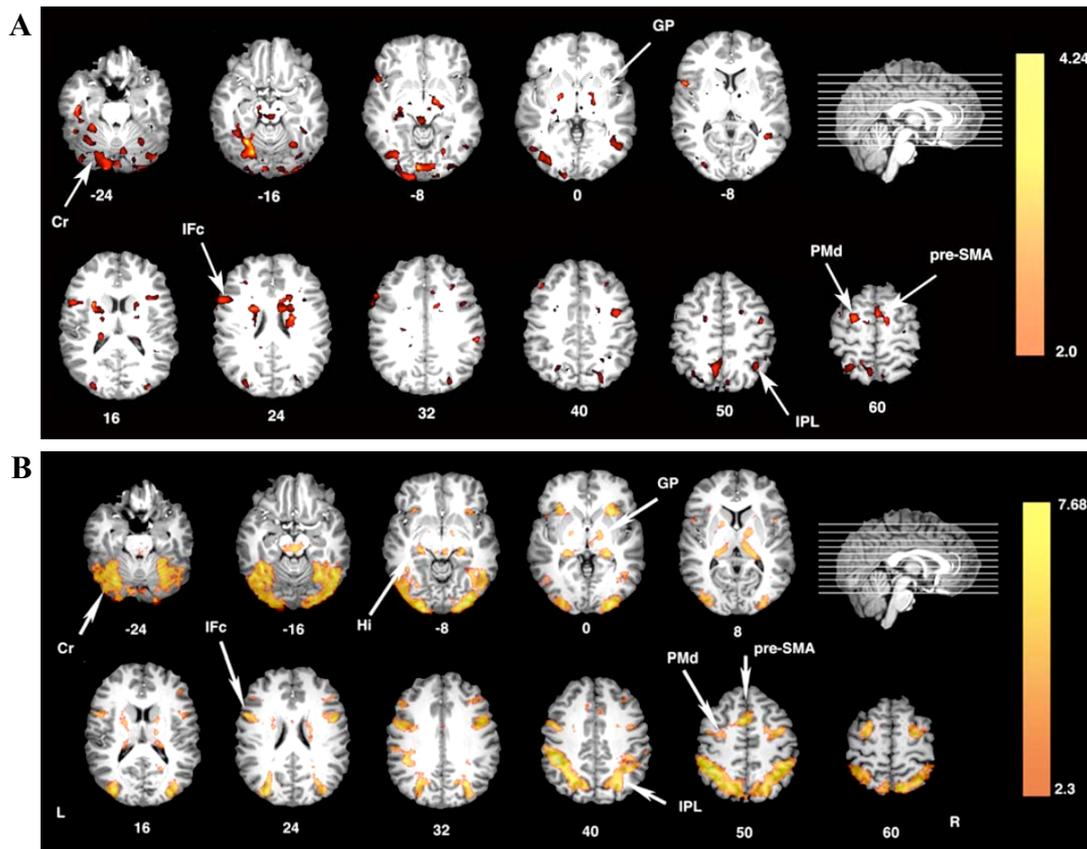
imitation itself (first a small pause and then repeating of the observed movements). When participants had to choose a chord of their own, activity was much lower. The human MNS thus seems to play an important role throughout the whole process of novel action imitation, from observing an action, through a short interval between observation and execution to execution itself. Also when only imitating very minimal actions far less complex than playing a whole chord, parts of the MNS show higher activation. For example when lifting an index finger while observing another hand doing the same, elicits a higher response in Broca's area and parietal regions than when performing the same action in response to a simple stimulus cue in the form of a dot (Iacoboni et al., 1999). Observation matching therefore seems to be an important role of the MNS. This study shows that in the MNS a clear difference is made between responding to a cue and imitating observed movements. Imitation and the MNS therefore seem closely linked. A following study by Nisitani and Hari (2000) in which MEG was the imaging medium also showed highest activation in Broca's area while imitating observed hand movements. Activation was clearly higher than when only observing or only executing the same actions.

Frey and Gerry (2006) used a more complex action to study activity in the brain using fMRI. Subjects watched a movie of a demonstrator assembling an object from several separate components. Activity in the MNS and several other brain areas (amongst which the cerebellum, as also seen in the Torriero et al. (2007) study) was highest when watching with the intention to imitate the assembly task in the exact same order. Somewhat lower activation was detected when subjects watched with the intention to assemble the object with the same result, but not necessarily in the exact same order (figure 7A). Activation was lowest during passive observation of the assembly task without any imitation intentions (figure 7B). This shows that the MNS is most active for exact imitation of an observed action, including the order of the order of action components. When only the goal of the action has to be imitated exactly, but not necessarily in the same way as in the observed action, MNS activity is less high. The authors ascribed this effect to the fact that the action components still were coded for, but that the exact order did not have to be memorized (Frey & Gerry, 2006). This might require less recombining activity and working memory.

