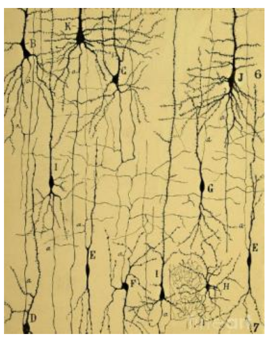
Universiteit Utrecht

Title: Could mirror neurons be sufficient to explain the origin and functioning of facial mimicry?

A literature study based on empirical evidence



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Broad Introduction

This thesis explores facial mimicry in the context of mirror neurons. Mirror neurons are recently discovered in macaques and are active in action execution and observation. They may or may not play a role in facial mimicry, the copying of facial expressions which is predominant in human interaction. Mirror neurons are a research topic in social neuroscience. Neuroscience which investigates social phenomena, such as empathy and group influences on neuroscientific processes. The investigation of mirror neurons in facial mimicry has broader implications for artificial intelligence. Once we are capable of understanding the underlying mechanisms of facial mimicry, we may be able to compute social interaction in human-like robots or enable machines to have enhanced emotional behavior. Exploring mirror neurons in humans is therefore relevant for artificial intelligence. The topic had my interest because mirror neurons are recently discovered, often hyped and their concrete role in human interaction has been questioned. Some people suggest that mirror neurons are the reason for empathy, others say that mirror neurons play a minor role in empathy and mimicry. In this thesis, I explore two questions which relate to mirror neurons and facial mimicry. The first question is how mirror neurons are related to facial mimicry, and the second question is if associative learning can explain mirror neuron development in facial mimicry, Both questions are still open for debate and with this thesis I like to contribute to the existing evidence on the topic.

Structure of the thesis

Main thesis abstract

Two main question exist in this thesis. The first is: How do mirror neurons relate to facial mimicry? Can they explain the process of mimicking a facial expression or not? The second question relates to the debate on the origin of facial mimicry. How far can facial mimicry be explained by associative learning? An associative learning process is prevalent in the development of mirror neurons and means that visual neurons correlate with motor neurons in a network. Also known as Hebbian learning. There are presumptions that mirror neurons explain empathy and mimicking of facial. Whether facial mimicry can be regarded as a mirror neuron property has to be answered first in order to understand the origin of facial mimicry. When facial mimicry can be seen as a mirror neuron property, the research on the origin of mirror neurons is evident for facial mimicry as well. The first chapter is an introduction to the topic of facial mimicry, where I provide an overview of the literature of facial mimicry and explain the influences of other cognitive processes on mimicry. For example cognitive load and group dynamics. The goal of the chapter is to show that facial mimicry is more complex than basic muscle imitation, an unconscious muscle response measured early by Dimberg. In chapter 2 I look at mirror neurons, which might be the possible neurobiological bases of mimicry. The function of mirror neurons is discussed here. The first research question: What is the contribution of mirror neurons in facial mimicry? will be answered in chapter 3. Facial mimicry is discussed as a complex process that accompanies basic action imitation and also two pathways for emotional processing. The basic action of mimicry can be explained by mirror neurons but the emotion recognition pathway can only partly be explained by mirror neurons. At the end of the chapter, I introduce a model which contributes to the explanation and which shows the relevant processing stages into one model. There are three separate information streams, one for action-perception and two for emotion recognition. The answer on the research question is in short that facial mimicry can only partly be described as a property of mirror neurons, both for action perception and emotion recognition. The last chapter, chapter 4 focusses on the origin of facial mimicry. I answer the question about the relative contribution of associative learning and genetic explanations for facial mimicry. The answer on the second research question is that humans are born with neurons that code for imitation of facial expressions. One of the reasons is that Infants already copy the gestures of their peers. But associative learning is also present in mirror neurons. It seems that there is a role for both, which is shown in an interesting computer model at the end of this chapter. The theoretic boundaries are mainly formed by an exploration of facial mimicry literature, mirror neuron literature and sensorimotor learning literature. With the literature combined I like to give a well-rounded answer whether facial mimicry can be regarded as the activity of mirror neurons and provide an answer to the question about the origin of facial mimicry.

Relevance

The relevance of this study is the contribution to the theory about facial mimicry and mirror neurons and to conquer prior presuppositions on the role of mirror neurons in empathic facial mimicry. I suggest a model based on the existing literature through which we can understand the several paths in facial mimicry. The questions about the origin and relative contribution of mirror neurons in facial mimicry is relevant because there is a gap in the literature which explains the origins of facial mimicry. There is a large amount of literature on the origin of mirror neurons but not on the origin of facial mimicry. This is mainly a qualitative research project, because research reviews and articles will be reviewed to answer the questions posed. The neurobiology of facial mimicry has applications for artificial intelligence because when we would be able to know the underlying processes of mimicry, we could be able to build more human-like artificial devices.

Chapter 1 Facial mimicry

Facial mimicry is the process of copying facial expressions or emotion and implementing them in your own expression. As early as 1872 Charles Darwin noted that “Joy, when intense, leads to various purposeless movements—dancing about, clapping the hands, stamping, etc., and to loud laughter.” (Darwin 1872) This is an example of a broad emotional state. Often, the emotional states are mimicked by the observer, the happiness of one person in the group may lead to happiness in other persons. When everybody around you starts dancing at a party, you are likely to start dancing too. You mimic the actions and emotions of people around you. This happens with postures, accents and even facial expressions. (Hess, philippot, Blairy, 1999). A paper by Lakin suggests that people who mimic body postures more are liked more than those who do not mimic. Thus, mimicry can be regarded as a form of *social glue*. (Lakin et al. 2003). The impersonation of an emotional state can be seen at the facial level – congruent with the other person’ emotional state. This process is named facial mimicry (Dimberg, 1982). When we see a sad face for example, we tend to look sad as well. Such facial mimicry reactions occur spontaneously and rapidly already after 300–400 milliseconds after a static stimulus is presented (Dimberg and Thunberg, 1998). When certain facial muscles contract, the same facial muscles appear to contract in the observer. Specific muscles correspond to particular emotional expressions. When people look at a happy face, there is activity of the *M. zygomaticus major* in the observer. This is a muscle that pulls the mouth corners for a smile. When there is an angry or sad face there is activity in the curator supercilii, the muscle that knits eyebrows when frowning. These results can be measured by EMG analyses, a behavioral measure to test for these muscles in facial expressions. Basic facial mimicry will be the main focus of this review but when other factors are not investigated, this will not fully regard the complex processes that influence facial mimicry. There are many factors which influence facial mimicry, we will briefly take a look at these factors to understand facial mimicry in its broader context. The focus will be on the emotional process which accompanies facial mimicry, theories of facial mimicry and other influences on mimicry.

Facial mimicry can be a form of emotional contagion
Facial mimicry can be a prerequisite for empathy. Empathy is the understanding of the other person and relating to the person. For example, when a person gets hurt, an empathic person

will ‘’feel’’ the pain and relate to the feelings of the person in pain. At a social level, empathy is important for the understanding of others and relating to other persons. People can express and understand the feelings of each other. People with certain diseases lack empathy. People with autism often do not have the same social skills as controls. Empathy is required to recognize facial expressions. Autistic people are not as good as controls in recognizing emotion from facial expressions (Celani et al.1999).

In the general adult population, facial mimicry accompanies the recognition of emotion in others too. Emotion recognition might be one of the significant aspects of facial mimicry. A study by Ramachandran tested whether blocking of facial mimicry has effects of emotion recognition. The change in an emotional face is detected later when facial mimicry is blocked in the observer (Ramachandran, 2007). When the participant holds a pencil between the teeth which blocks facial muscle activity, the happy or sad facial expression is detected later. This is direct evidence of the interplay between facial mimicry and emotion detection. There is a difference between detecting happy versus sad expressions, because emotions differ in the degree to which they are expressed in the face (Ekman, 2004). For example, happiness is associated with distinct changes in many facial regions and is more prevalent in muscle activity than sadness. In a natural setting we can observe that humans who are conversating mimic both the actions as well as the facial expression of their partners (Hatfield et al. 2011). Facial mimicry effects are more prevalent for natural faces than for artificial faces, shown by an experiment of gradual change from neutral to emotional faces in both videoclips of simulations and videoclips of natural faces (Sato, 2007). Through mimicry, people are brought together and can relate to each other. The tendency to automatically mimic and synchronize facial expressions and to relate emotionally shows the importance of facial mimicry in emotion recognition, a process that is known as emotional contagion (Hsee, Hatfield, & Chemtob, 1993)

Why does facial mimicry occur?

