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Mirror neuron system: Mechanisms and functions

Zrcadlové neurony: Mechanismy a funkce

Bachelor thesis

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Declaration:

I hereby declare that this bachelor thesis is the result of my own work and to the best of my knowledge, it contains no materials previously written by another person. All used sources are listed on the References.

Prague 2018

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Alisa Loginova

Abstract:

Mirror neurons (MN) are a group of neurons with extraordinary visuomotor character. Their activation is connected to an observation of a certain action and its execution, if the action was already in motoric repertoire of the observer. MN were firstly identified in macaque´s brain, with later identification in human´s brain. The most important structures where we can find the MN are Broca´s area located in the inferior part of frontal gyrus (IFG), premotor cortex and superior parietal lobule (SPL). The functions of MN are various, they take part in action understanding, imitation, learning and language. According to present knowledge, they were assigned a role in social cognition – while experiencing empathy and theory of mind (ToM). Empathy can be defined as sharing of another person´s emotions. ToM highlights the importance of one´s ability to represent metal states of other people, knowledge, wishes and experiences. It leads towards understanding and anticipating of another person´s actions. Additionally to MN, amygdala, insula and basal ganglia are also important in processes of social cognition. Impairments of social cognitive skills are in autism, schizophrenia and psychopathy.

Key words: mirror neuron system, motor area, social cognition, empathy, theory of mind

Abstrakt:

Zrcadlové neurony (MN) jsou výjimečnou skupinou neuronů s visuomotorickými vlastnostmi. Jejich aktivace je spojena jak s pozorováním konání druhé osoby, tak i s prováděním stejného úkonu, pokud již tyto činnosti patřily do motorického repertoáru pozorovatele. MN byly poprvé identifikovány u makaků, později došlo k jejich objevu u člověka. Nejdůležitější struktury, kde můžeme nalézt zrcadlové neurony, jsou Brokova oblast, která se nachází v inferiorní části frontálního gyru (IFG), premotorický kortex a superiorní parietální lalok (SPL). MN jsou nedílnou součástí pochopení činů ostatních, imitace, učení a jazyka. Dle dnešních poznatků mají také roli v sociální kognici – při prožívání empatie a teorie mysli (ToM). Empatií lze definovat jako sdílení pocitů druhé osoby. ToM zdůrazňuje schopnost reprezentovat mentální stavy jiných osob, poznatků, přání a zkušeností. Vede k schopnosti správného pochopení a anticipování konání pozorované osoby. Kromě MN se sociálně kognitivních procesů účastní i amygdala, inzula a bazální ganglia. Poruchy sociálně kognitivních schopností jsou pozorovány v autismu, schizofrenií a psychopatií.

Klíčová slova: zrcadlové neurony, motorická oblast, sociální kognice, empatie, teorie mysli

Table of Contents

Alphabetical list of abbreviations:

AE - affective empathy

AS - Asperger syndrome

ASD - Autistic spectrum disorder

ASL - associative sequence learning

CE - cognitive empathy

DBH - dopamine-beta hydroxylase

EEG - encephalography

fMRI - functional magnetic resonance imaging

fT - foetal testosterone

IFG - inferior part of frontal gyrus

IPL - inferior parietal lobule

MEG - magnetoencephalography

MN - mirror neurons

MNS - mirror neuron system

mPFC - medial prefrontal cortex

PCC - Posterior cingulate

REA - Relative empathic ability

SMA - supplementary motor area

SPL - superior parietal lobule

SPL - superior parietal lobule

STS - superior temporal sulcus

TMS - transcranial magnetic stimulation

ToM - theory of mind

vACC - ventral anterior cingulate

vAI - ventral anterior insula

Introduction

This bachelor thesis aims to make a profound knowledge summary about mirror neurons (MN) and especially their function in social cognition. Thanks to advances in imaging techniques, research in neurosciences makes giant steps forward. It is therefore necessary to access and evaluate all the available information correctly, in order to obtain a correct starting point for all the upcoming research in this field. The review is also aimed to provide the reader with a critical view on MN system.

The thesis is divided into two main parts. The first part covers the general topic of mirror neurons. It is known that apart from being the center of whole body management, brain also plays a crucial and leading part in our social behaviour. There are several main parts of the brain with structures activated in social behaviour – the temporal lobe, where amygdala and limbic system are located and diencephalon, represented by hypothalamus. Later, more structures have been proposed to play a role in the maintenance of social behaviour.

It all started in 1995, when Rizolatti and his team discovered a special group of neurons with an unusual combination of functions in monkey´s brain. In comparison with other neurons, which tend to have only one main function according to their precise brain location, these neurons were reacting to more complex stimuli. While having their brain activity recorded, monkey subjects were firstly set up to watch an experimenter make a meaningful hand movement towards food, which preferably belonged to monkeys´ repertoire of movements. Secondly, they were to do the same goal-directed hand movements themselves. Data collected from the recordings showed an activation of F5 brain region during both movement observation and execution by the monkey itself. More studies followed and resulted in a discovery of a region with homological function called Broca´s area. As a result of numerous following studies, it became clear that these neurons possess a combination of motoric properties, or so called visuomotor properties, connected with an ability to represent previously seen action. In other words, they are activated when a motoric task is performed, as well as when it is simply observed. This is where their name comes from. Mirror neurons do not only react on the individual parts of an actions, yet they focus on the complexity of the action to provide the best possible judgment of the action context. Moreover, these neurons provide an accurate action representation, which eases the eventual proceeding action execution. It is believed that more roles of the mirror neuron system are yet to be discovered. What we know today is that these neurons have major motor properties as well as being a key substance in skills as language, imitation and social cognitive abilities as empathy and the Theory of mind (ToM).

The second part is focused on the role of MN in social cognition. Basically, the mirror neuron system (MNS) can be considered as a bridging tool, which provides the observer with the understanding of an action through an inner simulation of the same action. As the social cognitive skill require a number of centers being activated, distinguishing the MN from the rest would not fully explain its function in social cognition. The core and the complexity of these abilities lies in a tight cooperation of perceptual, emotional, reward and motor centers. Result of the cooperation are prosocial skills like empathy, compassion and the ability to mentalize, all resulting in strengthening of social bonds. There are two different anatomo-physiological pathways how the MN deal with the information – direct and indirect. Apart from parieto-frontal circuit, there is a certain role of dopamine an oxytocin in the social cognitive circuit.

Even though the evidence for the MNS is substantial, it is still important to note some of the critique aimed at the mirror neurons and provide the reader with questions emerging from the popularity of the MN.

1. Mirror neuron system

1.1. Anatomy

Mirror neuron system (MNS) consists of specialized neurons responding to sensory and somatosensory stimuli. In primates, the most active area is described as F5 area, dorsal convexity of the cortex and the posterior part of arcuate sulcus to be exact (fig.1). Respectively in human brain, the area is described as Broca´s area – frontal gyrus and its left inferior part (fig.2). These two areas are considered to be homologous, mainly in its role in neurophysiology in social cognition. (Rizzolatti & Fadiga, 1996)

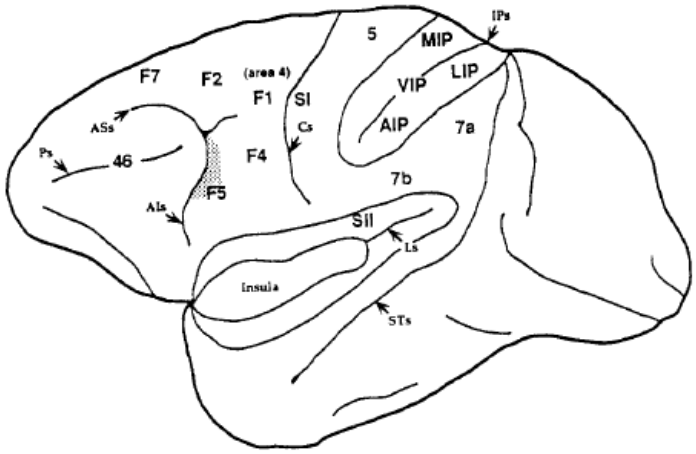

Figure 1: Schematic view of a monkey brain. Abbreviations: AlP, anterior intraparietal area; AIs, inferior arcuate sulcus; ASs, superior arcuate sulcus; Cs, central sulcus; IPs, intraparietal sulcus; LIP, lateral intraparietal area; Ls, lateral sulcus; MIP, medial intraparietal area; Ps, principal sulcus; SI & SII, primary & secondary somatosensory area; STS, superior temporal sulcus; VIP, ventral intraparietal area (Rizzolatti et al., 1996)