All these imaging studies show that the MNS, among other brain areas, is not just active during action observation, but reacts stronger when one already has the plan to subsequently imitate the observed actions. This indicates that MNS activity can be modulated consciously by planning to imitate new actions. Although activity is also seen when one is passively observing actions, this rather leads, as in monkeys, to the understanding of actions happening around us. To do this consciously would be rather inefficient and could be very distractive. Recognizing actions already in our motor repertoire, and also sometimes imitating them as in the chameleon effect, happens automatically (Buccino et al., 2004; Rizzolatti & Craighero, 2004; Iacoboni, 2005), but for true imitation we need to focus our attention stronger on observed actions and recombining of action components needs to take place. This could explain why during imitation learning the MNS is extra active. But what exactly happens during this recombination phase? Does recombination occur within the MNS, or are other brain areas also possibly involved in the process?

#### *Imitation learning theories*

One rather vague theory for the imitation of observed action is that of active intermodal matching (AIM) (Heyes, 2001). This theory holds that an observed action is transformed into a set of 'organ relations' by an innate imitation mechanism. These



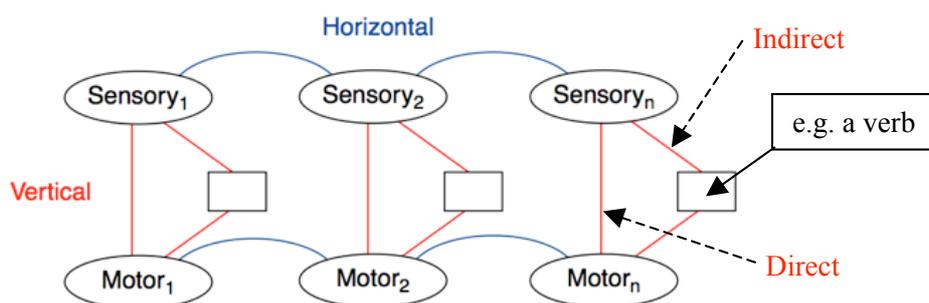
**Fig. 7.** Significant differences in brain activity between different conditions while observing a demonstrator assembling an object. **(A)** Difference between observing with the intention to imitate the exact same sequence and observing with the intention to imitate the goal, but not necessarily using the same sequence. Activity is higher in the first condition in the cerebellum (Cr), globus pallidus (GP), parietofrontal mirror system (IFc and IPL) and in PMd and pre-SMA. **(B)** Difference between observing with the intention to imitate the exact same sequence and observing passively. Activity in the first condition is much higher than in the second, with more pronounced differences in the same areas found in the previous comparison, as well as in the hippocampus (Hi). From Frey & Gerry, 2006.

organ relations are matched to another set of organ relations created from the observer's motor output and those that match will form a certain connection for favoured use in future imitation actions. The exact way in which the organ relations are coded for in the brain is not clearly described in this AIM hypothesis (Heyes, 2001). Since ever more evidence is accumulating that experience plays an important role in actions used for imitation, the validity of this theory becomes ever less likely.

Another theory for the shaping of connections between the MNS and other brain areas through imitation, now often seen as a good explanation is the 'associative sequence learning theory' (ASL) (Heyes, 2001; Iacoboni, 2009, but see Oberman & Ramachandran, 2008). This theory holds that through repeatedly experiencing action observation and simultaneous motor output vertical links form between sensory input and corresponding motor output areas. These vertical links in humans can either be direct or indirect (figure 8). Direct vertical links directly connect sensory and corresponding motor areas without any other areas in between. Some of these direct vertical links are already present at birth (e.g. smiling, yawning and tongue protrusion) (Heyes, 2001), which might explain imitation of such actions reflexively at a

very young age (e.g. Ferrari et al., 2006). Other direct connections form through experience due to simultaneous firing of sensory and corresponding motor units during imitation (as was for example shown in the study by Catmur et al. (2007)). Indirect vertical links are formed when something else often happens in combination with observing or executing a certain action. In humans this can be the sound of a word for example. In this way, a link is formed between hearing the word that describes the action and the action itself (both observation and execution) (Heyes, 2005). The existence of audio-visual mirror neurons could explain the formation of the indirect vertical links by linking a sound (a word) to a certain visual image (an action) (Iacoboni, 2009). This theory, however, does not necessarily include mirror neurons, because it describes links forming between separate sensory and motor areas, while mirror neurons are single cells already coding for both processes.

A third theory concerning imitation learning is the ideomotor framework (Prinz, 2002; Iacoboni, 2009). According to this theory, a connection between a goal and the action(s) needed to achieve it, forms when one has a goal in mind with no other conflicting ideas, and when subsequently a certain action is performed to reach that goal. When having the same goal in mind afterwards, the action connected to it will be performed automatically (summarized in Prinz, 2002). This framework would cause imitation by observing someone reaching a goal and subsequently activating ones own motor plan to reach the same goal (Iacoboni, 2009). This of course does not have to lead to imitation of exactly the same action, but rather leads to goal imitation. However, lifting a finger (whether as part of an action or as an action itself) is also a goal that can be reached. Reaching sub-goals of separate action components can lead to more exact imitation of an observed action and can still be accounted for by the ideomotor framework. In humans, as in other animals, the goal of an action often seems more important than the action itself. However, the action itself can sometimes also be the goal if the action does not lead to reaching an obvious goal (Iacoboni, 2009) (for example a dance movement). Next to this, due to human language capabilities one can also be instructed to take an observed action as the goal to be reached, even if this action itself does reach a visible goal.