Facial mimicry can be seen as an imitative process of facial gestures. This could be regarded as pure motor copy of facial muscles, also known as the perception and behavior link. Another view is that facial mimicry is part of a broader emotional state and forms a communicative link between people which is also likely. This distinction between direct action and perception and deeper emotional processing will be discussed in chapter three, however de Waal et al. suggest the PAM model, the perception and action model which accompanies both the activation of the motor system in mimicry and the emotional system. De Waal and Preston propose that these emotional states are understood through embodied representations that allow empathy. (de Waal, Preston, 2002) An embodied representation occurs both at the muscle level as the emotional level. I defend that facial mimicry consists of both emotional processing and perception of facial muscles but they may not occur simultaneously. It is important to know what happens in facial mimicry in order to understand the underlying neuroscientific theories, discussed in the next chapter. Two theories are prevalent about what happens in facial mimicry. The first theory states that the emotional state is observed and acted upon by the observer. For

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example someone looks sad, has accompanied muscle activity, and this elicits sadness in the observer, who shows the same muscle activity (Hatfield, Cassipo and Rapson, 1994). The second view is that that facial mimicry reflects an internal simulation of the perceived facial expression in order to facilitate understanding of others' emotion. (Atkinson & Adolphs, 2005; Niedenthal, Brauer, Halberstadt, & Innes-Ker, 2001; Wallbott, 1991). Both theories propose a perceptive feature of facial mimicry. Either the muscle activity is interpreted and is accompanied by an emotion or the perceived facial expression is simulated first which elicits an emotion. Both theories may be together true when facial mimicry is muscle activity as well as an emotional state. The second view has high overlap with the view that facial mimicry is accompanied by mirror neurons for the simulation of the perceived expression. And the first theory relates to the perception of emotion accompanied by facial mimicry or emotional contagion (Hatfield,1993). The precise mechanisms of internal perception of facial mimicry was often theorized. Research in facial mimicry could only be done by behavioral measures. Research in facial mimicry reobtained interest when mirror neurons were discovered. Nowadays mirror neurons can be investigated by neuroscientific methods such as fMRI. Mirror neurons support the theories of internal perception in facial mimicry. Mirror neuron properties, could form the missing neurobiological link between the observance of a facial expression and the execution of the same expression.

Higher cognitive influences on facial mimicry

Context dependency of facial mimicry

To show that facial mimicry is not simple muscle imitation many studies have shown higher cognitive influences on facial mimicry. There could be differences in direct facial mimicry, facial mimicry in static images which onsets after a few milliseconds, which is unconscious. And more complex facial mimicry, which occurs after a short while when dynamic images are presented. Complex facial mimicry includes other cognitive processes which will be reviewed. One of these cognitive processes are emotion recognition as we have seen. Other cognitive processes also interfere with facial mimicry. These influences can be divided in 1. Context dependency 2.Current perceptual state and 3. Group dynamics in facial mimicry. These views support that facial mimicry involves higher order cognitive functions such as attention and emotion. Facial mimicry is more than just motor copy of facial expressions. A view that is in line with the theories that facial mimicry involves internal representation of the facial expression. The influences contribute to the broader context for the theory on facial mimicry and relates to the view that facial mimicry is not a reflexive muscle mechanism.

Context dependency

A review by Seibt et al. suggests that facial mimicry is context dependent (Seibt. 2015). Most experiments are during lab settings of static and dynamic facial images. These experiments do not express the natural situation. In a natural setting there is often background noise. For example, other stimuli or conversations exist during facial observation in a natural situation. When you are at a party or in a coffee bar, there is background noise while processing facial expressions. Natural facial mimicry is context depended and differs across changing social interactions. Different social settings require different facial signaling, social norms and scripts. They develop regarding the normal, correct or desirable facial behavior in a setting. (Seibt et al. 2015) During natural observations in shopping malls with direct response coding by an observer, about half of the smiles of experimenters were returned but hardly any frowns (Hinsz and Tomhave, 1991). So, mimicry depends on the context and is according to standards in an environment. Facial mimicry is limited by background noise or cognitive load. When people had to report the color of a face together with the emotion, instead of only an emotion, facial mimicry was reduced. When the observer had to listen to a video with sound, facial mimicry was reduced compared to the non-background noise condition. (McHugo et al., 1985)These results suggest that interpretation of a facial expression relates to other cognitive tasks. The amount of information, or cognitive load, interferes with facial mimicry and the processing of a facial expression requires the limited attentional resource and information processing. Further research is necessary to find out whether there are differences in facial mimicry itself. What exactly are these internal processing mechanisms of facial mimicry? And could there be two different streams in facial mimicry. One for unconscious muscle imitation and the second for emotion recognition? Other processes also interfere with facial mimicry, one process that relates to facial mimicry is self-focused attention.

The state of the perceiver

The way in which information is observed and interpreted influence facial mimicry. Empathy from the side of the perceiver is positively correlated with the outcome of facial mimicry. The high empathy group rated both expressions, happiness and sadness as more intense than the low empathy group and they showed more facial mimicry (Dimberg et al. 2011) A specific emotion in the perceiver influences facial mimicry. For example, those with higher scores for fear show weaker Zygomaticus major responses to a happy face than those with lower fear scores. Participants in a fearful mood, after watching fearful movie clips, showed a fear response to angry faces. An explanation for this phenomenon is the extra awareness of the environment which comes with fear. When you walk an ally in a fearful condition, you most likely pay attention to possible dangers in the environment. Participants in a sad mood, after they watched sad movie clips, did not show any significant reaction to a perceived facial expression and only showed reduced corrugator activity in response to a happy face. (e.g., Wood et al., 1990; Sedikides, 1992; Green and Sedikides, 1999). The emotional state of the perceiver thus influences facial mimicry. This can also be explained by self-focused attention. People are focused on their own emotion and these emotions interfere with the facial expression of others. This would predict that people who are depressed show little response to happy faces and more mimicry to sad faces. Further investigation needs to prove this. Self-focused attention is important because it suggest a large emotional processing component in the processing of facial expressions. The facial expression likely elicits an emotional response which can interfere with other emotions. People in a certain mood which have self- focused attention seem to respond more according to their own point of view. What happens then when people are in a happy mood? The people in a happy condition showed standard responses to both sad and happy expressions. They responded with corrugator activity for sad and zygomatic activity for happy faces (Seibt et al. 2015). These results suggest that a happy mood is the indicator when it comes to facial mimicry. A happy mood is also perceived as stronger in naturalistic settings, in shopping malls, smiles are more readily mimicked than sad expressions. Those in a happy condition are able to read facial expressions and respond correctly. Finally, direct eye gazing influences whether an emotional expression is perceived more robust. When an avatar directs itself to the receiver directly without looking away, the receiver responds with more zygomatic activity for a happy face and more prevalent corrugator activity for a sad or angry face in comparison with a non-direct gaze. (Soussignan et al. 2013). Direct gaze influences facial mimicry which could be due to better recognition of the emotional expression when gaze is direct. So, the way in which information enters the brain, the current emotional state of the receiver and other cognitive processes such as attention all relate to facial mimicry and this makes facial mimicry an advanced and complex process.

Group dynamics on facial mimicry

Prior judgement and emotions in the observer influence the outcome of facial mimicry, which would also be in line with the theory that there Is an internal processing mechanism for facial expressions. Facial mimicry has been researched several times in combination with familiarity. Agreeableness and familiarity influence our muscle responses to a facial expression. The way in which we view each other matters. When another person is a romantic partner there is more zygomatic activity for an angry face, to compensate with a smile for the angry looking person. Close relatives have little disgust mimicry when there are faces presented. This is in line with the theory that people tend to approach people with positive characteristics and avoid those with negative characteristics. (Chen and Bargh, 1999; Neumann and Strack, 2000;Neumann et al., 2004; Seibt et al., 2008). If mimicry can be seen as communicative approachable behavior, there will be more mimicry for those with positive characteristics. Recall that facial mimicry plays a role in empathy, so the view that facial mimicry is more when we like somebody is very likely. This has been investigated by Hess et al. Zygomatic activation was stronger for happy faces of positive characters than to those of neutral and negative characters. There was incongruent corrugator activity with those to which we attribute negative characteristics. In-group mimicry may occur more frequently in comparison with out-group mimicry since we have more empathy towards people that belong to our own group (Hess 2001).

The external factors on facial mimicry which influence mimicry such as in-outgroup, the state of the perceiver and cognitive load are important because they suggest that other cognitive processes play a role in facial mimicry. There is also a large emotional component of facial mimicry. In this review I would like to focus especially on immediate facial mimicry. The unconscious direct facial mimicry is part of the full process of comprehending a facial expression. Other cognitive processes provide a broader context for facial mimicry and explain that facial mimicry is not only muscle imitation but involve: 1. Emotion recognition and 2. Cognitive processes such as attention and agreeableness. The underlying neural processes of facial mimicry in neutral participants who tend to mimic both happy and sad expressions would presumably be mirror neurons. Neurons that fire when an action is observed and executed. The third chapter answers whether facial mimicry is a mirror neuron property.

Chapter 2 Mirror neurons

The underlying neural mechanisms of facial mimicry may rely on the mirror neuron system, just like motor acts. The mirror system is involved in many processes that involve empathy and goal-directed motor acts. In chapter 2, I will discuss shortly what mirror neurons are and how they contribute to the performance of motor acts. In chapter 3 I will discuss whether facial mimicry can be seen as a property of this interesting finding of mirror neurons.

The discovery of mirror neurons happened by chance. Mirror neurons were discovered in the research labs of (Rizollati, 2002). A group of neurons started firing when a monkey performed a goal-directed motor act (Rizollati, 2002). In this case the grasping of a peanut. It was the same group of neurons located in the premotor and inferior parietal cortex of the macaque that fired when seeing a motor act of somebody else, the experimenter, when he performed the same action of grasping a peanut. The same neurons fired as if the macaque performed that action himself. These neurons were given the name of mirror neurons. ''Or monkey see, monkey do'' neurons. They are located in the inferior parietal cortex and the premotor cortex of the macaque brain. These can be named classical mirror neuron areas and are connected to the superior temporal sulcus for visual input. Together they account for the classical mirror neuron system (Ferrari et al. 2011).