Areas of our concern are interconnected by various functional circuits. Thanks to the functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS), encephalography (EEG) and magnetoencephalography (MEG), discovery of these circuits was made much easier. As a result, MN were localised in numerous brain regions (Fig.2) – premotor cortex and its supplementary motor area (SMA), inferior (IPL) and superior parietal lobule (SPL) and inferior frontal gyrus (IFG) with Broca´s area (Iacoboni & Dapretto, 2006; Rizzolatti & Craighero, 2004). Tight functional connection with MNS was found with Wernicke´s area, as together with Broca´s area, they are main players in language learning, (Iacoboni & Wilson, 2006). Moreover, the somatosensory cortex brings sensory stimuli towards motor cortex, which is responsible for motor output (Molenberghs, Cunnington, & Mattingley, 2012). Last but not least, among functions of insular gyrus are awareness of body movements and interoceptive stimuli like pain, thirst, exercise or sexual arousal (Craig & Craig, 2009).

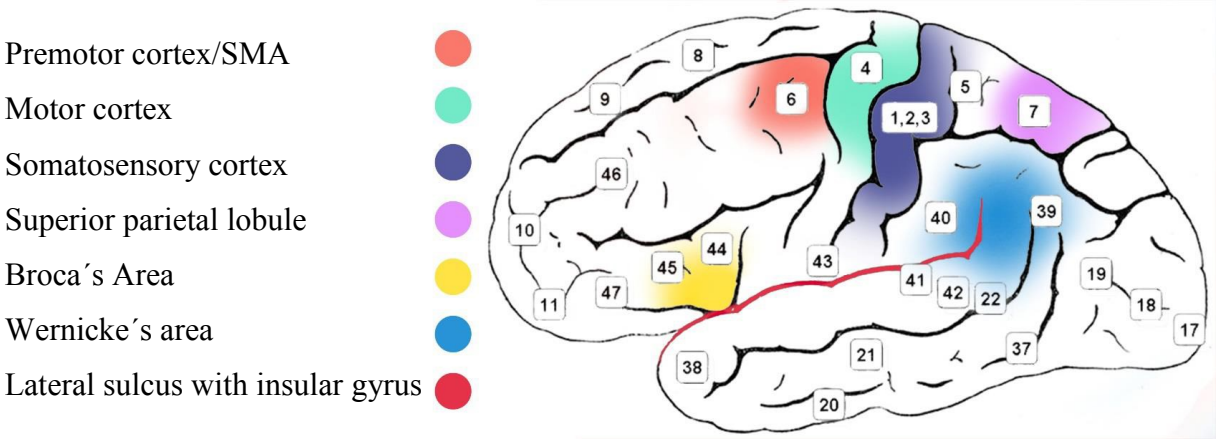

Figure 2: Schematic view of human brain and overview of MN regions and regions with tight functional connection, numbers indicating individual Brodmann areas. (Wikipedia: Brodmann area; Edited by PhDr. Marie Bendova)

One of the main circuits is called the parieto-frontal circuit found both in humans and monkeys with a slight difference in variety of regions (Rizzolatti & Sinigaglia, 2010). Human parieto-frontal circuit consists of inferior part of precentral gyrus, posterior part of the IFG and the IPL and its cortex in intraparietal sulcus (Rizzolatti & Sinigaglia, 2010). In macaque monkey brain, the main actions of events of parieto-frontal circuit concern the already mentioned F5 area – ventral premotor cortex, which is divided into 3 parts - F5 convexity, F5 posterior and F5 anterior part. Two more areas are important – parietal lobule of prefrontal gyrus and anterior intraparietal area, which interact with F5c and F5a respectively (Rozzi, 2005).

There is present scientific evidence of neurons with mirror properties of songbirds. The fact is that these mirror properties are slightly different from those described earlier. The system is called auditory vocal mirroring system to be precise. Functional MNS of birds consists of two interconnected pathways – a song motor pathway (SMP) and anterior forebrain pathway (AFP) (fig.3). The high vocal center of caudal nidopallium (HVC) is the main part of both pathways. In the AFP, the HVC is followed by interaction with area X in the paraolfactory lobe, the dorsolateral division of the medial thalamus (DLM) and the lateral magnocellular nucleus of the anterior neostriatum (IMAN) of bird's brain. The SMP pathway starts in the HVC, followed by the robust nucleus of the Archistriatum (RA) and tracheosyringeal division of the hypoglossal nucleus (XIIts/RVG) (Mooney, 2014).

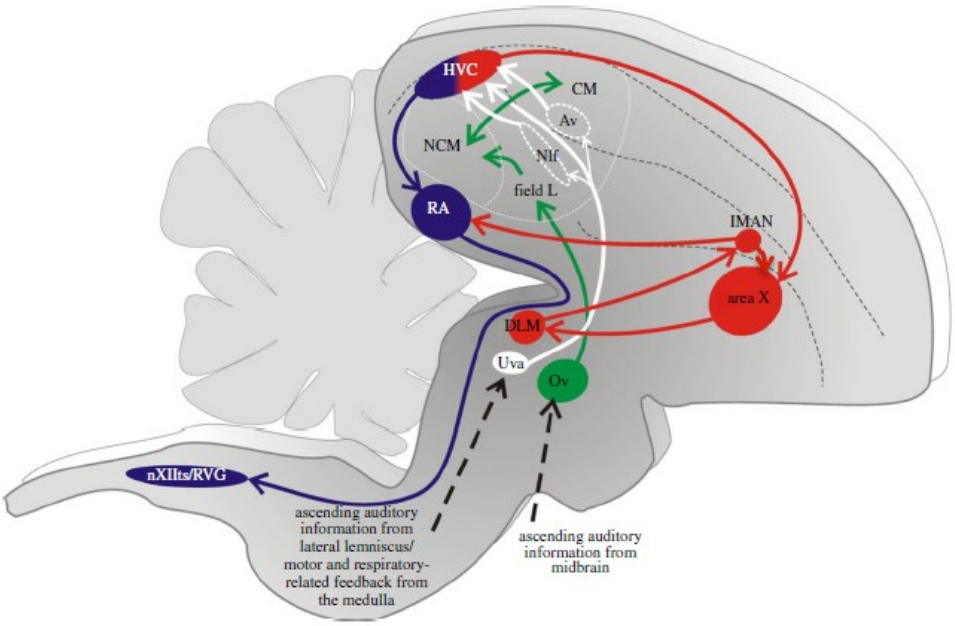

Figure 3: Schematic image of a songbird brain and its song system "SMP (blue) and AFP (red), the ascending auditory pathways (green) and the auditory inputs to HVC (white). At the microscopic level, HVCX and HVCRA cells are randomly intermingled within HVC. Av, nucleus avalanche; CM, caudal mesopallium; DLM, medial part of the dorsolateral thalamic nucleus; HVC, abbreviation used as proper name; LMAN, lateral magnocellular nucleus of the anterior nidopallium; NCM, caudomedial nidopallium; NIf, nucleus interface; OV, nucleus ovoidalis; RA, robust nucleus of the arcopallium; Uva, nucleus uvaeformis; VRG, ventral respiratory group; nXIIts, tracheosyringeal division of the hypoglossal nucleus." (Mooney, 2014)

Exact functions of mirror neurons are highly dependent on their location in the brain. The decision about which circuit is to be activated is upon the sort of the incoming stimuli. Complementary to the mirror neurons are canonical neurons (Garbarini & Adenzato, 2004). They are located in the lower part of the Brodmann area – rear part of arcuate sulcus. These canonical neurons with visuomotor properties fire as a reaction for observation of a three-dimensional object being presented or any related objects, which allow the same type of interaction of the agent and the object. They are size specific – if they are active in precise grasps of small objects, they do not fire to presentation of a big object and vice versa. Both mirror neurons and canonical neurons can fire at sole observation of an object. Nevertheless, canonical neurons react to visual presentation of an action related object and to basic interaction of the agent and the object. On the contrary, the mirror neurons require observation of a goal-orientated action using the object in order to be activated.