**Fig. 8.** The associative sequence learning model. Through experience direct and indirect connections form between sensory and motor areas in the brain. Further associations can be made through existing horizontal connections, which could be important for association between different actions or action components. For example, horizontal connections could form between areas coding for different action components, enabling the observer to put observed action components into the right order. This ability, however, is probably not unique to imitation processes (Heyes & Ray, 2000). From Heyes, 2001.

The last two theories are both based on experience dependent imitation capabilities. This also seems to be the case in real life. A combination of those theories could well be a good explanation for what is really happening during imitation (Iacoboni, 2009). Both theories seem at least partly to be supported by evidence from multiple studies. The only difference between the two theories is that the ASL theory assumes that sensory areas become linked to motor areas, whereas the ideomotor framework is based on overlapping areas for representation of action observation and execution. In the MNS, mirror neurons fire both when an action is observed and when it is executed. This would make the ideomotor framework a more plausible option. However, the MNS consists of separate areas and also connects to other brain areas which provide support and to which the system itself provides support. When looking at it from this direction, the ASL theory seems also partly explanatory, because the connections between all those areas can be viewed as the vertical connections described in this theory. Imitation therefore seems to be an interplay between both the ASL and ideomotor theories (Iacoboni, 2009). At least the shaping of imitation by experience seems to be an important component.

#### *Conclusions on imitation and the MNS*

There are plenty of studies suggesting a close relationship between activity in mirror areas and imitation. Many of these, however, also show activity in other brain areas while imitating or observing certain actions for subsequent imitation. This makes the idea of the MNS being ‘the’ system responsible for imitation unlikely, but it nevertheless seems to play an important role. As other areas like the cerebellum and Brodmann area 46 it is likely to be an essential part of the brain enabling imitation learning in humans. The debate about whether or not monkeys are able to learn through imitation is still ongoing. Although there seems to be some evidence that monkeys can imitate certain actions, it is not really clear how far learning through this process has developed in monkeys (Iacoboni, 2009). Probably this is mostly limited to actions leading to a visible goal. It is clear, however, that imitative abilities in humans have developed much further and that, for instance, also highly abstract actions can be imitated and learned through this way. This can also form the basis of the principle that enables us to transmit culture and social skills to next generations. Many cultural habits, like certain rituals or the use of tools, are abstract actions that could be understood and learned through a mechanism like the MNS. As Järveläinen et al. (2004) showed, activity of the primary motor cortex in response to grasping actions with chopsticks, likely elicited by MNS activity, positively correlated with previous intensity of chopstick use by participants. Although the number of participants was low, this seems to be a first indication that prolonged exposure to use of certain tools becomes incorporated into the MNS.

Abstract hand and arm signals are also often used when humans are orally communicating. Could there be a link between such sign language or abstract movements and language comprehension? Or could there be a more direct link between words and MNS activity, as suggested in the ASL theory? Because a lot of teaching and learning in humans is mediated through the use of language, it is interesting to look what the role of the MNS might be in language comprehension. Because this could then well be another way in which this system contributes to learning.

## 5 | WORDS AND LANGUAGE RELATED SIGNALS

**T**he idea of a link between the MNS and language first arose when intransitive actions, also seen in sign language, also seemed to activate parts of the human MNS. Sign language might have its origins in grasping and other hand and arm movements in the monkey, which over evolutionary time became more ritualized and produced symbolic gestures (e.g. Arbib, 2002). With the discovery of audiovisual mirror neurons the theory became more plausible, for now there was a system able to link sounds to actions (Keysers et al., 2003; Tettamanti et al., 2005; Iacobini & Dapretto, 2006). However in monkeys the audiovisual mirror neurons, like almost the whole monkey MNS (Buccino et al., 2001; Ferrari et al., 2003) only respond to object related actions, which is not sufficient for a well functioning communication method. The symbolization of gestures in humans (pantomimed and intransitive actions) probably provided a good gestural communication system to which words could be linked (Rizzolatti & Craighero, 2004). The first signs of communicational gestures can already be seen in monkeys, where some mirror neurons do respond to communicative mouth actions (Ferrari et al., 2003). They seem, however, not completely freed from their origin in ingestive actions (Rizzolatti & Craighero, 2004). These communicative mirror neurons (see chapter 2) could still also have played a part in the origin of language. The same goes for the discovery of area F5a in the monkey brain coding for intransitive actions. This area is probably homolog to Broca's area in humans, thought to play an important role in language processing (Nelissen et al., 2005).

