MIRIAM HEYNCKES

The predictive vs. the simulating brain: A literature review on the mechanisms behind mimicry

Review

Is it possible to understand the intentions of other individuals by observing their actions? And how does unconsciously mimicking the behavior of other people relate to this? Mimicry is an important element of social cognition. Its settings and effects have been well studied. However, the neurobiological mechanism behind it remains uncertain. This review illuminates two neuroscientific approaches to explain the mechanism behind mimicry. On the one hand, simulation through the mirror neuron system (MNS) describes mimicry as a by-product of simulation by certain motor-neurons. On the other hand, forward and inverse models, an internal prediction about future events, are an important concept in motor control theory and have been suggested to be involved in social cognition as well. The author proposes a model in which mimicry relates to forward and inverse models by acting as a facilitator of social cognition. A better prediction, due to mimicry, leads to a better understanding of others. Furthermore, limitations of the given approaches are illuminated.
Keywords: social cognition, forward models, mirror neurons, mimicry

Miriam Heynckes; Research master student Cognitive Neuroscience
Maastricht University, Maastricht, the Netherlands

m.heynckes@student.maastrichtuniversity.nl

INTRODUCTION

One of the main aspects of being human is being a social individual. In the broadest definition, social cognition is what we think about ourselves and other people and how the processes involved influence our behavior and judgment in social contexts

(Hewstone, Stroebe, & Jonas, 2012). Social cognition as a research field has important sub-elements: for example the interest revolving around the Theory of Mind (ToM), the understanding and acknowledging of beliefs. Another element of social cognition and of importance to this review are social interactions. Interpersonal communication – the coordination between two interacting individuals – is one of the key features of social interaction. A complete picture of social cognition is far too complex for this review and therefore themes such ToM for an example are outside the focus of attention of this review. Interpersonal communication is about communicating information, meaning and feelings through verbal and non-verbal messages (i.e. gestures) and on the other hand, understanding intentions and messages from the other person. Accordingly the main focus of this review is on social interactions and mimicry.

Mimicry is an important element of interpersonal communication which can occur at non-verbal and subconscious levels. Mimicry reflects the similarity of behaviors during a social interaction. An example is the image of two women sitting in a café talking to each other and unconsciously sharing the same body postures while they talk. Both have the same leg crossed over the other and seem to be driven by the same idea when crossing their legs over again. This realistic example illuminates how omnipresent mimicry is. However, it still tends to go unnoticed most of the time. Particularly of interest is the finding that mimicry in social contexts leads to an increase in liking and vice versa (Chartrand & Bargh, 1999). It shows an important consequence of this ubiquitous but often unnoticed behavior. The effects of interpersonal coordination have been the topic of interest in a large amount of research. However, the larger role of mimicry when it comes to social cognition and understanding others' actions still needs further investigation. Therefore the focus of this review is to illuminate the mechanism behind mimicry by reviewing two approaches. On the one hand is the mirror system and on the other hand applications from predictive coding framework, namely forward and inverse models. Before reviewing these, a more thorough overview is given about what mimicry entails.

In general mimicry can be defined as "unintentionally doing what others are doing", and research has shown that it's often part of social encounters and occurs automatically (Hove & Risen, 2009). Mimicry was empirically observed for the first time in the 1970's in a study by LaFrance and Broadbent (1976). They observed students in a classroom and noted that automatic copying of laughter, movement, body posture and behavior is adopted several seconds after the observed original behavior, concluding that body postures function as non-verbal indicators of relations.

Furthermore, research during this time revealed a correlation between mimicry and liking (Lakin & Chartrand, 2003). Chartrand and Bargh (1999) demonstrated in a study that mimicry enhances rapport and liking. Within this study, a confederate mimicked the participants in one condition and strictly avoided mimicking them in the control condition. Mimicked participants reported liking the confederate significantly more than those participants not being mimicked. Experiments such as this study highlight the effects of mimicry on social coordination. In addition, recent research revealed that the relationship between mimicry and liking is bi-directional; two persons who mimic the behavior of one another on a non-conscious level promote liking towards one another and vice versa. In other words, affiliations can be expressed through non-conscious mimicry (Lakin, Jefferis, Cheng, & Chartrand, 2003). However, mimicry can also have negative effects on affiliation (Bailenson, Yee, Patel, & Beall, 2008). Using computer agents that mimicked head movements of individuals confronted with them showed that explicit detection of mimicked movements had negative effects on affiliation.