1.2. Pathways

1.2.1. Direct pathway

The first one to be described is the direct pathway. As the name suggests, this pathway is heading directly from the sensory input to the motoric output. It is primary active in neonatal

and infant stages of life (Ferrari, Bonini, & Fogassi, 2009). It turns out that visual stimulation of infants – tongue and mouth movements performed by an adult – support their own movements of the same type and therefore are the direct moving engine of the action mechanism. Direct pathway relies mainly on MN and their mirror-like activity (Ferrari et al., 2009).

1.2.2. Indirect pathway

Indirect pathway, on the other hand, is a crucial circuit for mediation of delayed responses like emulation, contagion, true imitation and response facilitation. All of these neural responses require more than just MN for adequate functioning. If we have a closer look at response facilitation, the main thought behind the indirect pathway becomes clear. Response facilitation is based on observance of certain behaviour, which is later unconsciously repeated in the same situation, simply based on two conditions – certain observance frequency and its presence in motoric repertoire of the performer. However, it is not necessary to follow the same motoric movements. The main focus of any movement is the goal, which motivates all the motoric actions (Ferrari et al., 2009). As this goal bears the importance of the action, MN require cooperation with prefrontal cortex, which is responsible for including motivation and context into the motor action, as well as proper action organization (Ferrari et al., 2009). For the indirect pathway, it is therefore necessary to keep the goal in one´s mind, not only perceive and process the actual motoric behaviour which leads to the desired finish line. The truth though remains that the most complex behaviour which utilizes this indirect pathway is imitation.

1.3. Functions

MNS is a neuronal base for numerous behavioural circuits, which are necessary for correct function of social abilities. The demonstration of the mirror nature of these neurons is through two different anato-physiological pathways – direct and indirect. Both direct and indirect pathway are highly dependent on the development stage of the organism.

1.3.1. Action understanding

Action understanding can be considered as a basic ability, which enables the receiver to react adequately to stimuli, in order to learn, imitate, understand and produce speech or feel empathy towards another person. There exist two major theories proposing neural circuits, which might be responsible for action understanding – thanks to motor simulation or the ability to mentalize (Brass, Schmitt, Spengler, & Gergely, 2007; De Lange, Spronk, Willems, Toni, & Bekkering, 2008). Theory of motor simulation is based on the sensorimotor properties of mirror neurons in

the premotor cortex – an observation of a certain familiar action activates these special neurons, which would further activate the adequate movement. By a mental repetition of the movement and its linkage to its own movement repertoire, observer understands the action and some reasons behind it (Gallese & Goldman, 1998). Action understanding might have also been achieved by the theory of mind framework. This theory suggests that in order to understand an observed action, the network of mentalization located mostly in the posterior part of the superior temporal sulcus (STS) needs to be activated, as any action does not possess only motor properties, but a significant deal of mental background as desires, believes and experience (De Lange et al., 2008)

Having said that, there is not much information left which could potentially decide whether the first or the second possible option is the right one. However, there is still one issue, which has been omitted – it is whether the action is a novelty for the observer or it has been previously perceived. If the action, and its goal in particular, is familiar to the observer, it is the mirror neuron system which is responsible for action understanding. On the other hand, if the observed action looks unfamiliar, a certain portion of mentalizing and inference needs to be applied, in order to potentially understand the actual goal of the action (Brass et al., 2007). It is therefore possible to say that action understanding is context dependent, be it a simple hand movement towards a glass of water or a complicated one like opening the fridge by feet with hands full of groceries. These two systems are complementing each other, as they both utilize different networks and react to different stimuli, thought altogether, they serve the purpose of action understanding (De Lange et al., 2008).

1.3.2. Imitation

Imitation is a rather important function of the MNS. Imitation itself can be interpreted as an observation of a performed task proceeded by its reproduction, influenced by observer´s previous experience. In 1999, the involvement of mirror neurons was confirmed in imitative tasks. Using fMRI techniques, Iacoboni and his team set the subjects to imitate a previously seen finger movement. Afterwards, they used a screen command for the same movement and finally, the subjects were set to watch the same movement. Activation was seen in the areas of mirror neurons - Brodmann area 44 and the rostral part of posterior parietal cortex (Iacoboni et al., 1999). It is an undeniable fact that it is simpler to imitate a familiar gesture than to perform an activity experienced for the first time, as imitation is considered to be the most effective form of learning. There is a common tendency towards imitation of effective behaviour rather than enduring one´s own pathway of finding - trying and failing, until finally reaching the

desired destination of effective, energy and time-saving performance to reach the desired outcome (Huber et al., 2009).

There are two central models used for explanation of imitative circuits. The first and pervasive one is an ideomotor circuit. This model needs two points to be fulfilled – observing a goal-achieving action and observer´s ability to perform it. Performer´s goal-orientated task activates motoric neurons by sensory stimuli, what subsequently leads to activation of exact muscles for the action to be performed (Iacoboni, 2009).

The second model is called associative sequence learning (ASL) (Cooper, Cook, Dickinson, & Heyes, 2013). This model is based on unnecessity of a specific imitation pathway to exist and emphasizes a strong influence of observer´s personality, environment and previous experience. These factors in particular are the linkages between the sensory and motor neural circuits of action execution, which are not otherwise interconnected. In case of ideomotor model, the performer and the observer are two different subjects. The ASL proposes that the subject can observe its own hand grasp or oneself in a mirror and it is still considered to be imitation, as both actions are visually guided. Additionally, the learning through association is also supported by the convergent evolution, as imitative skills have been observed within primates, birds and dolphins (Iacoboni, 2009).

Why do people imitate previously seen actions? In my opinion, there are several reasons. If someone else regularly takes certain steps to achieve a certain goal, wasted energy must be worth the achieved aim. If the goal of the intended action and the observed action are similar, it is the most energy-efficient way to imitate the behaviour and avoid own pathway of uncertain success. Moreover, previously learned pathway to achieve a certain goal may be collaborated on, in order to use its modification in a different goal-orientated task. It is therefore possible to say that imitation itself is an innovation to one´s repertoire of motor behaviour.

Imitation possesses a significant importance in social cognition. In human society, empathy and imitation are closely related to each other as they both serve a purpose of strengthening the social bonds through re-feeling or reacting of emotions or actions. In this concept, there are two main pathways of imitation in human society – a low and a high road. As the name indicates, the low road is the direct and simple one, as it is based on imitation of body language. The high road is thought to be the harder one, counting with an ability to prime people (Bargh, Chen, & Burrows, 1996) or to make indirect connections of observation and induced feelings in observers. Consequently as two people share the same feelings (or body language), their mutual likeliness also increases, which leads us to the fact that imitation in a social environment

promotes formations of positive bonds. (Eisenberg, 2000; Tangney, Stuewig, & Mashek, 2007) These types of imitation are rather automatic, serving the main purpose of socializing and bonds strengthening. This phenomenon is already well known amongst scientists. It is called the Chameleon effect due to its resemblance to a chameleon changing its skin´s colours in accordance to the physical environment it is being placed in. To make a parallel with human behaviour – action recognition and emotional processing, in other words, copying human actions and behaviours tends to strengthen one´s empathy in the eyes of others, consequently amiability, which is definitely a highly desired outcome (Chartrand & Bargh, 1999).