Functional properties of mirror neurons

The functions of mirror neurons were soon to be discovered, Ferrari et al. found that discharge of mirror neurons is related to object oriented hand actions such as grasping, holding and manipulating an object. But they have also been found for mouth actions of two kinds 1. ingestive and 2. communicative. Mouth ingestive mirror actions are the interactions between the mouth and an object, holding (with mouth), suck-ing, chewing and breaking. When a macaque sucks juice from a straw for example, mirror neurons are active (Ferrari et al., 2003). Communicative mouth action relate to lipsmaking or tongue protusion. They play a role in macaque face to face communication. From a young age macaques are already able to act out these communicative mouth actions and these may be inherited at birth (Ferrari et al.2003) Inheritance is an aspect of mirror neurons which I discuss in chapter 4. The communicative mirror neurons are likely the mirror neurons that are active in facial mimicry. Since we have seen that facial mimicry plays a role in empathy and communication of non-verbal information, smiles or frowns, it is likely that these mirror neurons play a role in facial mimicry. Even though mirror neurons respond with particular actions, they do not only fire for specific acts or movements. Nearly 1/3 of the mirror neurons are precisely congruent, which means that there is a one to one relationship between action observance and mirror execution. Nearly 2/3 of mirror neurons are broadly congruent, which means that there is not a one to one relationship between the exact observed action and the firing of mirror neurons. (Iaboni, 2007) A hand action of the sender may have an impact on mirror neurons but a slightly different hand action may elicit the same response. An interesting phenomenon occurs when a screen is in front of an object. When the action is performed partly under a blind condition, and the object is visible, the mirror neurons still fire. But when the screen is present and the object is not visible, the mirror neurons do not fire. Mirror neurons also fire when a sound associated with the action is present. (Iaboni 2007). The sound of tearing paper elicits a mirror neuron response in the observer. This suggests a response mechanism to what we have learned because we are not born with knowing the sound of tearing paper. Rizolatti suggests that mirror neurons code for understanding intentions. Different set of Mirror neurons respond to different intentions. For example, the response of a mirror neuron was different for grasping a cup to clean versus grasping a cup to drink. (Iaboni, 2007) This suggest an intention specific response of mirror neurons to the social context. It suggests that a positive facial expression elicits a positive intention and this intention elicits a mirror response because mirror neurons respond to the intention. It could be that the mirror neurons correspond to the positive intention which accompanies a smile. This view would be open for further consideration However, it has not been established yet whether these intention specific mirror neurons are also the origin of facial mimicry in humans.

Mirror neurons in humans

Until now we have only shown that mirror neurons exist in macaques, they are certainly prevalent for motor hand actions. Although mirror neurons were originally found in macaques, indirect evidence suggests that mirror links exist in human populations too. There is a body of evidence which goes in the direction that humans also have mirror neurons systems. In some papers however, the existence of mirror neurons was questioned. Until an interesting discovery by Mukamel et al which will be discussed. Originally, mirror neurons in macaques were found solely for motor acts. Recall from the last paragraph that mirror neurons were found for 1. Goal-directed motor acts and 2. Communicative acts. But psychologists suggest that the functions of mirror neurons are not limited to the observance and execution of motor acts. Mirror mechanisms play a role in imitation, mouth gestures, language and may play a role in autism as well (Cook, 2014). Both evidence for motor mimicry and communicative mimicry exist in humans. Only indirectly, based on neuroscientific methods. TMS studies in humans show that passive observation of arm, hand and finger movements result in selective activation of the same muscles that produce the action (Aziz, Zadeh et al. 2002, Catmur et al. 2007; Fadiga et al 1995). It has also been found that passive observation of an action and executing of a hand action highly tend to overlap with areas where mirror neurons have been found in monkeys. (Aziz-Zadeh et al. 2006; Buccio et al. 2004). (based on Heyes, 2009). Another study from Dinstein et al. used fMRI to test for mirror neurons in humans. They found five movement selective cortical areas, in the ventral premotor, anterior parietal, superior parietal and posterior parietal, anterior frontal sulcus when using a habituazion method. Habituation means that neurons stop firing when a biological stimulus is repeated many times. When the neurons in these areas received consequent stimuli, these areas habituated both for action execution and action observance

(Dinstein et al.2008) Which also suggest overlap between observation and execution of an action. Evidence for communicative mimicry also exist in humans. Both humans and monkeys share common cortical and subcortical circuits for facial processing (Paus, 2005, Caria et al. 2012) which involve the emotional areas beyond traditional mirror systems. It is found that the anterior part of the amygdala in humans is similarly active in humans and macaques when processing happy and angry facial stimuli. The ACC and the anterior insula relate to the processing of disgusting stimuli in humans when viewing a face with the expression of disgust. This overlaps with the area in macaques as well (Wicker et al. 2003) To conclude whether mirror neurons exist in humans, further research needed to contribute, the paper of Heyes and Iaboni suggests that single cell recordings in human populations can find the direct evidence for motor neurons to fill the gap between human mirror systems and macaque mirror systems. (Heyes, 2010) (Iaboni, 2006) Now the gap consisted of the weak temporal resolution of fMRI and the indirect measurement of the mirror areas in humans. In reverse, fMRI BOLD signals and TMS in macaque populations could also give us insight. Single cell recordings in humans are often unethical and can only be done on test animals. The direct evidence of mirror neurons is therefore more readily available for macaques than for humans. These doubts questioned whether mirror neurons existed in humans based on the difference in methods between macaques and humans.

Doubts of a human mirror system

A meta-study by Turella et al. tried to show that most fMRI data didn't show whether humans had mirror neurons, even when certain areas show overlap between humans and monkey brain areas when there was action performance and action observance (Turella, 2009). There were doubts whether fMRI measures were sufficient to find mirror neurons in humans. Recall that the methods to test for mirror neuron in humans are with fMRI. An example of a fMRI study to look for mirror neurons is relating the observation condition vs. a rest condition. In the first condition the human looks at an experimenter who performs an action. The fMRI signal is then measured and compared to the rest condition. Another method is to look whether there is simultaneous activity when observing and executing a movement since mirror neurons share the same property (Dinstein et al. 2008). These two methods do not show whether there are mirror neurons, single neurons that fire, but instead measure whole cortical areas. This approach has several downsides. Because fMRI measures the whole cortex instead of targeted areas, other processes may be active as well in these cortical areas when tasks are performed. These tasks to test mirror neurons also involve visual recognition, working memory etc. ''Mirror neurons are only a small portion of the neurons in these areas'' (Dinstein et al. 2008). In macaques, the mirror neurons are targeted individual cells measured with single cell recordings. Single cell recordings in humans could give sufficient evidence for the existence of mirror neurons in humans. In 2010 a study by Mukamel investigated mirror neuron activity in people with epilepsy with single cell recordings. This study could provide the sufficient evidence for mirror neurons in humans. They implanted electrodes in a single human cell, just like in the macaques. Normally, single cell recording would be impossible in humans, but these people were willing to assist when they had an epileptic surgery. Mukamel and colleagues presented 21 of these patients with movies of two types of facial expressions (frowns and smiles) and two types of hand actions (precision grips and whole hand prehensions). The neurons which were recorded behaved like broadly congruent mirror neurons in macaques. The activity of mirror neurons was beyond the classical areas, and involved the primary somatosensory cortex and temporal lobe as well. In the traditional areas of premotor and the inferior parietal lobe It showed mirror activity in single cells as well. This suggest that mirror neurons in humans exist beyond the classical macaque mirror neurons system but also exist in traditional mirror neuron areas. A surprising finding was that they found that the primary motor cortex acted like an antagonist. Neurons in this area fired when an action was performed, but decreased its activity when an action was observed (Mukamel, 2010). There was also evidence of anti-mirror neurons in humans. These neurons decrease their firing rate when an action is observed. These neurons can only be measured by single-cell recordings because they can use the same amount of energy to discharge as mirror neurons. An fMRI scanner would not detect the difference between anti-mirror and mirror neurons. The study with epilepsy patients showed proof of mirror neurons in humans, both involved in facial recognition and in broad hand movements just like the communicative and action specific mirror neurons. There is a role for mirror neuron systems in empathy, an aspect of facial mimicry. One theory suggests that facial mimicry occurs with emotion recognition. That the observance of a smile or frown elicits an emotional response through the facial muscles and these emotions are internally perceived by higher cognitive processes, but this has not been proved yet.

Mirror neurons in emotion recognition

When observing an emotional face, observers do not only participate in synchronized mimicry, they also understand the relevance of the agent's mental state for social interaction (Grosbas & Paus 2006). This process is also known as emotional contagion. (Ferrari et al. 2013) The definition of emotional contagion is the transfer of a certain mood among individuals through automatic mimicry and synchronization of facial gestures, vocalizations and postures (Ferrari et al 2013). Studies show the involvement of mirror neurons in emotional processing. When mirror neuron activity when viewing grasping actions was related to empathy scores, there was a robust correlation between activity in mirror neuron areas and empathy scores. (Iaboni, 2007) This suggest that mirror neurons, just like facial mimicry, play an important role in emotion and that people who score high on empathy tests have correlated activity in traditional mirror neuron areas. Note that this study measured hand actions and not the interpretation of facial expressions. In another study, subjects listened to action sounds after they filled in an empathy questionnaire. In this study they found a correlation between empathy scores and mirror neuron activity as well. (Gazolla et al. 2006) (Iaboni 2009). Neuroimaging evidence also shows a positive correlation between the mirror neuron system and empathy. (Gazolla, Aziz-Zadeh & Keysers 2012). Execution of an act as your own act can psychologically be described as re-afference. It has been suggested that deficits in mirror neuron areas play a role in autism (Ramachandran 2007) and affect re-afference. Autistic people often lack social skills that involve empathy and the lack of mirror neurons could be one of the causes of autism. The lower the activity in mirror neuron areas, the more severe the autism (Dapretto et al. 2006). A metastudy however contradicts the prevalent role of mirror neurons in autism (Hamilton, 2013) there seems to be involvement of mirror neuron areas in autism, but this can't be regarded as the sole cause. In youngsters, mirror neurons account for a large part in observational learning. Babies stare at their own hands when an action of a parent is observed. This suggests that re-afference occurs in youngsters, which can be an important given to explain the origins of facial mimicry. (When children already mimic from a young age, this leads more towards an genetic explanation which will be discussed in detail in the fourth chapter). Based on the evidence, mirror neurons seem to play a role in emotional just like facial mimicry. It seems that mirror neurons describe facial mimicry, at least partly, but is that the full story?