Patients suffering from autism spectrum disorder experience many problems related to social cognition. A better understanding of the mechanisms behind social cognition is necessary to address and eventually alleviate these problems. The occurrence and effects of mimicry have been investigated thoroughly and a lot is known about the behavioral consequences. Nonetheless, looking at mimicry leads to asking why the human brain is sensitive towards the observation of other people's behavior. Answering this adds to the knowledge on social cognition. Therefore, this review has the objective to introduce two approaches explaining a mechanism behind mimicry.

The first approach concerns a topic that has received a lot of interest, with many supporters and as many people who disagree with the suggested concepts. Mirror neurons have received a considerable amount of attention since their discovery by Gallese and colleagues at the University of Parma. Since then many promising but also speculating hypotheses have been formed involving the mirror neuron system. While some researchers deny their importance in understanding other people (e.g. Hickok (2009)) other researchers strongly support the idea that mirror neurons enable humans to understand the meaning of other's actions (e.g. Gallese & Goldman (1998), Rizzolatti, Fogassi, & Gallese (2001)). Many researchers have investigated the mirror neuron system and argue that they function as the neural basis of human perception and action coupling and in a wider sense the understanding of actions and intentions of other people (Gallese, Keysers, & Rizzolatti, 2004). Therefore, it seems plausible to delineate how the MNS possibly relates to mimicry and to illuminate limitations of this approach.

Forward and inverse models have been shown to predict self-produced movement in the field of motor control. These prediction models often are also referred to as the predictive brain approach, the Bayesian brain or the predictive coding framework. They are gaining an increasing significance, reaching as far as describing predictive coding as the general principle of how the brain works. It is interesting to reflect mimicry from this perspective. The predictive coding framework basically states that large parts of information processing, namely perception, understanding and action (a great deal of what is happening in the brain) can be modeled and explained by predictions. Complex cognitive processes such as social cognition have been included in this framework (Brown & Brüne, 2012) and in this review the possible relation to mimicry is considered. Both approaches, the MNS and the predictive coding framework, are influential and a large amount of interest has been devoted to them. This leads to the question whether these two concepts from the field of neuroscience are able to explain mimicry, and which limitations they bring about?

PREDICTION VS. SIMULATION

Social cognition through the Mirror Neuron System

Gallese and Goldman (1998) introduced mirror neurons; a system of neurons partially located in the motor cortex. These mirror neurons fire when executing a movement but also when the person observes the very same movement. Gallese (2006) stated that "the hard problem in 'social cognition' is to understand how the epistemic gulf separating single individuals can be overcome" (p.2). The influential findings on the Mirror Neuron System (MNS) guided research strongly towards a future in which this problem will eventually be solved.

Research on macaque monkeys showed that mirror neurons are located in the ventral premotor areas in the cortex. They do not only respond to goal directed movements made by the monkey himself, but also when he solely observed or heard a performance of a similar action. This similar action could be observing how a nut is being picked up or hearing how this nut is being cracked (Gallese & Goldman, 1998). According to this idea, the monkey knew what the observed person was doing by using his own motor system (motor areas in the brain) as an internal simulator. Comparable findings have been also been made in humans (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995).

It has been suggested that the MNS could be the bridge between individuals, a neural mechanism that creates a social link (Gallese & Goldman, 1998). The activation of these cells creates the intuitive understanding of another person's actions that human take for granted when observing someone else. They are, according to Gallese, Keysers and Rizzolatti (2004), the neurophysiological basis of social cognition.

The "double-function" of mirror neurons refers to the ability of these neurons to fire when own movements are initiated, but also to fire when comparable movements are observed. This double- function enables to link 3rd-person experiences to 1st-person experienced events by simulating the neural event. This has been referred to as simulation by Gallese and Goldman (1998). This mechanism not only allows to see or hear what other members of one's species are doing, but enables an understanding in the observer as if he was experiencing the action himself. However, as discussed in depth in the limitation section a major weakness of this approach is that no empirical evidence has been found supporting how the mirror neuron system could accomplish action understanding.

Furthermore, the mirror neuron mechanism has been proposed to mediate the understanding of others' emotions. A study focused on patients suffering from epilepsy with an implanted electrode located in the insula. The insula is an area in the brain involved in the perception and experience of emotions, amongst one of them being disgust. Findings suggest that the anterior insula is active when perceiving disgusting odorants as well as when the person is observing the facial expressions of disgusted people (Krolak-Salmon, et al., 2003).