1.3.3. Language

To fully understand the meaning of MN in language, it is crucial to define what is the language itself. There are numerous possible explanations, depending on the viewpoint of the narrator. Language, as all the main functions of mirror neurons, can be described as a sender performing a gesture or vocalization, which is decoded by observer´s neural circuit. To achieve observer´s understanding of emitted information, it is necessary for the neural circuit to activate the exact motoric pathway, which dominantly leads to the same outcome as the sender´s gesture or vocalization. In order to understand each other, both the sender and the receiver have to share common explanations of words and gestures.

The discovery of areas activated in language procession and production happened thanks to two patients who suffered a loss of speech. The language center was located and called for the Broca´s area (Iacoboni & Wilson, 2006). MN were years later discovered in F5 macaque brain region, which is considered to be homologous to Broca´s area in human brain. Having connected these two information, it soon became clear that MN are activated during formation and usage of language. Another evidence of participation of MN in language is the similarity between areas activated throughout imitation and language - Broca´s area, Wernicke´s area and rostral part of the posterior parietal cortex (Iacoboni & Wilson, 2006).

If we take a closer look at evolution of gestures in primates, monkeys´ communication lacks meaningful gestures though apes´, as bonobos´, gesture communication possesses this additional meaning. For example, MNS of the macaques are activated during observation of a performer ingesting food (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003). If we compare lip-smacking, which is a usual communicative gesture, to a gesture connected to ingestion, we can find some strong similarities between these two - in terms of brain activated regions (Fogassi & Ferrari, 2007). Moreover, meaning of their message gains precision when they use vocal or

facial signals. With all above in mind, we can say that ape gestures might be the soil for evolution of spoken language (Pollick & De Waal, 2007).

It is known that gestures remain a rather crucial part of human communication. For a vast group of people with hearing impairments, sign language and lip-reading are the only ways how to communicate or to pass certain information from one another. For the rest, gestures, as a way of nonverbal communication, play a role of additional source of information about the speaker´s intentions, goal, and emotional states (Friedman, 1979). Experiments conducted on perception of language, using the eye-tracker, confirmed the importance of nonverbal communication as a source of additional informational cues for the receiver (Allison, Puce, & McCarthy, 2000). The major activation was found in the STS, which forwards the received information into the MNS. MNS, in this case, evaluates the obtained data from emotional standpoint in order to give the most reasonable reaction to the obtained verbal and nonverbal information (Iacoboni & Dapretto, 2006). Gestures, as the language itself, are a highly symbolic way of sharing information. To understand the symbols correctly, both the receiver and the speaker ought to share a common database of signs and their meanings. As have signs acquired meaning throughout their evolution, one of the present theories suggests that they might be a starting point, from which the spoken language evolved by gaining sense and vocalization (Pollick & De Waal, 2007).

After years of research, it has become clear that MN are not the first neurons to deal with the incoming language stimuli. However, it is the auditory system as the acceptor of the incoming vocalization and processes it further on to the brain. As studies show, a damage dealt to MN does not alternate the ability to perceive language as would do the damage to the auditory regions in the temporal lobe (Rogalsky, Love, Driscoll, Anderson, & Hickok, 2011).

Strong evidence has been found that language procession is lateralized to the left hemisphere (Frost et al 1999). The same case was with another type of auditory stimuli, which led to activation of left motor cortices was observed, both in right-handed and left handed participants (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004). This agrees with the widely accepted fact that language is located mainly into the left hemisphere.

Communication, in particular language is used to propose ideas, express thoughts and feelings or just share one´s mindset with someone else. Without communication, any social interaction would be harder as it is not always easy to come to terms with a mind state of someone else. In order to understand another person´s mind state, we have to both listen the spoken words and observe the used gestures.

1.3.4. Social Cognition

Neuroscience and psychology have been walking hand in hand for quite some time. As both these fields are continuously developing, both separately and altogether, is it necessary to bear in mind the necessity to openly view the researched topics and avoid splitting them because of the either biological or psychological focus of the scientist. Without doubt, social cognition is one of these subjects, which interests both neuroscience and social psychology, even more so in the recent years.

Social cognition is a functional pathway, which enables the observer to manage incoming stimuli in order to understand the reasoning behind the performers actions (Happé, Cook, & Bird, 2017). Social cognition as a term can be used to describe a wide range of social abilities and processes, which are used daily to facilitate interactions in groups. Social cognition roofs several prosocial behaviours as compassion, empathy, Theory of Mind (ToM) (Saxe, 2006). Social cognition requires both action and emotion understanding, in order to achieve the final prosocial behaviour. It is clear that sharing emotions and acting according to these emotional cues strengthens the prosocial bonds between the individuals. If we feel understood, it eases our pain or magnifies our joy. The understanding of another person´s emotions comes through activation of those particular regions, which are substantial in experiencing the same feelings, in other words some sort of inner mirroring is particularly necessary (Gallese, Keysers, & Rizzolatti, 2004). In this case, it is not only about the functions of MNS, but also the functions of amygdala (Adolphs, Tranel, Damasio, & Damasio, 1994), insula (Craig & Craig, 2009) and basal ganglia (Ring & Serra-Mestres, 2002) are also substantial, as they are responsible for emotion recognition.

1.4. Species

MNS has been, up to now, described in three groups – primates, humans and birds. However, birds have a rather analogical system. As this research of MNS in other species is still in its beginning, there is no certainty about the total number of species that possess this special type of neurons.

1.4.1. Primates

MNS was first described relatively recently, in 1995 by G.Rizzolatti (G. Rizzolatti et al., 1996). It all started with a discovery that certain neurons in a macaque monkey´s brain are associated with hand and finger movement (Hepp-Reymond, Hüsler, Maier, & Qi, 1994). Many studies were afterwards interested in researching this phenomenon. It soon became clear that F5

neurons possess both motor and sensory properties and discharge primary during an observation or a performance of a goal orientated hand movement. (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Moreover, there is a minor window in a neonatal developmental stage of a rhesus macaque monkey when it can surprisingly imitate facial expressions of a researcher (Pier F. Ferrari et al., 2006), which leads us to the idea that imitation may be evolutionary chosen as a learning and bonding facilitator, easy enough to be performed by a neonatal monkey, while remaining complex to process the facial expression from visual input to motoric output.

1.4.2. Humans

Discovery of the MN in the macaque brain was the first impulse to proceed with conducting the research on humans with the main task to distinguish similar neurons in human brain and uncover all the pathways which activate the MNS. Many studies tried to provide data on presence of MN in human brain using EEG and MEG, which can be considered as indirect sources of evidence. The first in vivo study on a cellular level was conducted on patients undergoing a surgery. Activity of neurons of anterior cingulate was measured by single cell recording during pain observation and perception (Hutchison, Davis, Lozano, Tasker, & Dostrovsky, 1999). Years later, intracranial recording of extracellular activity of individual neurons directly confirmed change of state of neurons located in premotor cortex during perception of actions (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Surprisingly though, there were some neurons activated during action execution but inhibited at action observation. These findings may suggest necessity to distinguish between self or other as the agent of an action. Later, fMRI provided the final evidence for existence of MNS in human brain – IPL, IFG including the Broca´s area and STS. (Giacomo Rizzolatti & Craighero, 2004).

1.4.3. Birds

Birds primary use their MNS as a learning circuit, which enables them to acquire new notes into their own songs. Furthermore, providing them with better social skills as courtship facilitation and recognition of individuals based on their voices (Mooney, 2014). Humans, on the other hand, tend to use their MNS as a basic way of gathering information. It is important to note that human and bird MNS are more of analogous than homologous structures.

There are a few bird species with a functioning song and consequently MNS – Zebras, Bengalese finches and swamp sparrows, just to name a few. Needless to say, these birds find their imitative abilities given by the neuron system equally necessary as the social cognitive

abilities as they enable them to interact adequately with their own and other species and have the biggest possible profit in a closed socially active flock.