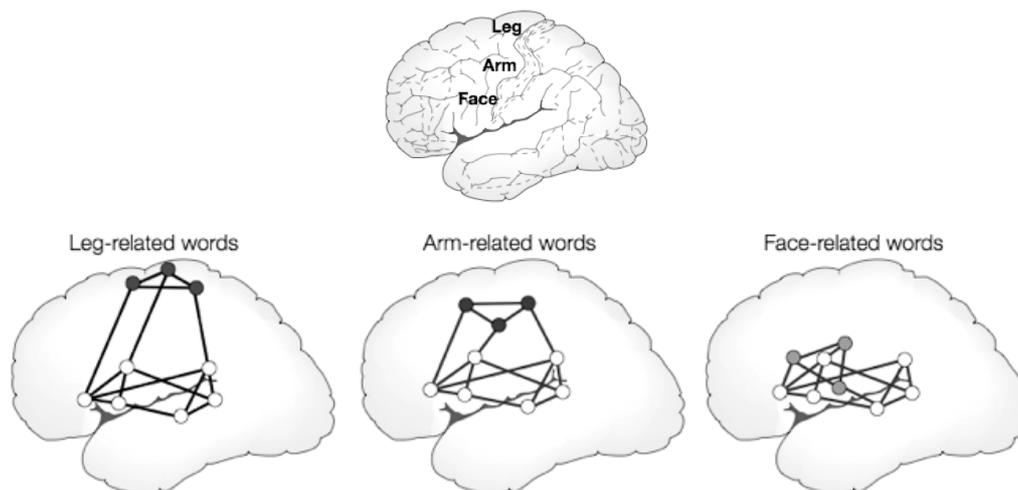
In humans the larynx is positioned in a way that allows production of a larger diversity of sounds than in other animals. It is therefore that we are able to make connections between many gestures and specific sounds (Arbib, 2002) or objects and sounds. These sounds became the words we know today and pass on to next generations, who in their turn learn to associate certain gestures, actions and objects with specific words. Like a monkey might associate the sound of a breaking peanut with breaking a peanut (Keysers et al., 2003), we associate the word 'kick' with the actual action. The only difference is that in humans the sound is not necessarily produced by the action itself, but rather is a product of our vocabulary. Of course it is the gesture and action coupled words in which the audiovisual mirror neurons might have played an important role. For object related words, this is less likely.

### *Language-MNS connections*

The theory of language evolution described above has been suggested by several authors as being a good possibility, but to make it plausible, experimental evidence needs to be provided. Not long ago Floël et al. (2003) detected a possible link between gesture and spoken language. When subjects performed language tasks like reading and speaking, MEPs in hand muscles from TMS stimulation in cortical hand areas, were larger than for non-linguistic tasks (e.g. observing abstract 'Kimura pictures'). This could show a tendency to move the hands when speaking, but also (possibly mirror) activation of hand muscles when listening to speech. Indeed people tend to move their hands when talking to each other. Several studies have shown that observing someone gesturing while he or she is explaining something in words or telling a story, helps in remembering more details and learning the explained matter better (Skipper et al., 2007; Cook et al., 2008). It is not clear whether and to what

extent the MNS plays a role in processing these gestures and linking them to the words heard, although, as Skipper et al. (2007) showed, during gesturing, activity between Broca's area and the IPL seems to be fairly low. The authors conclude that during speech accompanied by gestures the IPL could play a role in language comprehension by coding for the associated gestures. This could lower Broca's area activity because not all information has to come from the words only. More research into this area should be done, however, to find out exactly what the role of the MNS might be in language-gesture situations.

Next to its supposed role in language production, Broca's area also has mirror properties mainly for mouth and hand actions (Heiser et al., 2003; Rizzolatti & Craighero, 2004). Therefore it is part of the MNS. When listening to speech this area always shows activity due to the fact that it mirrors mouth actions and speaking involves mouth actions (Pulvermüller, 2005; Rizzolatti & Fabbri-Destro, 2008). This could indicate that humans also possess audiovisual mirror neurons. Especially because this activity is detected in Broca's area, the human homolog to the monkey area F5, where audiovisual mirror neurons were first discovered. Broca's area is a complex brain region, showing activity in language related tasks as well as during gesture and other hand, mouth and foot actions (Rizzolatti & Craighero, 2004; de Zubicaray et al., 2008). There is still much debate about the exact functions incorporated into this area and what the observed activity really means. It might well have an important role in recognizing and categorizing action words, because listening to action words seems to activate premotor and IPL areas involved in the activation of specific effectors described by the action words. As well as other parts of a widely distributed language related network with some long distance connections (among others the MNS; figure 9) (Rizzolatti & Craighero, 2004; Pulvermüller, 2005). This seems to be the case both for listening to or reading action words separately or imbedded into a sentence. Tettamanti et al. (2005) showed that this activation was specific for sentences describing actions and was absent when listening



**Fig. 9.** The much observed somatotopic division of the (pre)motor cortex (top). Different brain network activations while listening to action words involving different effectors (e.g. kick, pick, lick). There seems to be a basic activity pattern when hearing action words, involving Broca's area, the STS and IPL (the MNS). Next to that premotor activity varies according to the action word used, following the somatotopic organization of the (pre)motor cortex. From Pulvermüller, 2005

to abstract sentences. It is possible that again such links form through experience, when areas for action execution are active while hearing certain sounds (words) (Pulvermüller, 2005).