Relating back to mimicry the question arises how the MNS could relate to it and what it contributes to the findings of increased social liking during mimicry. Gallese and Goldman (1998) showed that internally activated mirror neurons cause the execution of a planned movement. So to say, mirror neurons function as typical motor neurons. However, the very same mirror neurons when externally activated (i.e. when observing someone) show comparable activity but do not lead to an execution of the movement. They seem to be inhibited with regard to the usual self-initiated movement or as Gallese and Goldman call it "taken off-line". This seems counterintuitive, as there is neural activity in motor areas but no movement follows as a consequence. Gallese and Goldman (1998) concluded, that the MNS functions as a simulation mechanism to put the observer "into the same 'mental shoes' as the target".

A study by Fadiga et al. (1995) exploited transcranial magnetic stimulation (TMS) to stimulate the motor cortex of a subject. TMS is an established technique, which uses a strong magnetic field to stimulate certain areas of the brain. In this study the subject was observing hand movements grasping an object, while motor evoked potentials (MEP's) were being recorded from his hands. The researchers were able to demonstrate that this led to significantly higher MEP's in the same hand muscles, as the ones being observed. This condition was compared to conditions where the subject was only looking at the object or tracing the confederate's finger drawing geometrical figures in the air. This is further evidence supporting the idea of a human system that matches observing an action and the execution of the same action on a neural level. Comparable results were made with MEP's recorded from the tongue (Fadiga, Craighero, G.Buccino, & G.Rizzolatti, 2002).

The author suggests an explanation how mimicry could be the result of a mirror neuron system. Facilitated motor responses through the MNS then act as the basis of mimicry. Mimicry is essentially the unknown copying of an observed behavior, which comes into existence, as the necessary muscle groups used are facilitated, as explained in Fadiga's (1995) TMS study on MEP's. Motor responses are facilitated through the activity of mirror neurons in motor areas corresponding to the observed movement. Mimicry then appears to be a by-product of the simulation mechanism of mirror neurons. According to Gallese (1998) the purpose of mirror neurons is to serve as a simulator leading to action understanding of others. This is then accompanied by mimicry, which is essentially synchronized behavior (*for clarification purposes the author created Figure 1*). The given explanation entails that research investigating mimicry, was looking at observable instances of a simulation mechanism (the MNS). Simulation through mirror neurons is a form of neural synchrony between the observing person and the person performing an action and being observed. Self-other overlap refers to an understanding of another's intention such as putting oneself "into the same 'mental shoes' as the target" (Gallese & Goldman, 1998). Neural synchrony, by means of mirror neuron activity, thus leads to action understanding (a self-other overlap) and it leads to mimicry.

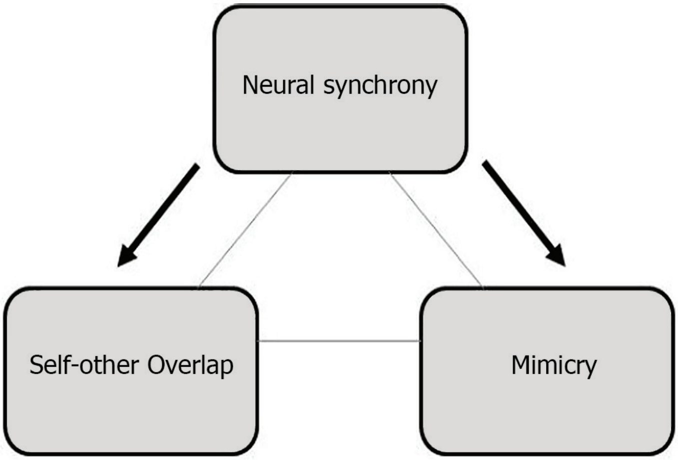

Figure 1. Simulation leads to an understanding of the other (self-other overlap) and to mimicry through facilitated motor responses

Wheatley, Kang, Parkinson and Looser (2012) state that the MNS evolved to function as a bridge between two individuals thus promoting social understanding. First they conclude that neural synchrony (MNS) is an efficient process, which is supported through its ubiquity of forms within the brain and the fact that simulation through mirror neurons leads to a self-other overlap reducing processing capacities. Efficiency of any kind in the long term sustains throughout evolution and is often naturally rewarded. Their second argument is based on similarity functioning as a cue of kinship. The broad concept behind kinship is that there is a kinship mechanism that favors social behavior towards relatives, due to evolutionary relevance, which leads people to be more comfortable with similar people. When mimicking behavior, the similarity in it, even if not perfect, functions as an implicit cue of kinship and this might lead to liking. In other words, shared movements suggest shared genes.