1.4.4. Other species

Though the research concerning the MNS makes huge steps forward every single year, it remains unclear how many species do possess these neurons. It has been discussed that social species as dogs, which are known for their interaction with human beings, may have a sort of MN network. One research conducted by Frederike Range and his team (Range, Viranyi, & Huber, 2007) may have confirmed the actual presence of MN in dogs. Dogs do not use language in order to communicate. In this experiment, researchers showed that dogs use imitation as the basic way of learning when observing another dog performing an unusual action in an imitation-selective task. In my opinion, there is a great probability of social cognitive skills as empathy among dogs. Many dog owners would swear their dog understands them well and interacts as if was the questioning of presence of empathy rather inadequate. One thing still has to be taken into account – thanks to the close relationship between people and dogs, there is a certain inevitable level of anthropomorphism present in the evaluation of this animal´s cognitive abilities. It is certain that more research needs to be done in this field in order to achieve a complete understanding of MN´ capacity of man´s best friend. Nonetheless, no one can deny the love that have dogs acquainted throughout the thousands of years spent on the interactions with people.

2. Social cognition

Social cognition is a psychological construct, scrutinized in social psychology, which deals with information from the outer world and the way how a person processes it. Social cognition itself includes subconscious perception of other people´s behaviour in various social situations and interactions between one another, the processing itself of the abstracted information, its storing and finally a correct application of knowledge based on the previous social experience. Social cognition is a term valid not only for one-to-one interactions and inside of a group of individuals, but also representations of inner states. Moreover, each and every individual included in the processed interaction may be processing different information though abstracted from a single social experience. Reason for this is a different character, social background and experience, all of which provide the rules for processing any situations and social interactions. This fact is what makes the field of prosocial behaviour such an attractive and rich field, both on new discoveries and yet unconfirmed theories.

The term social cognition is a term, further branching into several domains, which include empathy, ToM and more visually based domains like perception of the body with certain facial features and movements (Saxe, 2006).

2.1. Empathy

Empathy is a cognitive ability of inner representation of mental states, which helps us to understand actions of another person by experiencing emotional states, beliefs, ideas and desires of others (Corradini & Antonietti, 2013). The term "empathy" was introduced by Theodore Lipps in 1903, in German "einfühlung", as a description of a relationship of an observer towards an artwork (Gallese, 2003). For more detailed historical overview see an article by Gallese (Gallese, 2003).

If we question the motivation for being empathetic, it might be our will to understand behaviour and intentions, in order to adequately evaluate actual goals of another person´s behaviour and reasons for experiencing that exact emotional state. We may, but not necessarily, become concerned and willing to provide the best possible emotional conditions for the person to feel accepted and safe. All mentioned above results in strengthening of interindividual relationships. On the other hand, there are not only positive results of being empathetic, but also rather negative outcomes like malevolence or envy.

Empathy, from the positive and widely accepted point of view, is thought to be one of those personal qualities, which ensures the person´s amiability amongst others. Its impairment results in poor, unstable and malfunctioning relationship within the group, as often seen in autistic

spectrum disorders or sociopathy (Preston & De Waal, 2002). Empathic ability is a rather consistent quality as empathic people tend to act similarly under various conditions. However, it is possible to strengthen the empathic response by empathy enhancing meditation, which uses a special training to promote loving and empathic reactions to the outer world (Lutz, Brefczynski-Lewis, Johnstone, & Davidson, 2008).

Even though both empathy and compassion are socio-affective abilities, they should not be interchanged, as the feeling of compassion can be characterized as a subdivision of empathy. Compassion includes understanding on emotional level, but also a substantial urge to help the person one feels compassionate with, which is accompanied with pleasantly warm feelings and a certain level of motivation to ensure the other person´s well-being (Singer & Klimecki, 2014). Even when the inner force to help gets out of hands, it still leaves a positive effect on the compassionate person, maybe not so on the over-cared receiver. However, when we over-share someone´s negative emotions, the caused distress might be even harmful for our own well-being, as we are suddenly living through the pain of someone else, instead of providing him with comfort and care.

The first experiments dealing with empathy were directed at feelings of physical pain or those in pain (Bastiaansen, Thioux, & Keysers, 2009). Disgust is an evolutionary important feeling, as in the older days, sharing this emotion with someone midst eating a certain poisonous food would discourage the observer from eating it. Moreover, basic form of physical disgust can be considered ass a precursor for moral disgust, which is an undeniable part of social cognition (Bastiaansen et al., 2009). Pain incorporates both sensory and motor triggers, as the person should either remember the physical pain or imagine how painful is the stimuli in order to give and adequate response to the person in pain. The team from University of Washington in Seattle provided evidence for areas activated both when experiencing pain and observing another person in pain (Jackson, Meltzoff, & Decety, 2005).

The current studies define two types of empathy – affective (AE) and cognitive (CE), which are cooperating to ensure the correct empathic experience (Cox et al., 2012). AE or emotional contagion is considered to enable understanding of emotional states of others, in other words to feel what the other person feels. It is suggested that the actual mirroring is stronger than in CE, providing the observer with more accurate information about the emotional state (Nummenmaa, Hirvonen, Parkkola, & Hietanen, 2008). CE uses perspective to understand the emotional state of the other person. A certain level of mentalizing and higher cognitive skills is needed, enabling the observer to extract all the necessary information about the emotional state of the

other person and consequently understand it. Cooperation of both systems is necessary to provide the most adequate empathic response. However, this cooperation is not balanced equally as CE and AE abilities vary from person to person. This balance is called relative empathic ability (REA) and is reflected in brain dynamics and architecture of the individual units of both CE and AE (Cox et al., 2012).

Empathy facilitates social interactions, relationship establishment, promotes strong societal bonds. Feelings of concern and care do not exclusively come towards family members or partners, it is rather common that people experience these feeling while interacting with total strangers. However, the mechanisms are slightly different. In case of strangers, empathy is based on understanding of the situation through mentalizing, rather than direct sharing of emotions, which is utilized in empathic reactions with friends (Meyer et al., 2013). Feeling of pity for those, whose house was taken down by a hurricane or those suffering by lethal illness is a part of human nature, or empathic concern to be exact. Once the concern is induced, the one who is concerned becomes genuinely interested in the outcome of the situation, not to mention the well-being of the care receiver (Konrath & Grynberg, 2013). On the other hand, there is a certain level of differences in terms of the degree of empathy. Studies suggest, that empathy is not universally strong towards strangers, but rather depend on the race and even religious beliefs of the receiver (Chiao & Mathur, 2010). Chiao and Mathur suggest, that people tend to feel concern for feelings of the other members of the same race but do not have equal interest in the emotional states of members of another race. In their opinion, reason for this might not only be the strongly built prejudice but also rather long running intention to strengthen own social group and not to lose any substantial energy to empathize with strangers and potential enemies.

Generally, empathy helps in making predictions about someone´s objectives and needs (Preston & De Waal, 2002). As, by these means, empathy strengthens bonds with others within social groups, it is necessary to highlight its importance in close relationships. Two contexts which count with empathy are kinship and parental care (Swain et al., 2012; Decety, 2015). The very first encounter with empathy happens in infanthood as it is a crucial attribute to formation of bonds between new-borns and parents. Parental care in general offers a wide range of benefits for both the giver – parent and the acceptor – the infant. The first and obvious one is to ensure lifelines of the infant, its safety and adequate quantity of food and sufficient living conditions and provide with protection against infanticide. Consequently, it lowers the stress and anxiety levels in both parent and infant. New studies have shown that parental care becomes addictive

for the parent, as the care bears a meaning of reward for them. Consequently, neural reward pathways are activated by dopamine and encephalin, which bring the parent the addictive feeling (Gammie, 2005). When talking about hormones, it is crucial to pinpoint maternal behaviour as it activates the mesocorticolimbic dopamine system (Coria-Avila et al., 2014). As a result, mother – infant relationship is strengthened as mothers feel the need for care, rewards as their dopamine system suggests, and infants are happy to be surrounded and protected by a caring mother. More on hormones connected to empathy in the next chapter.