Chapter 3 Can facial mimicry be explained by mirror neuron properties?

Introduction

Recall from the last chapter that basic motor imitation can be regarded as a mirror neuron property (Iaboni, 2005). Imitating tongue movements can be a mirror activity, and mouth gestures such as drinking from a straw are seen as an ingestive mirror neuron activity. Seen by peers, infants and young macaques tend to copy tongue gestures from a young age, which suggests that the very basic form of imitation may be inherited. The activity of mirror neurons was found for facial expressions as well, (Mukamel, 2010) and for motor mimicry of hand actions. Motor imitation is regarded as a mirror neuron property because it involves mirror neurons that fire when an action is observed. Facial mimicry is more complex than basic muscle memory because it involves more complex forms of understanding the action as we have read in chapter 1. I would divide two important components of facial mimicry which form the boundaries in what the mirror neuron mechanism can explain. 1. is the recognition and the execution of muscle activity (such as activity in the zygotic major for smiles and for the corrugator for angry expressions). A basic perception-action link: an action of a facial expression that is perceived and elicits a response in the observer. 2. Emotional contagion, which accompanies facial mimicry. Emotional contagion can be seen as the interpretation and emotional understanding which relate to facial mimicry, described earlier as relating to the mind of the other person. These shared representations of emotions and motor acts are referred to in the PAM model, (De Waal, Preston. 2012) and the neurobiological bases of these representations could be the mirror neuron system or involve different processes which will be discussed.

I suggest that facial mimicry does not only consist of direct shared representation of motor acts which would be only prevalent in motor mimicry. But propose an internal processing mechanism of emotions which is separate. We can look at facial mimicry as a sophisticated process which involves emotional contagion, relating to the person's state of mind which is influenced by self-focused attention. The process of emotion recognition would likely be an internal mechanism that involves the perceivers own emotional state and the interpretation of the emotion in the facial expression that is seen. Recall from chapter one that facial mimicry depends on the surroundings, and attention. Mimicked responses can be inhibited and altered based on the state of the perceiver, or self-focused attention (Seibt. 2015). Mirror neurons explain the shared muscle activity in facial expressions, but attributing a mental state requires a different set of brain processes. To discuss facial mimicry simply as a form of basic imitation will not explain the full process of relating to another person's facial expression and state of mind, then emotional contagion comes in (the mentalizing system, or theory of mind, as will be described). The role of emotions in facial mimicry is further explained by Carr et al, 2003 who described the underlying pathways for emotion recognition which do not overlap with traditional mirror neuron areas for hand movements and communicative motor actions. In this chapter I would suggest that the action-perception link in facial mimicry can be explained by mirror neurons but more complex processing needs accompanied brain areas which do not have to have mirror neurons.

Motor imitation in relation to mirror neurons

Early studies found that the process of facial mimicry happens automatic after a couple milliseconds. Even without awareness, facial mimicry is present in human subjects. Effects are unconscious, automatically controlled processes (Dimberg et al., 2000; Dimberg, Thunberg, & Grunedal, 2002). According to current literature, the neuronal base of this direct action-perception link for (facial) mimicry is presumably the "mirror neuron system" ((Iacoboni et al. 1999), Blakemore and Frith 2005; Iacoboni and Dapretto 2006; Niedenthal, 2007). Who found overlapping areas in mirror neurons when actions were perceived and executed both for mimicry of hand actions and for mimicry of faces. A problem for measuring mirror neurons in facial mimicry is that automatic facial responses can only be measured by behavioral testing, mirror neurons are tested by neuropsychological methods such as fMRI. (Heynes 2009). There is still a large gap between research with behavioral measures versus neuropsychological like fMRI in relation to facial mimicry. But Mukamel showed mirror neuron activity for single cells in epilepsy patients which were active for facial expressions. It has also been suggested by Rizolatti et al. that homologues areas to the parietal and premotor areas of the macaque brain are active in humans when facial mimicry occurs (Rizolatti et al. 2011) ''Facial mimicry involves both classical, parietal, premotor areas and extended mirror neuron areas in humans''. Sato also describes in his paper that mirror neuron activity accompanies dynamic rather than static emotional images because of activity in the inferior frontal gyrus (Sato, 2007). The area of the inferior frontal gyrus is homologous to the anatomical locations of the macaque brain areas with mirror neurons. To area F5 in the ventral premotor cortex and area PF and PFG in the rostral sector of the inferior parietal lobule. (Iaboni, 2009). These are all examples of studies which suggest mirror neuron activity for goal directed motor actions. Both hand actions but also for facial mimicry. This is only proof that there exists an overlap between areas corresponding to the motor actions and not yet to the accompanied emotional contagion. The involvement of mirror neurons in emotion recognition comes from Ramachandran et al. in 2007. They propose a mirror neuron link for facial mimicry because Inhibition of facial expressions leads to inhibition of mirror neuron properties that understand emotions. Test subject responded later if they had to recognize an emotional face on the screen when facial mimicry was inhibited. (Ramachandran, 2007). Ferrari et al. suggest that coordination between actions and perceptions supports the hypothesis that a mirror mechanism is instrumental in coordinating facial expressions within social contexts (Ferrari et al. 2016). Even though mirror neurons accompany facial mimicry in traditional motor areas (premotor and the parietal cortex), the process for recognizing emotions seems to be separate from mirror neurons and evidence for the connection between the two systems is not well established even though there is clear evidence of mirror neuron properties in relation to motor mimicry of facial expressions.

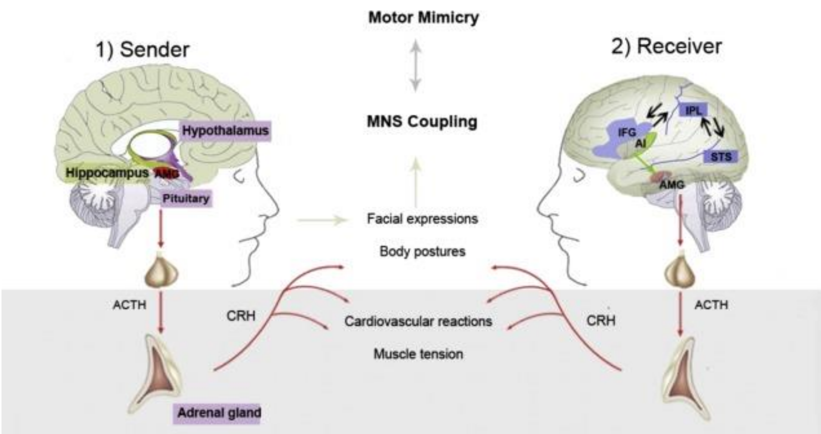


Figure 1 The standard pathway for motor mimicry (1) Observation of bodily movements activates the STS which is involved in early visual description of actions. (2) The STS projects to the IPL with mirror neurons tracking precise kinaesthetic movements and (3) passes this information to the IFG coding for 'the goal of the action'. (4) The goal directed motor plans are sent from the IFG via the IPL back to the STS. (5) The MNS coupling initiates motor mimicry '' cited from Eliska Prochazkovaa bMariska E.Kretab ‘’

Emotion recognition and mimicry

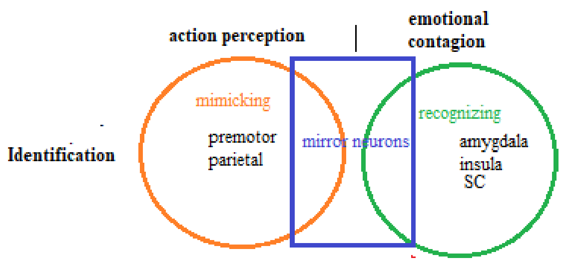
The emotional reaction in mimicry involve mimicking in heart rate, emotional processing of faces and responding accordingly. That emotion and facial mimicry are related is shown by Ramachandran et al. When mimicry was blocked by holding a pencil between the teeth, a change in emotion was detected later. So beyond the basic perception-action link in facial mimicry, evidence exist on the emotional processing of facial expressions. Lips proposes in a theory that there is a feedback mechanism by a three step model (Goldman & Sripada, 2005; Lipps, 1907). ''First, during emotion recognition, an observer mimics an expression, presumably in a subtle and covert manner. Second, facial feedback generates the corresponding emotional state in the observer. Third, the observer understands or classifies the emotion he or she is experiencing as the emotion expressed by the other person. The Lipps model suggests even that emotion and mimicry are not only related but that mimicry is a prerequisite for emotional understanding. This link can be doubted. an experiment by Botsard and Matsymoto investigated people with the Moebus syndrom. People with this syndrome lack the ability to mimic facial expressions because they were paralyzed in their facial expression. If Lipps' theory was true, it would suggest that these people were not as good as controls in recognizing facial expressions. The results showed no lack in recognizing emotional expression in people with the Moebus syndrome. They had the same results as controls. Since the facial paralyzed people were still able to recognize emotions, the prerequisite of facial mimicry is not a necessity for emotional recognition to occur. But emotional recognition and facial mimicry are two processes that both occur hand in hand when a facial stimuli are perceived. Emotional recognition could be a separate process from mimicking or a parallel process and involve both separate and non-separate brain areas. It seems that the areas for emotion recognition and motor mimicry show little overlap.