Finally, leading back to the introduction of this paper is the approach of looking at mimicry from the MNS viewpoint. Mimicry can be explained through the concept of the MNS. Within this approach mimicry is seen as a by-product of neural synchronization/simulation through the mirror neurons. These motor neurons fire when observing someone but no motor execution occurs due to inhibition of this neural command to move. Mimicry to observed actions occurs quite often. However, the link between MNS and an increased social liking through mimicry needs a stronger argumentation than currently suggested by the author. Wheatley et al. (2012) note that the critical point is, that neural synchrony (MNS activity) appears to ensure efficient processing by means of a rewards signal, which explains findings by e.g. Chartrand and Bargh (1999) on the link between mimicry and liking.

Limitations of the MNS approach

Mirror neurons are an important neurobiological discovery and have a strong intuitive appeal as to their importance for understanding social cognition. The MNS is often described with general explanations and functions which make it easy to understand and appeal as an explanation for many phenomena. However, empirical evidence for a concrete mechanism is lacking. Gallese (2006) stated that: [...] "We do not have a clear neuroscientific model of how humans can understand the intentions promoting actions of others they observe". And still eight years later the same question remains: if the MNS is in fact in charge of mediating understanding of actions and social coordination, how could it accomplish this?

Building onto this criticism are questions about the interpretation of fMRI data used to infer MNS activity. Gallese's and Goldman's (1998) initial study focused on single-cell recordings that specifically show the activity of certain neurons in the monkey cortex. However, how can we be sure that the activity measured in one voxel (which is by far not equivalent to one neuron) originates from the same neurons when observing action and when executing the very same, they could merely be neighboring cells.

Research has contributed a lot to specify where the exact parts of the MNS are located within the monkey brain and also partially within the human brain (Miall, 2003). However, this knowledge has often been oversimplified by the media and applied to many aspects of social cognition. Mirror neurons were claimed to create empathy when watching movies, leading to experience the same emotional moments seen on screen (dailymail.co.uk, 2013). Furthermore, in relation to the recent soccer world cup it has also been claimed that mirror neuron activity reflects higher understanding of the game. More experienced soccer players have higher activity of the MNS when watching a game (focus.de, 2014). However, there is no research that confirms the exact function of mirror neurons.

Research has shown that these cells are part of a complex interacting network of neurons. Also the category of what qualifies as mirror neurons is very large, comprising cells that fire when observing an action, hearing an action or seeing biological motion. Of these cells many fire only under very specific circumstances and others fire to a broad range of movements. (Gallese & Goldman, 1998).

Research is still at the beginning and the limitations stated earlier should be kept in mind. Generalizing from areas of the monkey brain to areas of the human brain should be done with caution and also using human brain imaging data has its disadvantages, as it cannot depict single neuron activity. Single cell recordings give more detailed insight into the functioning of the MNS. However, it is invasive and seldom done in humans; only if medically necessary.

A different proposal for a mechanism behind social coordination and eventually the understanding of others' intentions is the predictive approach of the brain, stating that the brain is able to predict events close in time. This mechanism has been suggested in the framework of the sensorimotor system and recent approaches focus on applying this concept onto social cognition. The following section illuminates on this.

Social coordination through internal models of forward and inverse planning

Forward and inverse models are established concepts within the Central Nervous System (CNS) to explain motor control in an individual. These models make use of a prediction of what a sensory event will be (Wolpert & Flanagan, 2001). The following section outlines forward and inverse models and their function in motor control. Furthermore, a link to mimicry is established by explaining social cognition through forward and inverse models.

Forward models of motor control

Research established a general acceptance of the concept of forward models in motor control and these forward models predict the sensory consequences of our executed movements (Wolpert & Miall, 1996). Forward models of the motor system use a neural copy of a motor command. This neural copy is referred to as corollary discharge and is used to establish a prediction of the position of the body. This prediction is then compared to the actual position of the body after executing the movement.