Is this somatotopic activation the result of motor imagery after hearing or reading action words? This seems like a plausible explanation because of the involvement of the MNS without really observing an action. However, activity seen in the (pre)motor cortex is observed very shortly after action word perception. The time between action word perception and onset of activation is not long enough to allow motor imagery. It is therefore likely that fast connections exist between perception and execution areas through which action words are automatically coupled to execution areas (Pulvermüller, 2005; Tettamanti et al., 2005). Linking action words directly to the (pre)motor areas instead of through motor imagery can indeed be a better way for processing language. It is both less energy and less time consuming than through motor imagery. For now these are only indications and further research into this mechanism is required.

### *Problems*

As mentioned above, there is still doubt about the actual role of especially Broca's area in language comprehension. Because this area seems to be active while listening to language in general and even non-words and also shows overlapping mirroring properties for different effectors (de Zubicaray, 2008). However, language studies can obviously only be done in humans, and in humans single cell studies are not being carried out. This makes that up to now conclusions have to be drawn from imaging studies, which often do not have a high enough resolution. As seen in the monkey single cell studies, area F5 does not only contain mirror neurons. There are also other neuron types with different activity patterns. Furthermore mirror neurons do not have to be in separate clusters according to effector. The organizational pattern might be different than that which is often expected, or resolution of imaging studies is simply too low to reveal subtle effector specific patterns within Broca's area. Looking at the findings of differential, somatotopic activity patterns in the premotor cortex and IPL when listening to action words involving different effectors (e.g. Tettamanti et al., 2005), it seems that there should be some system coupling the sensory information to the right motor stimulation. The MNS could be a good candidate for this, but to verify this hypothesis single cell studies or higher resolution imaging techniques are needed.

Taken together, currently the exact processes behind development and comprehension of language are not completely clear. Several studies have shown premotor and IPL activation of areas corresponding to those used for stimulating effectors involved in heard action words or sentences. Another study has also shown that TMS stimulation of the arm motor cortex leads to faster processing of arm action words. The same also goes for leg motor cortex stimulation (Pulvermüller et al., 2005). Interesting to note here is that this only seems to be the case for left hemispheric arm and leg motor areas and not for their right hemispheric counterparts. The left hemisphere is also the one mostly involved in language processing. This could also indicate that action word comprehension really involves stimulating the appropriate effectors. Since several MNS areas (Broca's area and IPL) are active when listening to action-related language, this could mean that at least in part the MNS enables the understanding of language. Next to that it could also play a role in word learning by coupling certain words to certain actions. This would require audiovisual mirror neurons and therefore

research needs to be done to see if such neurons are indeed present in humans as they are in monkeys.

Concluding from this, there are three ways in which the MNS could play a role in learning coupled with language. It could play a direct role in word learning (Pulvermüller, 2005) and it could play an indirect role by enabling (part of) language comprehension, either through activating effectors involved in described actions, or by mirroring speech associated gestures. We need to keep in mind, however that for now these are speculations still debated about. To come to more concrete answers, probably current techniques have to be refined or new ones developed.

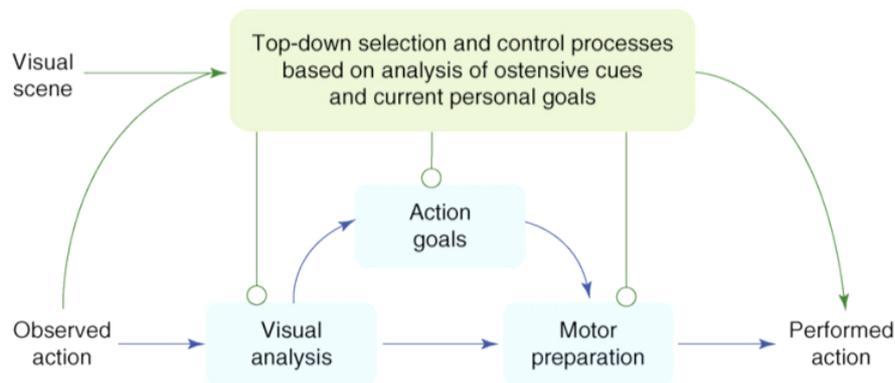
## 6| DYSFUNCTION

**W**hen looking at the function of the MNS and its role in learning it could be worthwhile to look at it in different ways. Until now I discussed in what situations the MNS is active to discover its role in learning. Another way of looking at the importance of this system is by studying the effect of a dysfunctional MNS. Symptoms observed in such situations could also clarify its role in learning. But again there are different ways of looking at a dysfunctional MNS.