Mirror like activity in emotions

Mirror neuron activity exists for recognizing facial expressions. Basically for actions which involve motor muscles. Emotion recognition is also present in facial mimicry. The PAM model by de Waal proposes a relational affective response, a shared circuit for emotion recognition. (De Waal et al. 2002) According to them, there is a shared system for muscle observation but also for emotions. Where can these mirror neurons been found that correspond to emotion recognition in both the observer and expresser? This pathway for emotion recognition has been investigated in relation to mirror neurons in several studies and seems to be more distinct from the traditional premotor and parietal cortex found for motor mimicry than overlapping. Emotional contagion is a closely related concept to facial mimicry that it is sometimes defined in overlapping terms, but it seems to be a distinct process (Hatfield et al. 1993). Limbic regions do not belong to the classical mirror neuron areas but play a role in emotional contagion. In addition to traditional mirror neuron areas of premotor and the parietal cortex, Carr et al. 2003 showed that two limbic regions, the amygdala and insula, were involved in both the observation and execution of facial expressions. Expressions in monkeys activate a subcortical circuit involving the thalamus, superior colliculus, amygdala, and anterior insula, which represent a fast and automatic encoding route for a rapid evaluation of facial expressions (Burrows,2008).

A summary of the overlapping areas in the receiver and sender with emotional processing of a facial stimulus has been given by Rizolatti and Coregana. 1. Stimulating the anterior insula produces a feeling of disgust in both humans as monkeys. As well as the observation of a facial expression of disgust activates the anterior insula. Lesions to the anterior insula impair the ability to feel disgust. Cellular activation of the insula in macaques elicits a disgust emotion and lip smacking, (Rizolatti, 2003) (Caruana et al.,2011). Second is the amygdala, which is active when fear is produced in humans. Fearful facial expressions create a faster response when compared with other expressions (for which evolution could explain, a danger in the environment has to be detected to survive. Selective destruction of the amygdala produce an impaired emotion of fear. The third is the anterior cingulate cortex. Stimulating this area produces laughing. Also, showing movies with laughter and not sad or neutral expressions alter the gamma band activity measured with EEG in these areas (Rizollati, 2003).

The pathway for emotion recognition of a facial expressions seems to relate to the Anterior cingulate cortex and insula for more detailed facial processing of emotions. (Burrows, 2008). The relation between amygdala and emotional expressions suggests a system beyond the classical system of premotor and inferior parietal cortices to evaluate emotional responses in facial mimicry. Visual information comes from the sensory cortex and thalamus and is processed in the amygdala, Anterior cingulate cortex and insula depending on the respective emotion which processes emotional cues (Haxby, 2006). These areas are active in both stimulation as well as observing which suggests that the system for emotion recognition involves some sort of mirror mechanism, which is active for observation and action execution. Further research has to find out if these are singular mirror neurons or pathways that connect to muscle imitation, but it seems that the two are separate pathways, because people with the Moebus syndrome can also recognize emotions even when they lack imitation. For the model of muscle imitation and emotion recognition see the figure 2 below.



This figure 2 describes the relation between mirror neurons and emotion recognition and motor mimicry. Both pathways involve mirror neurons based on the above evidence. (But only part of the neurons in these areas are mirror neurons) Direct evidence exists for motor actions but only indirect evidence for mirror neurons in emotion recognition. Both relate to the identification of a facial expression.

A separate mentalizing system beyond mirror neurons

Besides the emotional pathway for recognition or identification, emotional contagion requires another pathway. Referring to a person's mental state involves pathways which do not require mirror neurons at all. This system is different from muscle perception entirely and it may even be a distinction from the emotion pathway. This pathway becomes active when judgements are made. This relates not only to identification of an emotion but also to attribution of a mental state to the visible emotion. This pathway is active for example when asked: ''Why'' somebody is doing what he is doing? According to Spunt et al. This is the mentalizing system, or theory of mind. This suggests a third pathway for facial processing. Besides muscle perception and emotion recognition, there exists a separate mentalizing pathway.
Neuroimaging studies which ask participants to make judgments about the internal states of others, such as their beliefs (Saxe and Kanwisher, 2003), preferences (Mitchell et al., 2006) or emotional state (Budell et al., 2010; Ochsner et al., 2004), also include a different set of cortical brain regions beyond mirror neurons. These involve the dorsomedial and ventromedial prefrontal cortices, posteriorcingulate cortex/precuneus, temporoparietal parietal junction, the posterior superior temporal sulcus and the anterior temporal cortex (Frith and Frith, 2006; Mitchell,2006 ;Saxe,2003) also known as the mentalizing system. It has been suggested that this mentalizing system is not concurrently active with mirror neurons. This system is apart from mirror neuron.

Recall that Step 3 in Lips theory is the attribution of a mental state to the observed emotion. For example, why is the person doing what he is doing? This seems to be a separate system from motor imitation and consists not only of an attribution of an emotion but also the underlying reasons for the emotion. A meta-analysis of 220 neuro-imaging studies found that the mentalizing system, which corresponds to the reasons why, the judgement of an emotion or moral explanation why the emotion is perceived in this way, is not concurrently active with mirror neurons (Van Overwalle and Baetens, 2009*).* A famous task which involves the mentalizing system is the false belief test. A fictive character Sally place something in the basket, another person comes in and replaces the object. The question is, where will Sally look when she comes back? For judgements, and false belief tests, the corresponding neural mechanisms show little overlap with mirror neuron areas. Spunt and Lieberman agree with the two system account for facial mimicry. One system for muscle imitation, the basic action-perception link and the other for mentalizing or emotional contagion. Their experiment consisted of participants who watched videoclips with actors. After viewing videoclips of emotions, they observed that the mirror system was recruited for a behavior identification task. The question: ''what were the observed avatars doing''? But they observed that the other system, the mentalizing system, was recruited when adding causal attributions for observed emotional expressions. For example, ''what was the reason that the person in the videoclip acted in such a way''? In their discussion, they differed between identification of a stimulus (mirror neurons) and then attribution to a mental state (mentalizing) (Spunt et al. 2012) This is a two-process model is known as the I-A model, the identification and attribution model. There is little overlap between mirror neuron regions, that correspond to identification of a mental state, and the attribution system which consists of the temporoparietal parietal junction and other areas for explaining a behavior. The I-A- model, or two systems idea relates to the interpretation of facial mimicry. Muscle imitation exists for facial muscles, but the understanding of emotions involves both mirror emotion recognition pathways and the mentalizing system for attributing a mental state. Instead of only 2 streams, one for emotion recognition and the other for the action perception link we can add a third mentalizing stream for the processing of an expression.

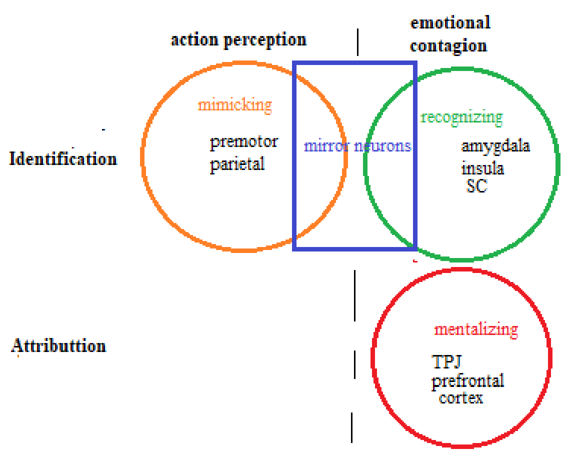


Figure 3. A full model based on the evidence. The figure differentiates between muscle action an

perception, emotion recognition, and mentalizing/attributing a mental state. This leads to a three way model as shown in the above image when a facial image Is presented. Note here that besides a distinction in identification and attribution, there is a distinction between recognition and mentalizing as well. Mentalizing does not involve mirror neurons but does relate to emotional contagion.

Can facial mimicry be explained as a mirror neuron property?

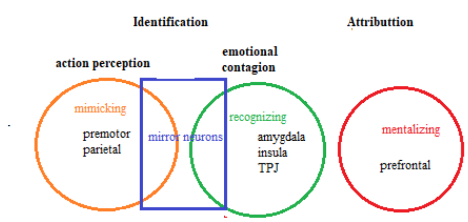
Facial mimicry is not simply imitation but a more advanced process that accompanies more brain regions than mirror neuron areas. It seems that facial mimicry, involves three streams of neural activity 1. A perception-action link, or a muscle reaction which involves mirror neurons. 2. for emotion recognition, based on the pathway which involves amygdala, insula and anterior insulate cortex for emotion recognition which responds to specific emotions, and a third mentalizing system for attributing a mental state which involves a description of the goal and an emotional judgement. The process of attributing reasons to an emotional state can be described as a separate mentalizing system. One view is the IA model which differs between the identification of an expression and the accompanied mental state, but this model does not explain the mirror neuron properties of emotion recognition. I thus describe a three stream model based on the evidence as shown in the image above. A mirror system for action and perception, a mirror system for emotion recognition and a non-mirror system for mentalizing. The mirror system is the action-perception link, and the system for emotion recognition since the evidence shows overlap for action and observation in these areas. And the non-mirror system, the mentalizing system, which involves the judgement and causal explanation of the emotion. These systems for mentalizing, emotion recognition and action-perception link could occur all at once. But it may be likely that they occur at separate times after presenting the stimulus for which an alternative is posed in the considerations. More research has to delve into the time lapse between these processes to see whether emotional processing is part of the same process or if these are separate processes.