We all know that both biological and non-biological parents tend to provide their child with support no one else can offer. Many children, even in older age, seek their parents´ attention, care or at least emotional connection throughout whole life as the bond between the child and the parents is unique. Verbal and non-verbal behaviour of a parent had a great influence on child´s level of stress during a cancer treatment procedure itself (Penner et al., 2008). The more concern was shown by the parent before the procedure itself, the less painful the treatment was for the child. As a result, the child was less distressed and felt more comfortable as the parent provided him with care, concern and support, which ensured the good mental state of the child.

Previously, it was long thought that infants under age of one lack empathy as their abilities and their use is rather self-orientated (Zahn-Waxler, Radke-Yarrow, Wagner, & Chapman,1992). As many emotional infant attributes remain unclear due to difficulties during organization and research realization, there is always a high level of interest when there comes a new theory or article concerning emotional states and abilities of infants. Many years after research from 1992 by Zahn-Waxler et al., it become clear that this assumption is wrong. Davidov with his team pinpointed that there are more than just self-reflective abilities, which is contradictory to the previously believed to be true article (Davidov, Zahn-Waxler, Roth-Hanania, & Knafo, 2013). Firstly, infants are capable of distinguishing between cries of other infants and equally loud sounds (Geangu, Benga, Stahl, & Striano, 2010). The team presented results of the research which stated that infants react with a various level of acoustic and facial distress to cries of other infants as early as in 1, 3, 6 and 9 months. Moreover, there was no connection established between the gender and the strength of the distress reaction. It is safe to say that empathic abilities of an infant are not on its whole life peak. As the experience mount, the growing child gets better insight on when, and how it is suitable to feel empathic concern for someone in distress or happiness and which is the adequate form of reaction to strengthen the bond.

Development of empathic abilities, as of any other abilities, are not finished until adulthood, as many outer conditions can form amount, target and strength of empathic concern. Even though

it is hard to predict how emotionally or rationally developed the child going to grow up, there is a certain precursor, which indicates the empathy potential of a child and it is the foetal testosterone (fT) (Chapman et al., 2006). FT is an interesting subject for cognitive neurobiologists as it influences the foetus´s development of various parts of brain, limbic system, hypothalamus neocortex to be exact (Geschwind & Galaburda, 1985). Both genders have a certain level of fT, though males tend to have higher level with an overall bigger variability, whereas females have lower level of fT with a smaller variability. More about the differences between empathic abilities of males and females in the following chapter.

Another situation when empathic concern is more than just visible are romantic relationships. In any kind of relationships, it is vital to understand what the significant other thinks, feels and, in the best circumstances, also wishes. In other words, being in a relationship requires rather unique mind reading skills and mutual understanding, simply to ensure the best conditions for a prospering relationship. Study by Thomas and Fletcher (Thomas & Fletcher, 2003) confirmed that close relationships are tightly connected with better empathic skills, as partners understand each other on higher level, in comparison with strangers or even friends. Moreover, the study suggested a certain link between the length, overall satisfaction and mind reading skills of both partners (Thomas & Fletcher, 2003). It turned out that longer relationship correlated with better mind reading skills and consequently higher overall relationship satisfaction. The reason for this might be the habit of discussing problems with the significant one and knowing when something is wrong. On the other hand, short-term couples - together for less than 11 months - show lower overall satisfaction though the mind reading accuracy is still rather high. As the relationship is still something rather new for both partners, they both feel insecure about their common future and therefore tend to react to any sign of upcoming turbulence in order to survive it or tear the relationship apart forever (Thomas & Fletcher, 2003).

2.2. Theory of Mind

Empathy is about sharing the emotional state, simple understanding would not be enough for empathic concern (Decety & Svetlova, 2012). ToM, on the other hand, is a socio-cognitive ability to mentalize – understand, explain and make certain predictions on how the person is going to act. In ToM, it is crucial to understand that one´s own mental state does not necessarily have to be a mental state of the other person (Frith & Frith, 1999). There are two general points of view on relationship between ToM and empathy and they both depend on how the authors defined both terms. The first one proposes that ToM is a basic form of empathy, giving empathy a more complex position as it has higher system requirements than ToM (Decety & Jackson,

2004). The second one suggests that ToM is more complex and empathy is only one part of it (Seyfarth & Cheney, 2013). Empathy is sharing someone´s feelings, ToM requires processing of several incoming stimuli - social environment, exact situation, observer´s inner state and the inner state of the observed person, their background and interactions. Mental evaluation of the situation has evolutionary built-up from more basic social instruments like imitation and empathy. As they promote affiliation and social bonds, their step-by-step cooperation has resulted in a more complicated cognitive ability ToM (Seyfarth & Cheney, 2013).

There are two explanatory theories of ToM, which have gained the most support from the neurobiological world. They are called theory-theory and simulation theory (Gallese & Goldman, 1998). Theory-theory is based on folk psychology – a common sense psychological approach of each person. It is used regularly in everyday life, when attributing others with a certain character quality, judging their mood or predicting their next steps, in terms of behaviour (Gallese & Goldman, 1998). Theory-theory is a way of explaining someone else´s psychological attributes by making a certain theory about them. The second theory is the simulation theory. On the contrary to the theory-theory, the simulation theory does not count with any general psychological laws applied to judgment of other people (Gallese & Goldman, 1998). It relies more on certain inner, individually obtained explanatory mechanisms. These inner mentalizing abilities enable the observer to achieve the understanding of mental processes, mostly through an imaginary substitution of the observed person with himself in a certain situation, consciously matching own mental state with the observed mental state (Vittorio Gallese & Goldman, 1998). This matching component might be where the MNS comes into the scene, as it does not only mirror the motor behaviour as used in imitation, but also enable the observer to go through the same, or at least similar pathway to achieve identical output, facial expression in particular (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995).

2.3. Neural mechanisms & Anatomy of Social Cognition

As we have discussed before, social cognition is a complex attribute of human psychology which promotes bond forming in a particular society, be it a classroom, football team or a nation. Due to the complexity, there is a number of areas which are activated in social cognitive processes (Fig. 4).

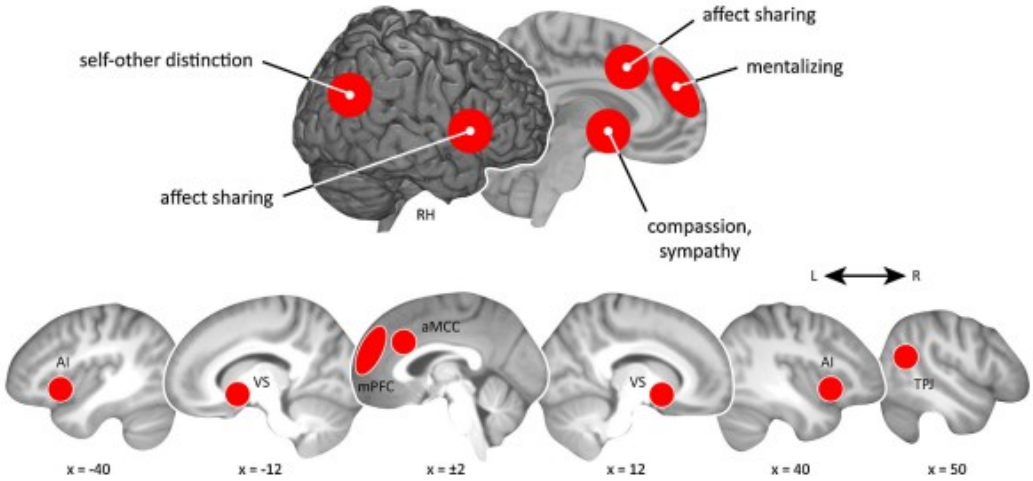

Figure 4: Brain structures involved in the social cognition (Lamm, Rütgen, & Wagner, 2017)

To pinpoint some of the structures, at the beginning of the chain (fig.5) is the STS with important somatosensory properties. The STS reacts both to observer´s facial and bodily movements and to a passive observation of a face or body (Allison et al., 2000).