### *Top-down research*

Over the past years several imaging studies have shown that people with autism spectrum disorder (ASD) show lower MNS activity than control subjects in action observation/execution situations. Nishitani et al. (2004) for example found delayed and weaker MNS activity in patients with Asperger's syndrome, a milder form of ASD, than in control subjects when they had to imitate lip forms from images. Théoret et al. (2005) showed lower motor cortex excitability in autists than in matched controls when observing finger movements. Because the authors did not find differences in motor cortex ability between the two groups, the differential activation was ascribed to a less functional MNS. During imitation of emotional expressions, Dapretto et al. (2006) found weaker frontal MNS activity in children with ASD than in a healthy control group. These differences likely were not due to the autistic children paying less attention to the faces than the healthy children, because other brain areas used for face recognition were active in both groups. Next to this, no differences in fixation of the eyes to an indicated location were observed in a test outside the scanner. This shows that the autistic children were as able as the healthy children to fixate their eyes on an indicated point. They even found a correlation between the severity of autism and activity in this part of the MNS; the weaker the activity, the more severe the form of autism and the less the functioning of the child in social situations. Overall there seem to be differences in activity between patients with ASD and typically developing people during different processes like action observation, imitation and emotion recognition (Iacoboni & Dapretto, 2006).

In theory such a dysfunction of the MNS could lead to impairments in imitation, theory of mind and social communication (Dapretto et al., 2006). However this idea proves to be more complex than it seems, especially for imitation, which is thought to be one of the main MNS functions in humans. ASD patients show considerable variation in their ability to imitate. Next to that, patients with a lesioned



**Fig. 10.** Schematic representation of processes possibly involved in imitation. Next to processes likely occurring within the MNS, there are also top-down processes from other brain regions (e.g. motivation, cues given by the observed actor). These processes can influence the imitation pathway in different stages, inhibiting or stimulating imitation in the observer. From Southgate & Hamilton, 2008.

MNS often show greater imitation impairments than ASD patients (Southgate & Hamilton, 2008). Therefore the exact role of the MNS in autism is still not clear. This system is, as discussed earlier, connected to many other brain regions and imitation is not regulated by the MNS alone (figure 10). It is not unthinkable that autistic individuals differ in one of those areas. When an area connected to the MNS is not functioning as it should, this could also effect MNS activity, but the symptoms could still be caused by the other area and not by the MNS. Therefore it is currently not really clear whether a malfunctioning MNS is the cause or the effect of ASD (Southgate & Hamilton, 2008). Not all symptoms of autism can be explained by MNS dysfunction (Lepage & Théoret, 2007).

#### *Bottom-up research*

Approaching the problem of the functions of the MNS as in most studies of ASD patients does not seem to be the most straightforward way. It can give some insights, but many factors remain uncertain. A better way to study the impact of a malfunctioning MNS probably is by studying patients with lesions. Current techniques like TMS also enable researchers to create virtual lesions in certain brain areas without actually damaging brain tissue. These methods have significantly moved the field of brain research forward. By ‘lesioning’ mirror areas one can get a more reliable idea of what role this area plays in normal brain functioning.

As was demonstrated in the study by Heiser et al. (2003) mentioned in chapter 4, inhibiting activity in Broca’s area and its right hemisphere counterpart using rTMS, negatively affected imitating abilities. Here it was nicely shown that the MNS indeed plays an important role in imitation. This finding was supported by showing that the motor system for finger movement was not affected. Participants were still able to execute a finger task in response to a cue in the form of a red dot. Here imitation did not play a role, since only an abstract goal (a red dot above a key) was visible and no recognizable action to imitate. Another interesting study involving decrease in activation of Broca’s area using rTMS, has recently been carried out by Gentilucci et al. (2006). Here participants had to verbally respond to an actress making communicative gestures by pronouncing the gestured word, or by pronouncing the colour shown on the actress’ hands. Subjects had more problems pronouncing the word

connected to the gesture when rTMS was applied over Broca's area than over two control areas (one of which was the right hemisphere counterpart of Broca's area). Next to that subjects had less problems pronouncing the colour when rTMS was applied over Broca's area than over the two control areas. This indicates that Broca's area probably plays a role in the coupling of communicative actions and words. In the first situation inhibiting Broca's area made connecting the action and the corresponding word more difficult. In the second situation the gesture seemed to automatically trigger a response using the corresponding word, which in normal situations slightly inhibits the pronunciation of other words as seen here with the colour. However subtly inhibiting Broca's area activation reduced this effect. This probably caused the link between gesture and word to weaken, showing that such links are probably made using Broca's area.

Studying patients with real lesions in the IFG, part of Broca's area, Goldenberg & Karnath (2006) found impairment specifically in imitation of finger movements. This is in accordance with studies showing activity in Broca's area mainly for grasping movements. These studies of dysfunction of Broca's area show that this region, being part of the MNS, is likely involved in both imitation and gestural communication. This adds to other studies, suggesting that the MNS indeed plays an important role in for example imitation learning and language learning.