Using tickling as an example illuminates how this mechanism works and explains why you cannot tickle yourself. An internal forward model supports attenuation of self-produced movements by using sensory predictions of the motor system (Blakemore, Wolpert, & Frith, 2000). Accordingly, there will be actual sensory feedback from your hand; for example proprioceptive information, which is information about the relative position of your hand in space. Furthermore, there will also be the predicted sensory feedback from the forward model, which is established through the corollary discharge and called the efference copy. The discrepancy measured by your forward model between the predicted and actual feedback is what establishes the "tickliness" of someone. If there is no sensory discrepancy between your executed movement and the predicted movement then a sensory attenuation occurs and the sensation is not as tickling. This is what happens if a person tickles herself. However, if for example someone is being tickled, the efference copy of the self-created movement is missing. Accordingly this person cannot predict the movement and no sensory attenuation occurs, due to a high prediction error. In consequence being tickled is experienced as a lot more tickling in comparison to self-tickling. Blakemore, Wolpert and Frith (2000) propose that this attenuation through the forward model has advantageous effects for an individual as sensory information is being filtered. Filtering of information, especially of external sensory information is a necessary element of many brain processes to avoid a cognitive overload and ensure efficient processing of the environment. This filtering is an important trade-off between sensing everything and recognizing what is important to an individual in terms of survival. Sensory feedback created by external events can be more easily discovered and self-produced movements, which are filtered, can be weakened (Blakemore, Wolpert, & Frith, 2000).

Inverse models of motor control

Inverse models are, as the name suggests, an inverse model of forward models. Inverse models form the relationship between intended goals or actions, and the motor commands to achieve those goals. So basically, inverse models use a given input to estimate an appropriate command. As an example, if you are hungry and intend to pick up a slice of apple, your internal inverse model transforms the visual input (sensory representation of relative positions of the apple and your arm) into motor commands. The flow of information along pathways in the brain would be from occipital visual areas to areas in the posterior-parietal cortex (PPC) and would then feed through pre-motor and motor cortex to execute the command (Miall, 2003).

It has been shown that forward and inverse models act together within the motor system to establish a functional motor control. This is achieved through the architecture of motor control that incorporates multiple pairs of forward and inverse models (Harumo, Wolpert, & Kawato, 2001). Functional motor control is achieved through a dynamic repetition of an inverse model giving a first command to move and a forward model calculating the error between the prediction of the movement and the actual position. This error is then fed back to the inverse model, which reacts with an upgrade command (Churchland, 2002). It follows that the combination of forward and inverse models presents a mechanism that is fast and reliable, an essential aspect of motor control. Constant monitoring through them allows correcting or reacting to unexpected events, such as lifting an object that is lighter than expected and motor responses occurring appropriately. And taking this concept one step further, assuming that forward and inverse models are capable of learning this combination of models would create a very efficient system able to acquire a broad range of sensorimotor skills and could be a fundamental mechanism for different cognitive functions (Churchland, 2002).

Social cognition through forward and inverse models

Forward and inverse models are not exclusively applicable to motor control. Forward and inverse models are a fundamental computational mechanism for sensorimotor prediction. This has been well researched and an increasing amount of attention and work is devoted to investigate how a predictive coding framework can include complex cognitive processes such as social cognition (Brown & Brüne, 2012). Research revealed a link between internal models of motor control and the understanding of one's own intentions (Blakemore, Wolpert, & Frith, 2000). The following section elaborates on this finding and illuminates how forward and inverse models function in relation to social cognition.

Research comparing schizophrenic patients with healthy subjects revealed important implications for the functioning of forward models. The efference copy of a movement is likely to have a more important role with regard to sensory attenuation than the re-afferent information from the body part being moved. A defect in the "self-monitoring" mechanism of the forward model that creates the sensory prediction of movements (the efference copy) causes schizophrenic patients to experience a passivity of their movements. This means they cannot distinguish between movements made by themselves or others through the sensory prediction that would attenuate the sensation. Healthy control subjects were compared to schizophrenic patients with symptoms of passivity. The subjects judged whether they tickled themselves or whether they were externally tickled. There was a clear difference in tickliness between healthy subjects and schizophrenic subjects. Healthy subjects reported a difference in tickliness when tickling themselves or being tickled. However, schizophrenic subjects did not report this difference (Blakemore, Wolpert, & Frith, 2000). This reveals the possible importance of internal forward and inverse models in relation to social cognition. Understanding how humans can become aware of their own intended actions is the first step in comprehending how humans are capable of understanding others.