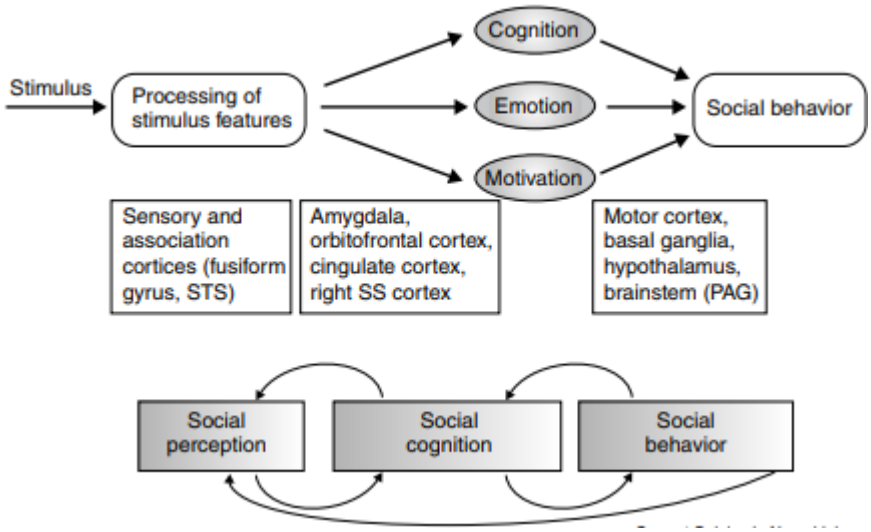

Figure 5: Chain of social cognitive processes and involved brain structures (Ralph Adolphs, 2001)

As for the further step of the cognition itself, it is necessary to mention amygdala, as it is important for its emotion recognition properties in facial expressions (R. Adolphs et al., 1994). Somatosensory cortices play a significant role in emotion recognition via inner simulation (Ralph Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000). Part of the somatosensory cortices – insula - has a crucial part in subjective feelings, self-awareness, love towards successors and decision making, all of which are adequately present in social interactions (Craig & Craig, 2009). Insula is also the main structure, which deals with auditory and visual stimuli usually accompanying basic emotions fear, but mostly disgust (Gallese et al., 2004).

Last but not least, the execution part, or the actual behaviour, requires activation of basal ganglia playing a role of a bridge between memory, motor behaviour and emotional functioning (Ring & Serra-Mestres, 2002). It is also important to mention temporoparietal junction (TPJ), as it is responsible for self-other distinction, self-awareness, beliefs towards outer world, comparison of inner predictions and outer events and perspective taking (Decety & Lamm, 2007).

From a neural point of view, empathy is a multilocational neural process. Apart from emotional contagion, regions of episodic memory and autonomic sensation have to be activated to fulfil the requirements and to have a fully functioning empathic circuit. It is untruthful to say that MNS is the only group of neurons activated during the feeling of empathic concern. As all the neurons are interconnected, the network cannot function on MNS only and need all the areas to be activated (Preston & De Waal, 2002).

It was long thought that both AE and CE share the same neural circuit though lesion study provided us with some contradictory information. (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009). A research from Cox at al, 2012 suggests that REA is based on the intrinsic functional dynamics and co-working of the CE and the AE (Cox et al., 2012). It turns out that the domination of AE suggests a better neural connectivity between social-emotional parts of brain as ventral anterior insula (vAI), orbitofrontal cortex (OFC), amygdala and perigenual anterior cingulate, whereas the CE domination showed major activation in regions of social-cognitive processing, interoceptive and autonomic monitoring as brainstem, STS and vAI. Moreover, there is an evidence of interconnectivity of measurements of RAE with aggression and impulsivity, as these characteristics are associated to deficit of empathy (Reniers, Corcoran, Drake, Shryane, & Völlm, 2011).

Proceeding with the discussion further, it turns out that these two empathy systems are of a different phylogenetical age. First clue is the complexity of both systems - MNS plays a massive role in AE whereas its role in CE is not that crucial as it needs ventromedial prefrontal cortices to be activated, in order to achieve more demanding cognitive understanding of actions (Shamay-Tsoory et al., 2009). Additionally, parts of the brain activated during CE and AE are slightly different too. In 1909, Brodmann described numerous areas of cerebral cortex, including area 44, which has a role in AE, and 10 and 11, which are important for CE (Shamay-Tsoory et al., 2009). Brodmann discovered a slight cytological difference between these areas – 10 and 11 have particular regions, which are fully developed and are not located in the area 44. This might be one of indirect clues that CE is phylogenetically younger, supported by the fact that AE found in other species as birds or rodents (Shamay-Tsoory et al., 2009).

Apart from the perceptual network, compassion also activates networks previously connected to the reward circuit – the ventral striatum, the nucleus accumbens, the ventral tegmental area, the medial OFC and the subgenual anterior cingulate (Preckel, Kanske, & Singer, 2018).

In ToM, medial prefrontal cortex (mPFC), STS and temporal poles play the most important role in the mentalizing abilities (C. D Frith & Singer, 2008), together with the temporoparietal junction (Van Overwalle & Baetens, 2009), which is the part contemplating explain the other mind.

There is a certain neural correlation of structures active in social cognition with those, which are a part of the default mode hypothesis. This hypothesis is the result of fMRI study and resting state brain activity compared to cognitive task activity (Greicius, Krasnow, Reiss, & Menon, 2003). Namely, it is the mPFC, OFC, posterior cingulate (PCC) and ventral anterior cingulate (vACC). Areas PCC and vACC showed the biggest change in these settings, with their activity low in cognitive tasks and high in the resting state measurement. Their activity was intact during basic tasks of visual procession (Greicius et al., 2003). PCC deals mostly with episodic memory, though its function is still a point of scientific interest. VACC is connected with subcortical areas, which are activated during affective and autonomic events. OFC and mPFC showed a certain activation in both PCC and vACC activation patterns and both play a role in both affective and cognitive processes. These results may suggest that there are important subconscious both affective and autonomic calibrating processes, which are supported by the high activity of these structures in resting state measurements (Greicius et al., 2003).

Social cognitive processes are also under influence of hormones. Oxytocin is known for its role in social cognitive skills – both when administrated externally or present naturally in human body on gene level. It influences body and brain, in terms of behavioural responses to the external stimuli, functioning as a peptide hormone and a neurotransmitter. Produced by paraventricular nucleus of hypothalamus and excreted by pituitary gland, oxytocin plays a certain role in numerous aspects of life as bonding, sexual behaviour in both genders and birth maternal behaviour. As for social cognition, oxytocin plays a crucial part in processing of emotional and social stimuli – stress reactivity and empathy (Rodrigues, Saslow, Garcia, John, & Keltner, 2009). In general, it promotes empathic response to external stimuli. Study by Kirsch et al (Kirsch et al., 2005) suggested that oxytocin also inhibited amygdala´s function in social cognition, lowering the levels of fear and suggesting that there are oxytocin-receptors in amygdala. Additionally, role of oxytocin receptor gene polymorphism has raised a certain level of interest. It turns out that there are certain allele combinations, which lead to better social

cognitive skills and those, which promote affective empathic response. (Wu, Li, & Su, 2012). Therefore, it is possible to conclude that there is a certain connection between the genotype and phenotype, with a visible variability, even in small genotype changes. These alleles also have different effect on both genders, confirming the fact that women tend to have stronger empathic response than man. More about gender differences in part VII. Last but not least, it is important to mention dopamine and norepinephrine and their role on social cognitive skills.