Not only Broca's area is important in imitation. Another part of the MNS, the IPL, has also been studied while dysfunctional. Uddin et al. (2006) applied rTMS over the left and right IPL and found that subjects had a reduced ability to distinguish self from other when the right IPL was inhibited. This could also lead to problems with imitation. Indeed lesions in the IPL region are known to cause apraxia, a condition in which patients have a reduced ability to recognize or imitate actions (Chong et al., 2008). The fact that only right IPL lesions were found to have this effect in the Uddin et al. (2006) study needs to be studied more closely. It could for example be that this area includes other functions not directly regulated by mirror neurons. It could also be that this area connects to other regions its left hemisphere counterpart does not connect to. Probably self-other discrimination is not the only factor important for imitation. Goldenberg and Karnath (2006) also found imitation impairment of hand movements in patients with lesions in the left IPL. The IPL as a mirror region seems to play a role in distinguishing self from other as well as in imitation. For now it is however not clear if it is really mirror neurons coding for these abilities because, as Broca's area, the IPL does not solely consist of mirror neurons. By lesioning this area it could thus be that other critical cells or networks are being affected.

## 7 | DISCUSSION AND CONCLUSION

**T**he aim of this thesis was to see whether the mirror neuron system plays a role in learning and if yes, to what extent it does so. Numerous studies using different techniques, measuring brain activity, peripheral activity in muscles, stimulating or inhibiting brain activity, point in the direction of involvement of the MNS in different learning mechanisms. While observing others, for example, the MNS probably enables one to understand the observed actions (Rizzolatti et al., 2001; Heiser et al., 2003; Iacoboni & Dapretto, 2006) and

even emotions (e.g. Arbib, 2002; Iacoboni & Dapretto, 2006). This could lead to associations between certain situations, actions and emotions by which one could learn how to behave in which situations. This does not necessarily mean that the MNS itself is fully responsible for making such associations, but it certainly contributes to the process. This goes for both humans and primates and is therefore presently thought to be one of the primary functions of the MNS (Iacoboni, 2005). Another feature likely coded for by the MNS in both humans and primates are goals of observed actions (e.g. Umiltà et al., 2001; Iacoboni et al., 2005). Therefore it is also likely that the learning of new goals belongs to the MNS repertoire.

One aspect in which the human and monkey MNS show clear differences is that of imitation. Monkeys seem very limited in their imitative capabilities and rather restrict their imitation to the goal level (Rizzolatti & Craighero, 2004; Iacoboni, 2005). Humans tend to imitate to a much greater extent and also imitate observed movements to reach a certain goal. Through this way we can also learn to use these movements to reach the goal in the future, or to just execute the same movements if this is the goal itself (e.g. dancing (Calvo-Merino et al., 2005) or simple finger movements (Catmur et al., 2007)). During the imitation process the MNS becomes active, which could indicate a role for this system in imitation. The fact that the human MNS responds to intransitive and mimed actions more strongly than does the monkey MNS (Rizzolatti & Craighero, 2004) could be one explanation for the difference in imitative learning capabilities. Another could involve a stronger supporting role of Brodmann area 46 in humans. This area possibly rearranges action fragments in ones own motor repertoire and recombines them into an action matching the observed action (Buccino et al., 2004; 2006). Finally the MNS could in humans also be connected to forming action-word connections, meaning it could be involved in learning language. This idea is both supported by the discovery of audiovisual mirror neurons in the monkey (Kohler et al., 2002) and by the fact that mirror areas in humans show activity when listening to language involving action descriptions (e.g. Pulvermüller, 2005).

It seems, when looking at these findings that the MNS is certainly involved in different types of learning involving natural actions; from context learning through action and emotion understanding in both primates and humans, to imitation and maybe language learning and comprehension in humans. One should, however, take care in interpreting the findings mentioned above. There are several issues that have to be taken into account. First there is the mirror neuron issue itself as also mentioned in chapter 2. In monkeys these neurons have actually been shown in single cell studies and found to be localised in a few different areas (see chapter 2). However in humans, as rightly brought forward by Dinstein et al. (2008), up to now it has not been shown directly that mirror neurons exist. The assumptions that humans also possess such neurons come from evolutionary logic and homologies with the monkey brain of areas active both when observing and executing actions. This activation, measured using imaging techniques, does not necessarily show mirror neurons. Since mirror neurons make up a limited part of all neurons in assigned mirror neuron areas, it could well be that also activity of different neuron types is measured. As shown in the monkey brain mirror neurons are very specialized cells, with only small clusters responding to very specific effector movements. Imaging studies are not refined enough to show such subtle activity. Attempts to find mirror neurons using an adaptation paradigm have so far resulted in mixed results (Chong et al., 2008). To get good evidence of the presence of mirror neurons in the human brain, for now single cell studies are still the best option, but hardly ever carried out in humans. First results

of a single cell study done with depth electrodes in a few epileptic patients carried out very recently seem to indicate the presence of neurons with mirror properties in the frontal lobe and medial temporal cortex (Mukamel et al., mentioned in Iacoboni, 2009). This could well be the first step in direct evidence showing the presence of mirror neurons in humans and thereby in strengthening the MNS theories.