In a large portion of literature, facial mimicry is explained as a mirror neuron property (Ramachandran, 2007 Sato, 2007) (Blakemore and Frith,2005, Iacoboni and Dapretto, 2006; Niedenthal, 2007).) and it is true that mirror neurons play an important role in facial mimicry. But it is only part of the story. Based on the reviewed experiments, facial mimicry involves the understanding of another person' emotion as well, emotional contagion instead of pure imitation of facial muscles. (Lieberman et al. 2005). Based on the evidence, there seem to be three systems when we process a facial expression. One for action- perception and emotion recognition which involve mirror neurons, and a mentalizing system which does not involve mirror neurons. Mirror neurons are not sufficient to explain emotional contagion fully and thus mirror neurons do not explain the full process of facial mimicry.

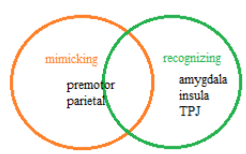
Some considerations

One process could be unconscious, identification and emotional processing. The other, mentalizing system could be conscious. It is like the system 1 and system 2 distinction based on judgement and decision research (Kahnemann, 2011). We need sufficient input to judge the causes and underlying research for emotions and this process seems conscious. It seems likely that emotional processing and the action perception link occur in parallel. But, that mentalizing comes in after conscious thought and occurs later after the stimulus onset, non-automatically. Further research in this area would be interesting to find out whether such a distinction is likely.

The model than has some presuppositions. A consideration for the prior model is that the model is parallel. Which means that the streams occur at almost the same time onset and that the defect of one aspect in the model does not interfere with another. However the process may be partly serial if the attribution and emotion recognition occur at different times, (alternative 2). In that case, the action perception and emotion recognition occur parallel, of which we can be quite certain based on the evidence and the mentalizing pathway serial. Attention models also have feedback and feedforward mechanisms which are left out in the figure. Finally, in situation 3, there is some overlap between the mirror mechanisms for emotion recognition and motor mimicry. For example it could be that mirror neurons for emotion recognition and motor mimicry overlap in the thalamus. In that case, these pathways interact or connect. We have situation 3 which shows overlap in the mechanisms for motor perception and emotion recognition. Finally, we may add conscious and unconscious to the model, if it is proved that emotion recognition and motor mimicry occur unconsciously versus conscious mentalizing.



situation 2 different time lapses, no feedback



situation 3 overlapping areas

Chapter 4 How can the origin of the perception-action link in facial mimicry be explained?

Introduction

Another question that is prevalent in the mirror neuron literature is the origin of these neurons. I would like to focus on the origin of facial mimicry. First I will look for similarities between the origin of mirror neurons and the development of facial mimicry. We know that facial mimicry can only partly be seen as a product of the finding of mirror neurons, Since there is more literature on the origin of mirror neurons, I would review the literature first. The implications for facial mimicry will be reviewed later. Mirror neurons most likely explain the unconscious automatic responses in facial mimicry, the action-perception link, since there is overlap in these areas for action observation and execution in facial mimicry. There could also be a similar mirror process in emotion areas for emotion recognition. In this section the focus will mainly be on sensorimotor learning and its contribution to the action-perception link in facial mimicry.

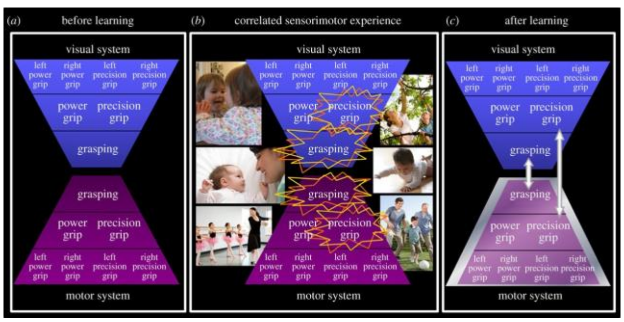
General sensorimotor learning

Sensorimotor learning is a form of associative learning. Associative learning plays a role in many different forms of learning. One of the earliest forms of learning was Pavlovian conditioning. When a conditioned stimulus is eventually associated with an unconditioned response. Basically sensorimotor learning is also a form of associative learning. In sensorimotor learning, basic sensory information is paired with motor information to come to an optimal decision for the next act. (Wolpert et al. 2011) In the review by Wolpert et. al, sensorimotor learning is mainly explained for complex movements like a tennis swing. Sensorimotor learning involves new mappings between sensory and motor variables. When performing a motor action that depend on motor learning, for example the hitting of a tennis ball or the execution of a facial expression, it requires the necessary processing of sensory information. Motor learning depends on eye movements for example. They should be in qualitative agreement with an optimal extraction of task-relevant information (Wolpert et al. 2011). The motor system then filters the important sensory information for the task by computing the possible states of the world combined with internal models of the body that map the motor commands.

Mirror neurons play a role in observational learning. Watching another person perform an action engages sensorimotor representations of the observed action (Wolpert, 2011). Activity is shown in the dorsolateral prefrontal cortex and ventromedial prefrontal cortex when an action is observed. It has been shown that the same area is active when observing errors of others than of self-generated errors (Wolpert, 2011). How do these sensorimotor representations occur? One answer on the neural level Is the process of Hebbian learning or Ricardo and Wagner learning.

Mechanisms of associative learning

An associative learning account proposes that when an infant views an action and later performs the action, both the motor neurons and visual neurons are activated together. These then wire together, they correlate. The next time they act together (Heyes 2009). On a neural level, Keyser et al. suggest that there exists Hebbian learning in mirror neurons. Hebbian learning on a neural level means that when two neurons are active at the same time these neurons become activated in a sequence. The next time these correlated neurons fire together and create a network. One argument for sensorimotor learning in mirror neurons is that mirror neurons exist in many more areas than classical mirror neuron areas (Keyser et al. 2002). Hebbian learning provides an explanation at the neural level for this phenomenon (Keysers, Gazolla et al. 2002) it is contra the evolutionary account for a mirror neuron property which states that infants are born with a mirror neuron system. According to Heynes there is no direct evidence that children have a mirror neuron system which supports the view that there is sensorimotor learning involved instead of only an adaptive view (Heyes, 2009). After sensorimotor learning, only a visual stimulus is enough to activate the corresponding motor neuron in the observer because these are active in a network.



This is a figure which shows sensorimotor learning for mirror neurons. First the visual and the motor system are two distinct systems with their own system of neurons. The first set of neurons in the visual system fires when there is visual input. The motor system is active when motor acts are performed. In the second picture, an infant observed the actions of a peer, observational learning. The infant watched how fruit is grasped from a tree (an act of precision grip). The infant performs the act herself while observing his peer. Now the visual neurons and motor neurons are activated at the same time, there is correlated sensorimotor experience. The third picture shows that after learning, these neurons correlate or wire together. The infant only has to watch a precision grip (visual system) and her motor system becomes activated, an example of mirror neuron activity.

Although Keyser et al. believe that Hebbian learning is the origin of mirror neurons, Cooper, R.P., Cook, R., Dickinson, A. & Heyes, C.M. (2012) have suggested that the associative (not Hebbian) Rescorla-Wagner model of learning forms the origin of mirror neurons. Rescorla, Wagner learning is associative learning in which two events do not co-occur but that two events relate to each other based on associative strength. They have based this on the experiment by Cook et al. who found several results for mirror neuron activity for hand actions (Cook, 2010). The compatibility effect is significantly greater with non-contingent training than with contingent training. When people had to close their hand when they observed an open hand action, training results were better than the group were hand actions corresponded with the observed hand action. Second, the compatibility effect is significantly greater with non-contingent training than with signalled training. With signaled training, the participants received also a neutral hand action stimulus. Third, the compatibility effects with contingent training and with signalled training are not significantly different. So there was no difference between matching open hand actions with open hand actions and adding neutral stimuli to the training phase. As a result of these findings, Cooper et al. developed a computer model which correlated better with the results of the Cook study (Cook, 2010). Hebbian learning would predict that contingent training gives better results, the actual observation of the action. Instead, counter actions lead to better results. The Rescorla Wagner model of learning also explained the non-contingent training. Even though this debate has not been solved yet, both Hebbian and Rescorla-Wagner learning provide an account for sensorimotor learning in mirror actions. However this contra stimulus learning of Rescorla Wagner learning seems to be more in line with the actual results of the investigations.

Heynes, Catmur et al. are in favor of an associative learning origin for mirror neurons. They have three reasons why sensorimotor learning is a more plausible account for the origin of mirror neurons than an adaptive view. They suggest that sensorimotor learning provides an empirically testable explanation for mirror neurons in humans versus monkeys. In humans, mirror neurons exist in more regions then standard parietal and premotor cortices. The additional mirror neurons, for example the mirror neurons that fire when a sound is correlated with an action, couldn't have been developed during different selection pressures but only exist through associative experiences. According to Heynes, mirror neurons also not play a specialized role in action understanding but play a role in many other cognitive functions (Heynes, Iaboni. 2009). An adaption tends to be tailored precisely to fulfill a particular function (Williams, 1966). The broad range of mirror neurons for several cognitive function such as communication and hand actions, could likely be associations between visual information and motor commands. Lastly, Heynes argues that sensorimotor training highly influences the mirror neuron system and the mirror neuron system can thus be trained which also proposes a sensorimotor learning account.