The author suggests a hypothetical predictive account initially suggested by Wolpert, Doya and Kawato (2003). Observing another person (here person 2) could function as visual input for an inverse model. The input replaces for example the relative position of one's hand and an object. Following this, an inverse model would generate communicative signals by initiating certain motor commands towards person 2 (e.g. speech gestures). A forward model of the individual would predict the sensory consequences of the motor command, in this case speech commands. Person 2 reacts to this by giving a motor command again, which closes the social interaction loop. His command provides feedback to the forward model of the first person; a prediction error is fed back to the inverse model which provides a new command through these consequences. As described earlier, a discrepancy between the prediction of another person's behavior and the actual observed behavior can be used to refine the inverse model (Wolpert, Doya, & Kawato, 2003). Furthermore, through an inverse model a person becomes aware of his intention why he wanted to move (e.g. pick up slice of apple). With feedback from the person being observed an estimate of what one's intention would have been for the same action can be inferred. This intention is then attributed to the person being observed (Blakemore & Decety, 2001). This social interaction loop functions by continuously predicting the other person. The following section illuminates how this social interaction loop based on forward and inverse models relates back to mimicry.

The human brain is all about efficiency. Communication between areas of the brain is created through synchronous firing of neurons in these areas. Also sensory input from the environment is processed in separate areas in the brain e.g. color and shape of objects are processed in different visual areas. These features of objects are combined again through synchronous firing (Engel & Singer, 2001). Neural synchrony in the brain is therefore an efficient process and the brain shows certain sensitivity to synchrony. This is also the case with mimicry. Mimicry of behavior promotes liking, on the other hand liking someone promotes this unconscious mimicry (Lakin & Chartrand, 2003). The author proposes that mimicry acts as a facilitator of social cognition. It is the result of interacting forward and inverse models of two or more persons respectively. Being in synchrony on a behavioral level (mimicry) promotes a synchrony on a neural level. This neural level refers to the prediction made by the forward models of two or more interacting persons. Understanding of others' intentions is promoted through a small prediction error of their forward models. Mimicry facilitates communication between two people by giving the forward models an "easy opportunity" to predict actions of the other person. This leads to a small prediction error. A small prediction error in our earlier example of tickling led to a sensory attenuation. However, in the social context instead of a sensory attenuation, a natural reward, namely liking towards the person is established. A more effective form of communication is established, and better understanding of the person one is interacting with has advantageous effects in evolutionary terms. But also the opposite relationship, in how far liking a person leads to an increase of mimicry, deserves attention. Interacting with a person means the brain is constantly predicting her actions. When liking a person the prediction error made by one's forward models is either small right away and promotes a facilitation of motor responses, which would reveal itself in mimicry. On the other hand the prediction error might be less accurate in beginning and then decrease over time as people become more similar behaviorally over time as well. Mimicry in this sense would then ensure mutual liking, while liking a person from the beginning on does not have an evolutionary advantage (this is not necessarily mutually), a mechanism that would promote mutual liking does have an evolutionary advantage. Mimicry in this sense would then function as a facilitator of social cognition.

Limitations of the predictive coding framework

Andy Clark (2013) concluded that predictive processing models offer the best clue until now for a unified science of mind and action. They promise to unite cognition, perception, action and attention within one framework. This framework suggests a hierarchical, bi-directional processing including top-down and bottom-up connections, where prediction- error minimization functions as the driving mechanism behind many cognitive functions (Clark, 2013).

However, a comprehensive understanding of the physical (i.e. neural) implementation of predictive coding frameworks remains yet to be shown (Egner & Summerfield, 2013). After all what has been illuminated on forward and inverse models within this review came from a computational point of view. According to Marr's (1982) different levels of information-processing, the computational level in itself has to be distinguished from the physical level, thus the implementation of the theory.

A disagreement exists on how this predictive mechanism is implemented. Additionally, it remains to be shown how the predictive and error messages are coded and transmitted via forward and backward connections in a hierarchy (Clark, 2013). Various implementations of the predictive coding theory have been suggested involving different cortical areas and circuits.

Nevertheless, the current lack of a general empirical demonstration of the predictive coding does not restrict its importance on generating theories involving prediction as a likely mechanism of brain functioning. Studies on the neural implementations of predictive coding have been scarce.

DISCUSSION

Summing up the main points, mirror neurons are motor neurons not only firing in response to goal-directed movements but also when the individual is observing or hearing the performance of a similar action. In this sense, mirror neurons are motor neurons used as an internal simulator to understand what another individual is doing

(Gallese & Goldman, 1998). Mimicry is a by-product of this simulation mechanism, which has been shown in higher MEP's recorded from muscles involved in a certain observed action (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). By highlighting how mimicry promotes neural synchrony it is emphasized that the opposite direction of this relationship is important as well. However, the MNS approach has often been oversimplified and put in a context in which this approach is used to explain a lot more than what has empirically been shown.