Secondly, because human MNS studies only made use of imaging techniques they are not easy to compare to monkey studies where often single cell measurements are done. It could be good to also study monkey brain activity using brain imaging more often. A good example of such a study is the one carried out by Nelissen et al. (2005). This makes comparing human and monkey MNS activity easier. Differences and similarities can be seen more easily when looking at activity patterns in areas thought to contain mirror neurons in those two groups.

A third issue to be considered is in how far the studies conducted represent real life situations. Almost all studies used videotaped actions shown to subjects on a screen as stimuli. It has been found, however, that both adult and infant brains respond differently to live actions and televised actions (Shimada & Hiraki, 2006). In the latter situation motor cortex activity was found to be significantly lower than during live action observation. Another finding connected to this comes from the Nelissen et al. (2005) study. Here it was found that, using fMRI on a monkey brain, mirror activity in area F5c was significantly higher when monkeys saw the whole actor performing a grasping movement compared to only a hand performing the same movement. Context, therefore, seems to play an important role in mirror activity. Since the first tests on mirror neurons in area F5c (di Pellegrino et al., 1992) were done using both live actions (the demonstrator was in front of the monkey) and context (monkeys could see the whole demonstrator), this seems to have been the best setting for studying mirror neuron activity. Many studies looking at human mirror activity have used televised actions with only the studied effector visible. This does not mean results obtained are wrong, but they could well be suboptimal. Maybe using a setup similar to that used in the study di Pellegrino et al. (1992) study would reveal more details or make weak results stronger. As long as single cell studies in humans are non-existent or rare at best, such refinements could possibly give a bit more insight in mirror activity. It also indicates that the MNS has developed to take into account a certain context and that it might be most important during direct social interactions.

The most direct evidence that the MNS is involved in action learning probably comes from the study by Ferrari et al. (2005) in which the tool mirror neurons were discovered in monkeys. This shows that new mirror neurons can form when new actions are learnt, or that existing mirror neurons acquire new properties. This makes understanding of or responding to observed actions easier in the future. Also other studies showing experience-dependent shaping of responses and brain activity point in this direction. When actions are actively associated through observation and execution often enough, these associations become integrated into the MNS and are made more easily and automatically. One example of this in humans is the chameleon effect, described in chapter 4, which plays a role in empathy (Chartrand & Bargh, 1999). Goals of actions seem to be the most important factors coded for by the MNS. What already subtly started to develop in the monkey MNS, but seems to be represented in the human MNS much stronger are responses of this system to action kinematics. Both this stronger development in humans and our extensive use of language could have made actions themselves our goals. For example when instructed (through language) to repeat observed movements. This is also a way of transmitting

culture and teaching next generations. When, however, humans do not observe an action with the explicit instruction or motivation to imitate the exact movements, the MNS codes for the goal of that action like in monkeys. Prerequisite here is of course that the action involves a visible object.

Overall the MNS mainly seems to be responsible for unconscious learning processes involving physical actions. It can help us understand and thereby learn the goals of other individuals we observe. In humans, this also can contribute to language learning. Without this system one would probably still be able to learn most things the MNS is normally involved in. This would, however, require much more time and energy. For example learning by observing others and extrapolating action components or goals to ones own motor system would be much harder, if not impossible. Therefore learning actions or goals without a MNS would involve much more conscious processes and own experience. Having to learn all those things through trial-and-error is much more costly and time-consuming, including the possibility of never acquiring certain goals or solutions to reach them. The same likely goes for learning and understanding of language, especially action related language. More attention and energy would be required for processing signals communicated through language, because the automatic coupling of words to certain motor systems would be absent. This likely requires the involvement of more brain circuits and therefore a much slower and more limited understanding of social signals like language.

The MNS is probably essential for the enabling of imitation learning as seen in humans, which would be impossible without it. It likely plays an important role in other types of learning from others, but is of limited importance of self-learning or learning of language not involving action descriptions. The main function of this system in learning is therefore likely to be saving time and energy, thereby extending the learning capacity. If one is able to understand observed actions and goals automatically (by the formation of mirror neurons for specific actions through experience) and only by observing, this saves the energy and time required for learning the same actions and goals through trial-and-error.

Concluding, it seems reasonable to assume that the MNS is involved in several types of learning like action goals and social interactions. This learning is limited to actions within the observer's motor repertoire. Different species, however still seem able to learn from each other. Monkeys, for example, can learn goals from watching human demonstrators (e.g. Umiltà et al., 2001). In humans also learning through imitation and language are included. As for now, however, mirror neurons have not directly been identified in humans, but certain areas clearly show activity during both action observation and imitation. It seems best in humans to refer to a 'mirror system', because it is not fully known what neurons play a role in the observed activity. Hopefully research in the near future will clarify this issue. The final important point is that the MNS should not be seen as an independent learning system, as sometimes seems to be done. As can be seen in figures 7 and 10 for example, during action observation and execution also other brain areas are active. For action integration, fragmentation, selection and recombining, the MNS seems to be supported by, among others, the cerebellum and Brodmann area 46. The MNS is an important link in the chain of learning new actions and their goals, but could never be held responsible for these processes entirely on its own.

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