Can the perception-action link in facial mimicry be explained by associative learning arguments in favor and against

Mirror neuron activity exists outside mirror neuron areas

A reason why mirror neurons can be acquired through sensorimotor learning is that (broadly congruent) mirror neurons respond to distinct stimuli and exist outside the traditional mirror neurons areas. When we are born there are not enough stimuli to explain the visuomotor connections that we can acquire. Recall that it has been found that particular neurons respond to action sounds, for example, the tearing of paper elicits a response in the premotor cortex. This is an example of a learned or acquired mirror action (Keysers et al. 2002). Another example of mirror neurons that respond to learned stimuli is mirror activity for written words, or language, these are learned correlations and cannot be acquired through genetics alone. Mirror neurons were themselves also discovered in area F5 of the monkey's frontal cortex, an area considered the homologue of Broca's area (Rizzolatti & Arbib, 1998). Heynes, Catmur even found fMRI activity in mirror neuron areas when they responded to geometric shapes. Because these associations happen only with sufficient stimuli it is difficult to fully explain them in genetic terms (Catmur, 2012).

Influence of sensorimotor training

Another view that accounts for a sensorimotor learning view of mirror neurons is that sensorimotor experience can enhance Press et al. 2007) and abolish (Heynes et al. 2005) mirror activation in humans. If mirror neurons would be genetically inherited, they would resist environmental influences or be protected against them. Several studies show that sensorimotor training influences the mirror neurons. Viewing foot movements while performing hand movements can reverse the dominance relationship in the parietal and premotor cortex (Catmur et al. 2008). This study indicate that the mirror system can transform. The effects of training in mirror neurons is shown with capable piano players, who watched another pianist playing the piano, there is more mirror neuron activity then in controls (Haslinger, 2005). The same is true for ballet dansers who watched ballet. Activation in mirror neuron areas was higher in comparison with capoeira dansers. These studies suggest that repeatedly observing or performing an action contributes to mirror neuron development. (Heynes, 2009). Another way to put this argument is that sensorimotor learning experiments change mirror neuron responses. For repetition surpression (Press et al. 2010) Motor evoked potentials (Catmur et al. 2007;2011; Dáusililio et al. 2006, Petroni et al. 2010) and automatic imitation (Heynes et al. 2005, Wigget et al 2011). Thus, there is some evidence that training changes mirror neuron responses (Iaboni, 2007)

Implications of sensorimotor learning

This view of associative learning in mirror neurons has several implications according to Heynes, it means that mirror neuron systems can be trained in other animals that can perform associative learning as well. A dolphin could have mirror neurons too for example. Or birds could have mirror neurons. If mirror neurons depend on training, then humans are capable of acquiring more mirror neurons as experience increases and can have a decrease in mirror neurons when they are not sufficiently trained anymore. In short, it suggests a more volatile account for mirror neurons during one's lifetime. This leads to the suggestion that facial mimicry could increase during the life span. Or the elderly would mimic more, since these connections can be strengthened in life. With practice, the visuo-motor connections could increase. However, it has been shown that facial mimicry does not improve with age (Seibt et al. 2008). This is an argument against the view that facial mimicry is learned and suggests that training can only explain some modulating activities of mirror neurons but not fully explain the causes of mimicry and mirror neurons in general.

Is a sensorimotor learning the only explanation? A genetic view

The general theory of genetics suggests that among common ancestors, some individuals had a stronger genetic predisposition to develop mirror neurons and these could reproduce more successful and spread the genes which coded for mirror neurons across generations. The mirror neuron system would also be protected against changes in the environment and would produce an advantage across generations. The genetic account thus suggest that mirror neurons facilitate a positive role in action understanding and that the development of mirror neurons had a positive role in reproduction. Several advantages of mirror neurons can be named. Mirror neurons play a role in observational learning. This has the advantage because mirror neurons accounted for training and learning from group members within a generation. Some researchers go beyond small advantages and suggest that the resulting increase in ability to imitate and learn (and teach) could explain the explosion of cultural change that we call the "great leap forward" or the "big bang" in human evolution. The generation can learn the action through the mirror neuron system and efficiently use it as an advantage (Ramachandran, 2010). Others also presuppose evolution. Rizollati et al. 2004 suggest that the mirror neurons are of great evolutionary importance through which primates understand action done by their conspecifics (Rizollati & Craighero 2004, p.172). This relates to an advantage based on empathy and communication. If mirror neurons are the driving force of communicative development than the evolutionary view is also likely.

infants already show mimicry

A view that strongly accounts in favor of evolution is when it is shown that children mimic their parents or peers. Since children have not had sufficient stimuli for sensorimotor learning to occur, the genetic account would be more plausible when they exhibit a form of mimicry. Heynes argues that no direct evidence exist for mirror neurons in new born children. But this could be due to measuring problems with young children. It is difficult to place a child under an fMRI scanner and measure mirror neuron activity. Evidence has been put that childrens do mimic. It has been found that imitation takes place in new borns already (Lepage and Theoret, 2007). Neonates already imitate tongue protusion and other basic communicative gestures. This is in line with findings in new born macaques, they express lipsmacking and tongue protusion (Ferrari et al. 2006, 2012). Facial mimicry also occurs soon after birth. Between day 1 and 7, perceptions of facial expressions produce facial responses (Ferrari et al, 2006). Human children also watch their own hands when a motor act is performed, known as re-afference.

Imitation in newborns has been widely accepted, but the question rises whether this is intentional behavior. Some have argued that the ability to mimic tongue movements may actually be the result of an innate releasing mechanism (Anisfeld, 1996; Anisfeld, Turkewitz, Rose, Rosenberg, Sheiber & Couturier-Fagan, 2001. This would be a reflexive mechanism and not a goal directed act. Recall from chapter 2 that goal directedness or intention is a core component of mirror neurons, mirror neuron activity requires an intentional act. The reflex mechanism suggests that there is no intention underlying tongue movements and some have argued that hand gestures and lip protusion may all be artifacts from tongue protusion, the same basic reflex mechanism (Meltzoff, 1998). Famous developmental psychologist Piaget suggested in 1952 that children cannot act at will, but van der Meer, 1997; van der Weel & Lee, 1995 suggest that infants can perform actions at will like elder humans. The earliest electrophysiological demonstration in infants suggests that the neural substrates for processing biological motion are in place by the age of 8 months (Hirai & Hiraki, 2005). This could be the prerequisite of a motor resonance mechanism, because mirror neurons are often act specific. For example only for grasping. It has also been shown that EEG activity in young children is active when observing and executing the same drawing motion, thus a mirror matching mechanism exists in children (Lepage, Theoret, 2007). Imitation already takes place from a young age without sufficient stimuli to learn from them. it seems likely that an action observation/execution matching system is already present at birth in some form. (Lepage, Theoret 2007). (Ferrari et al. 2009 Gallese et al. 2009) have also expressed the view that mirror neurons are already present at birth. Cassile et al. suggest that face processing and the mirror system, rely on a brain network that is largely present at birth (Cassile, 2009).

The observation that neonates already show mimicry may be showing that this is not learned but genetically inherited (Ferrari, 2013). this is true even when certain behaviors can be trained or mediated from the mirror neuron system. Another way of reasoning is that 1.facial imitation is mediated by mirror neurons 2. Both humans and monkeys imitate when they had minimal opportunity for visuomotor learning and therefore 3. The associative account for the origin of mirror neurons must be wrong (Cook, 2004). Alterations in the mirror neuron system can take place, or association of new neurons under different contexts, like learning across development, but the basic mechanisms of imitating motor actions seem to be present at birth.

Another argument in favor of evolutions is that not only humans have mirror neurons, but they also have been found in birds (for song recognition) (Mooney, 2009) and in macaques. This is likely not based on associative learning because these animals live under totally different conditions. Since imitating and mirror activity is widespread among different animals, and these animals experience a totally different world from ours, it can be suggested that mirror and imitating activity has been established during evolution and is genetically inherited and not because of learning alone, since these animals did not receive the same stimuli as humans did. Imitation behavior has been found in Orang Utangs for example. Orang Utangs that engage in playful activity show facial mimicry. They were videotaped when they engaged in such activities and they showed clear signs of mimicry (Ross et al. 2008). Gazolla et al. found that the sensorimotor structures are activated during early facial gesture observation in infant monkeys as well (Gazolla et al. 2001). It suggests that these species have evolved a system for emotional communicative exchanges that functions very early in life (Ferrari et al., 2006; Mancini et al., 2013).

Can the mirror system be modulated?

An interesting experiment by Borenstein and Rupin in 2005 made an artificial system with both Hebbian learning rules and general genetic features. One of the agents initial abilities was imitation. It seemed that after 2000 modulated generations, mirror neurons, neurons in the motor cortex that fired when an action was observed and executed, occurred spontaneously. They found the following basic figure:

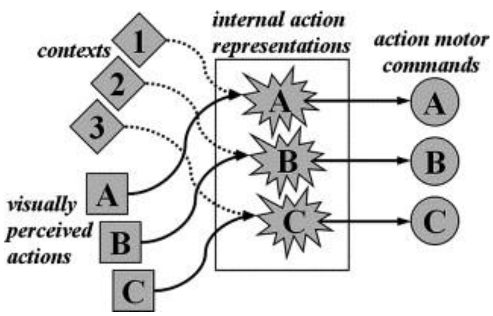


Fig. 7. A simple model of context-based imitation. Solid arrows represents innate associations, while dashed arrows represents associations that are acquired during the agent's life via Hebbian learning.

The correlations between visual neurons and action representations, seemed to be acquired by genetic inheritance, whereas the action representations in different context are acquired through Hebbian learning. This would explain why part of the mirror system is explained by learning (different contexts) across different situations, but that mirror neurons in general develop genetically when mimicry is present in the first generation.

How can we explain the origin of facial mimicry?