Forward models of motor control rely on a copy of a motor command, established by an inverse model, to calculate an error based on the prediction and the actual feedback from the motor command. A small prediction error leads to sensory attenuation which has evolutionary advantages due to an increased ability to differentiate between self-produced movements and external events. Using the motor system within this review to explain the functioning of forward and inverse models should not overemphasize the relation between forward models and the motor system. After all, a forward model is just a prediction. Seeing it like this, the brain often predicts events without necessarily involving the motor system. Visual perception and automatic processes of the brain, filling in the blind spot for example, are then also a prediction and a kind of forward model.

This functional combination of forward and inverse models has also been applied to social cognition (Wolpert, Doya, & Kawato, 2003). A social interaction loop is established, an interaction between individuals instead of forward and inverse models functioning within one individual. This social interaction loop creates mutual understanding based on predictions by the forward models of each person. Mimicry relates to this by functioning as a facilitator of social cognition. When mimicry is present, a small prediction error is made when predicting motor commands of the other person, which leads to efficient communication, having evolutionary advantages.

Leading back to the beginning of this review, the behavioral consequences of mimicry have been explained to a certain extent. However, what is the underlying mechanism and can neuroscience explain it? Both approaches have their strengths and weaknesses.

The MNS approach relates to mimicry by seeing it as a by-product of simulation. This concept is supported by findings from TMS studies (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). The simulation mechanism creates understanding of another person; this leads to liking this person on the one hand and mimicry as a by-product on the other hand. This approach is a reasonable explanation given the current knowledge on the MNS. Nevertheless, the reverse relationship, namely mimicry leading to enhanced liking deserves deeper attention from the MNS viewpoint.

Forward and inverse models of motor control are a well-established concept and based empirical findings. Forward and inverse models have been suggested as a mechanism to explain social cognition (e.g. Wolpert, Doya, & Kawato (2003)). However, linking these theories and findings to mimicry has so far not been approached. The author proposed in this review a possible mechanism, explaining why mimicry leads to enhanced mutual liking, based on forward and inverse models. Mimicry within this approach functions as a facilitator of social cognition, by leading to a small prediction error of the forward model. I think a lot can be gained when elaborating on this concept in future research. Its usefulness and application has been empirically shown with relation to motor control in humans and future research should aim to apply and proof this model in relation to areas of cognition, however with caution to avoid oversimplification.

When it comes to mirror neurons there has yet to be research, revealing the full functional significance of these cells. Mirror neuron research is still in its infancy and many different approaches using this concept have been elaborated. Forward and inverse models, however, have been an empirically solid proven concept in motor control and are presented as a less speculative concept than the MNS. Findings in relation to the MNS approach have been too vague until now to allow it being a solid independent concept. Especially the hype around mirror neurons in explaining social cognition and causes of autism should be evaluated carefully.

Forward and inverse models on the other hand, are also not the final answer. The concept of internal models can offer a lot to possible mechanisms behind social cognition. But again one could run the risk to oversimplify the topic and apply this approach too easily onto other areas besides motor control. After all, forward models are simply a prediction made by the brain of an individual to estimate future events. So the question arises whether a mechanism behind social cognition must be in the form of a forward model, or whether social cognition has a completely different mechanism behind it. Finally, both approaches reviewed here have been under a lot of investigation, especially mirror neurons. However, at this point in time no clear answer can be given to which mechanism leads to social cognition.

This review summarized findings from the field of cognitive neuroscience and aims to encourage researchers to look at social cognition and especially mimicry from a different angle. Future research should investigate the predictive account of the motor system in relation to social cognition to enlarge the existing concept and to illuminate the link between observed action, the motor system and social cognition (social understanding). Moreover, research focusing on the implementation level of predictive coding approaches is necessary.

Furthermore, many questions remain unanswered with regard to the MNS. For example, it is still unclear why mirror neurons seem to be specific for movements towards objects and food; in case of the macaque monkeys (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Also the exact definition of mirror neurons should be in the focus of research, since many different types of cells, in different functional and structural areas of the brain are now considered mirror neurons. It will most likely happen in the future that meaning and understanding of others will discovered to be not a single process or mechanism, but rather a combination of processes involving motor emulation, abstract cognition and other planning components of the cortex. And we are only beginning to understand their roles.

Acknowledgements

I would like to thank Sanne ten Oever and Stefan Gruijters for supervising this review and sharing their valuable suggestions and experience with me.

REFERENCES

Bailenson, J. N., Yee, N., Patel, K., & Beall, A. C. (2008). Detecting digital chameleons. *Computers in Human Behavior*, pp. 66-87.

Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews Neuroscience*, pp. 561-567.

Blakemore, S., Wolpert, D., & Frith, C. (2000, August). Why can't you tickle yourself? *Neuroreport*, pp. 11-16.

Brown, E. C., & Brüne, M. (2012). The role of prediction in social neuroscience. *Frontiers in human neuroscience*.

Chartrand, T. L., & Bargh, J. A. (1999). The Chameleon Effect: The Perception-Behavior Link and Social Interaction. *Journal of Personality and Social Psychology*, pp. 893-910.

Churchland, P. S. (2002). Self-representations in nervous systems. *Science*, pp. 308-310.

Clark, A. (2013). Whatever next? Predictive brains, situated agents and the future of cognitive science. *Behavioral and Brain Sciences*, pp. 181-204.

Egner, T., & Summerfield, C. (2013). Grounding predictive coding models in empirical neuroscience research. *Behavioral and Brain Sciences*, pp. 210-211.

Engel, A., & Singer, W. (2001, January). Temporal binding and the neural correlates of sensory awareness. *Trends in cognitive sciences*, pp. 16-25.

Fadiga, L., Craighero, L., G.Buccino, & G.Rizzolatti. (2002). Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *European Journal of Neuroscience*, pp. 399-402.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology*, pp. 2226-2230.

Gallese. (2006). Intentional attunement: A neurophysiological perspective on social cognition and its disruption in autism. *Brain research*, pp. 15-24.

Gallese, V., & Goldman, A. (1998, December). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, pp. 493-501.

Gallese, V., Keysers, C., & Rizzolatti, G. (2004, September). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, pp. 396-403.

Harding, E. (2013, February 14). *dailymail.co.uk*. Retrieved August 30, 2014, from http://www.dailymail.co.uk/news/article-2278360/Hugh-Grant-film-Love-Actually-wins-vote-movies-likely-mood-love.html

Harumo, M., Wolpert, D., & Kawato, M. (2001). MOSAIC model for sensorimotor learning and control. *Neural computation*, pp. 2201-2220.

Hewstone, M., Stroebe, W., & Jonas, K. (2012). *An introduction to social psychology.* John Wiley & Sons.

Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of cognitive neuroscience*, pp. 1229-1243.

Hove, M. J., & Risen, J. L. (2009). It's All in the Timing: Interpersonal Synchrony increases affiliation. *Social Cognition*, pp. 949-960.

Krolak-Salmon, P., Hénaff, M., Isnard, J., Tallon-Baudry, C., Guénot, M., Vighetto, A., . . . Mauguière, F. (2003). An attention modulated response to disgust in human ventral anterior insula. *Annals of Neurology*, pp. 446-453.

LaFrance, M., & Broadbent, M. (1976). Group rapport: Posture sharing as a nonverbal indicator . *Group and Organization Studies*, pp. 328-333.

Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological Science*, pp. 334-339.

Lakin, J. L., Jefferis, V. E., Cheng, C. M., & Chartrand, T. L. (2003). The Chameleon effect as social glue: Evidence for the evolutionary significance of nonconscious mimicry. *Journal of Nonverbal Behavior*, pp. 145-162.

Marr, D., & Vision, A. (1982). A computational investigation into the human representation and processing of visual information. *WH San Francisco: Freeman and Company*.

Miall, R. (2003). Connecting mirror neurons and forward models. *Neuroreport*, pp. 1-3.

Podbregar, N. (2014, July 13). *focus.de*. Retrieved August 30, 2014, from http://www.focus.de/wissen/experten/nadja_podbregar/fussball-wm-jubeln-trauern-und-besserwissen-die-spiegelneuronen-spielen-immer-mit_id_3983151.html

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, pp. 661-670.

Wheatley, T., Kang, O., Parkinson, C., & Looser, C. E. (2012). From Mind Percpetion to Mental Conection: Synchrony as a Mechanism for Social Understanding. *Social and Personality Psychology Compass*, pp. 589-606.

Wolpert, D. M., & Miall, R. C. (1996). Forward models for physiological motor control. *Neural networks*, pp. 1265-1279.

Wolpert, D. M., Doya, K., & Kawato, M. (2003). A Unifying Computational Framework for Motor Control and Social Interaction . *Philosophical Transactions: Biological Sciences*, pp. 593-602.

Wolpert, D., & Flanagan, J. (2001). Motor prediction. *Current Biology*, pp. 729-732.