The origin of mirror neurons is highly debated and controversial. Facial mimicry is explained often as a sensorimotor property that is obtained during a life time (Heynes et al. 2009). Here I argue that facial mimicry is genetically inherited with a role for sensorimotor learning in learning new associations. I based this on several arguments. That infants and young macaques already show mimicry, that facial mimicry is beneficial for reproduction due to observational learning and that mimicry has been found in monkeys, humans and other developed species who have different living environments. When both sides of the argument are considered, the evolutionary account has fewer hazards to overcome. It explains why different species share mirror neuron capabilities even when they had different stimuli. In a generation, communication plays a role in learning social norms and the training of capacities within a generation. The advantage for reproduction is that those with communication in the form of mirror neurons can better adapt to their environment and have a genetic advantage across situations. They pass their genes to the next generation. The genetic account also explains why children as young as 1 to 7 months old have the ability to mimic faces, why Orang Utangs show mimicry and why a basic biological mechanism exists within children for action observation and execution. This does not mean that these mechanisms can't alter or change. there is sufficient input for the child in order to learn. It's like language, partly inherited, because without enough input, children are able to generate a wealth of phrases, words and verbs through learning.

What is the role of sensorimotor learning?
This regards sensorimotor learning as a valuable asset for further development of mirror neurons. The view that sensorimotor learning influences the mirror neuron system has been proved in recent literature. The computational model of Borenstein et al. is particularly interesting, because it suggests that mirror neurons occur spontaneously after 2000 generations when imitation is the sole prerequisite. Sensorimotor learning is then necessary for activity in specific contexts and for slight adaption in function such as recognizing sounds and responding accordingly. The basic mechanisms of action understanding and execution already exists but can be modulated through sensorimotor learning.

General conclusions of the thesis

The first research question was, how far can facial mimicry be explained by mirror neurons? First of all, we found that facial mimicry is not a basic action and perception mechanism or simple muscle imitation. Based on the literature on facial mimicry, we can conclude that higher order functions, such as attention and cognitive load interfere with facial mimicry. This lead to a search for other mechanisms in facial mimicry, and we found that there is a connection between facial mimicry and emotional contagion. Ramachandran provided indirect evidence of the link between emotions and mirror activity. Inhibition of mimicry lead to later detection of emotions when people were not able to show a facial expressions. This link was further explained by correlations between empathy questionnaires and mirror neuron activity by Iaboni et al. To explain emotional contagion, we had to look for these pathways in facial mimicry.

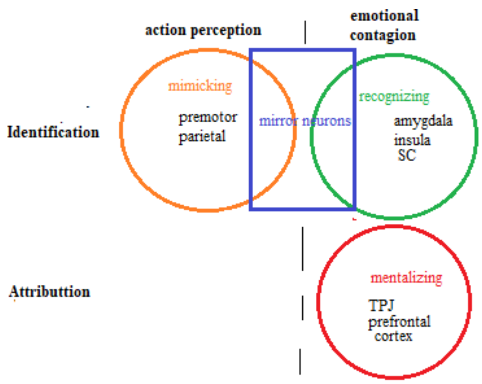
The investigation of emotion recognition in facial expressions lead to the Lipps hypothesis, which proposed that facial mimicry is a prerequisite for emotion understanding. People mimic the facial expression and causally feel the emotion. But the causal explanation was rejected by research with people with the Moebus syndrome. These people with facial damage could still recognize emotions, but they could not mimic a facial expression. Facial mimicry is likely facilitative in empathy but it is not a prerequisite for emotion recognition.

Mirror neurons then, were found especially for goal directed motor actions, both for communicative and ingestive acts in the parietal and premotor cortices. Based on the finding of Mukamel et al. in epilepsy patients, these neurons seemed active while viewing a facial expression in humans too. He found mirror neuron activity in traditional areas and areas beyond the premotor and parietal cortex when people are observed who execute a facial expression. Before, there were doubts whether a mirror neuron system actually existed in humans. Now they were found to be active in observing a facial expression. But still, we did not know what these mirror neurons could actually explain.

Based on the connection between hand actions and mirror neurons, it can be stated that mirror neurons are active in the motor part of the facial expression (the facial expression itself). But, according to some researchers, mirror neurons were active in empathy as well. The PAM (perception and action model) of the Waal focuses on shared representations for understanding of action and mental states. Carr et al found specific brain areas for emotion recognition, which involve the amygdala, insula and superior colliculus (Carr et al. 2003) and this is a distinct set of structures for emotion recognition. Now it seemed that mirror neurons were also involved in the understanding of emotions. We already found mirror neurons in the parietal and premotor cortices for the muscle action. But the indirect evidence, a similar mechanism for emotion observance and execution in the amygdala and other areas, lead to a mirror neuron explanation for emotion recognition as well.

However we found the interesting notion that there is a third pathway which does not involve mirror neurons, which is the mentalizing pathway. This was based on the findings of Spunt and Lieberman.

Spunt and Lieberman account for the IA model, which involves the identification and attribution of a facial stimulus. They found a mentalizing system which represents our ability to attribute causes to an act. But, the IA pathway fell short in explaining the mirror activity for emotion recognition in the insula and amygdala and the temporal parietal junction for disgust, fear and happiness. Then the following model could explain the relationships.



The answer on the research question whether mirror neurons can explain facial mimicry is that there are more pathways which accompany a facial expression. Facial mimicry involves both mirror neuron areas as well as non-mirror neuron areas. The three pathway model provides an answer to this question. One pathway for muscle imitation, one pathway for emotion recognition (which both involve mirror neurons) and a third mentalizing system which involves conscious thought and prefrontal functions to identify the emotional state. The latter two correspond to emotional contagion, or, the relation to the mental state of the other person. These seem to be parallel processes in the brain. But further research has to delve into this question whether these processes occur parallel or serial.

Now we knew that facial mimicry could partly be explained by mirror neurons, this raised the second research question, could associative learning explain the origin facial mimicry?
This was the subject of the last chapter. At first we looked at the general mechanisms of associative learning. There seems to be an influence of sensorimotor learning for mirror neurons in specific contexts. For example modulation because of skill learning has been proved in pianoplayers and dancers, and learning associations between sounds and visual stimuli exist only because we are exposed to these associations during our life time.

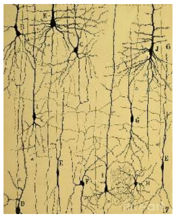
Interesting to point out is the phenomena of Rescorla Wagner learning for mirror neurons, instead of sole Hebbian learning which many researchers propose. Associations can also be made based on constant reverse input. Which pair the observation with another action. This opens a new world for the explanations of reverse facial mimicry. For example in romantic partners, because partners show a degree of likeness to an angry face. This could then be a learned reverse associative mirror neuron activity. Thus we could be able to associate anger with happy facial expressions and vice versa.

Even though the account of training should not be underestimated, it seems that the basic mechanisms of mimicry and mirror neurons can be explained genetically. Primates, our close relatives, and other animals such as songbirds live in totally different habitats and also show mirror neuron activity. Although they have different input, they are still able to express mirror neuron activity. And thus the learned associations may play a minor role, because the development of mirror neurons is not very context dependent. An argument which is just as strong is that young children and babies, also show imitation beyond basic tongue protrusion. It seems that a motor resonance mechanism is present at birth and that the development of mirror neurons is the natural consequence of these innate motor mechanisms.

The genetic account for the origins of facial mimicry explains that mimicry is important for learning and training which gave an evolutionary advantage for those members of the group who were able to communicate and understand each other and they passed their advantageous genes to the next generation. A clear image of a genetic modulation from imitation to the development of mirror neurons is depicted at the end of chapter 4. Which shows that genetics alone is enough for mirror neurons to appear with initial imitation after 2000 generations. Context sensitive mirror neurons on the other hand, develop due to associative learning. The answer then, is that the origin of facial mimicry can be explained mainly genetically and partly by associative learning.

Discussion

Further research has to investigate the slow and fast processes of facial mimicry and explore the relationships between emotional contagion and motor mimicry. In the presented model, the motor mimicry and emotional understanding show no overlap, but there may be a mediating pathway or an overlapping area. (This could be the thalamus, where sensory input comes together). Even though I pose the three way pathway in facial mimicry, the links between the emotional processing and the muscle pathway, remain an area of inquiry. Does activity occur at the same time or at different times? Do these pathways interact and how? Does the mentalizing system require conscious thought? The last question relates to the consideration of emotional versus rational thought. It seems that emotion recognition is purely emotional but the attribution of an emotional state is highly rational and thus requires prefrontal conscious thought. Also there exists only indirect evidence of mirror neurons in the emotion recognition pathway. Amygdala activity exists for observing and performing an action, but there has not been found direct evidence of mirror neurons in these areas. For the motor aspects in facial mimicry, the direct evidence has been found by Mukamel. The mirror neurons in emotion recognition areas such as the amygdala could be further investigated by placing electrodes in similar areas in other animals to find single mirror neurons in these limbic areas. Another aspect is to find the corresponding genes that are required for the development of mirror neurons. This could be found in test animals such as birds who have particular mirror neurons for song learning. Another question is, In what way do mirror neurons differ morphologically and structurally with other neurons? This could be an interesting neurobiological question to answer. The implications of this thesis are that the explanation of the relationships between mirror neurons and emotion recognition needs further clarification. The Lipps and IA model can be further investigated and enhanced based on the discussed literature. The model in chapter 3 could contribute to the explanation. This review also shows that many questions are still open for further consideration. Finally, modelling emotion recognition in machines has always been though. Emotions seem to be particularly for humans. Since these seem to involve mirror neurons, at least partly, the properties of these neurons can be modelled in machines to generate more basic emotional understanding. Understanding, or mentalizing is a whole other scope, which could be impossible altogether for machines.



drawings by Cajal et al.

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