Dopamine is a neurotransmitter from catecholamine family. It is mostly known for its part in motivational and reward circuits (Schultz, 1998). Dopamine is converted by dopamine-beta hydroxylase (DBH) into norepinephrine, which is responsible for mobilizing the body and brain activity in flight-or-fight situations of everyday life. Study of Gong and his team (Gong, Liu, Li, & Zhou, 2014) suggested an importance of the genes behind this enzyme. It turns out that cytosine-cytosine genotype promotes the activity of DBH, resulting in lower level of dopamine and higher levels of epinephrine. Cytosine-tyrosine and tyrosine-tyrosine acting as inhibitors of the conversion – higher levels of dopamine and lower levels of epinephrine. This genetic variance had an effect of empathic abilities – the CC genotype promotes the empathic responses and consequently CT/TT being genotypes are those which lead to lower empathic responses to social stimuli (Gong et al., 2014).

2.4. Sex differences

Social cognitive abilities vary not only according to age, but there are some quantity-orientated patterns of these abilities, which are frequent in population. First attempts to differentiate between emotional abilities of males and females are in their first year, as it is the time when encounters with other adults and infants happen on regular basis, compared to the period of in vitro development. There are many signs that point to the differences in early life reactions to living conditions and environment in general. Among other things, infant girls tend to be cuddlier or more responsive to emotional expressions than boys. (Alexander & Wilcox, 2012).

As stated above, foetal level of testosterones influences more than just the gender development. As it influences the development of certain brain regions, a question arose whether it might influence the functionality of these areas, or empathic abilities to be exact. Measurements of fT level were made during the second trimester of pregnancy at overall number of 193 mothers to be (Chapman et al., 2006). Years after the first measurement, the same children in the age of 6 – 9 went through two types of cognitive tests to confirm or neglect a connection between empathy and the level of fT – Empathy quotient and "Reading the mind in the eyes" task. Empathy quotient is a questionnaire based on self-observance, with 40 empathy-control and 20

filler-control items. The second task – "reading the mind in the eyes" is an eye test, which examines the overall psychological state and emotion recognition. The results were not surprising. Girls scored significantly higher points in both tasks, leaving boys counterparts far behind. This finding suggests that even pre-partum levels of this androgen hormone has a great functional influence on cognitive abilities - empathy to be exact.

The idea that men and women differ in their empathic abilities is not supported only by fT. Several studies in 1960´s and 1970´s targeted empathic abilities of children to 10 years of age to prove that girls tend to be more empathic towards acquaintances or strangers, whereas boys tend to modulate their empathic responses according to the social surrounding and exact situation when the response is expected (Christov-Moore et al., 2014). For more detailed description of the experiments, see the article by Christov- Moore from 2014. These findings may suggest than men possess better control over their emotional states and tend to evaluate how much of an emotional response is necessary in that exact situation. On the other hand, women tend to be concerned when they simply see someone in distress, not paying that much attention to actual situational surrounding or background of the person, which is the empathic response aimed at.

Throughout adolescence, differences in the quality and quantity of empathic response become even more visible and undeniable. Olweus and Endresen conducted a study on 13 – 16 year old students in Norway to find out how the girls and boys at this age differ in their empathic response (Olweus & Endresen, 1998). Using a questionnaire with sex-orientated items, they confirmed higher responsiveness of girls to various social stimulus. Moreover, they discovered a trend that boys showed more empathic concern towards girl-objects in distress though girls did not have this preference of sex and tend to be universally concerned about objects in distress. Moreover, this study also showed a surprising prevalence of highly empathic girls and boys with rather low level of empathic skills. Another finding from this research was a trend that empathic response increases with increasing age. As Olweus and Endresen state, the reason for this might be up-bringing, increasing emotional stability or personal maturity.

As the young people enter the world of adult´s life and problems, it is not only empathy, or social skill in general, that evolve under changing circumstances of the outer world, but many people find also the opposite side of these positive traits and develop rather psychopathic traits. As empathy is a highly prosocial skill, on the other side of this spectrum, there comes psychopathic traits, which are characterized by total lack of empathic skills, or at least their limitations to a big extent, connected with highly amoral behaviour (Blair, Mitchell, & Blair,

2005) . Furthermore, psychopathy is assembled of two characteristic features – affective-interpersonal and lifestyle-antisocial (Seara-Cardoso, Neumann, Roiser, McCrory, & Viding, 2012). Affective-interpersonal feature is characterized by easily induced aggression towards others, whereas lifestyle-antisocial is more about lack of respect towards opinions and rights of other people. The first study of this interest was conducted on men within a certain community, with a goal to establish or diminish a connection between empathy and psychopathy (Seara-Cardoso et al., 2012). Using a Self-Report Psychopathy Scale 4 Short Form, interesting results emerged. As for empathy and psychopathy connection, it was found in lower level of empathic concern towards fearful faces. However, these two features don´t have everything in common. Affective interpersonal feature is also characterized by smaller empathic reaction towards cheery stories, easier decision making in questions with moral dilemmas and general lack of interest in feeling any empathic concern. On the other hand, lifestyle-antisocial feature has no inner limitations in feeling the empathic concern (Seara-Cardoso et al., 2012).

It soon became interesting for the research team to uncover how empathic are women with psychotic traits (Seara-Cardoso, Dolberg, Neumann, Roiser, & Viding, 2013). The same battery of questionnaire was used to have the results as unbiased as possible. Outcome of this study was rather surprising as women and men were, in this context, rather different. Similarity, which should be further studied, is that women with affective/interpersonal feature od psychopathic behaviour tend to have lower empathic reaction to display of fear, as men with similar trait also do, though this characteristic is also valid for lifestyle-antisocial trait. Other differences in samples with lifestyle-antisocial trait need more evidence to be confirmed or neglected as the results showed only border values. From this point, most of the results were different. It turns out that AE is closely related to affective/interpersonal trait as it is responsible for development of emotions of morality as compassion and guilt. These emotions are thought to be mediators of prosocial behaviour and equally inhibiting antisocial behaviour. Consequently, women with interpersonal/affective trait tend to have lower level of AE, which leads them to have smaller empathic response to moral emotions of others, as well as lower concern about fearful and sad faces. When standing face to face to a moral dilemma whether it is better to harm one to safe many or not, women with affective/interpersonal trait had no problem with causing pain to one. This behavioural aspect was absolutely missing at men sample (Seara-Cardoso et al., 2013). The authors concluded that the basis for connection between empathy and psychopathic traits are the same in both genders. Differences come from various anatomical structures, behavioural templates and social roles which are accepted and followed in the society.

It remains undeniable that there certainly is a difference between cognitive abilities of males and females. It is also true that the question on exact developmental and evolutional basis remain unclear, offering a good ground for studies, which may further change our view of men and women in general, not only their emotional states and empathic abilities.

2.5. Impairments

Impairments in social cognitive skills have become an interesting topic for both neuroscientists and psychiatrists. The most studied impairments of these skills with the biggest number of studies is in schizophrenic patients. Schizophrenia is characterized by continuous fusion of self and other as patients often find problematic to distinguish who is an agent of an action (Gallese, 2003). In experiment conducted by Baez and his team in 2013, patients with schizophrenia and bipolar disorder were tested on their social cognitive abilities in contextual everyday situation, resulting in poor performance and insufficient ability to understand the context of the social environments (Baez et al., 2013).

Another group of patients studied in connection with impairments of social cognitive skills are patients with autistic spectrum disorder (ASD) and Asperger syndrome (AS). Patients have difficulties with emotion recognition and their sharing. Additionally, they also have characteristic traits like repetitive behaviour and strong tendencies towards stereotypes (Baron- Cohen, 2009). One of the first articles discussing this issue was written by Baron-Cohen and his team in 1985 when they questioned existence of ToM in autistic children. In accordance with the results of their research, children with ASD are less mentally retarded than patients with Down syndrome, but their social cognitive skills are missing (Baron-Cohen, Leslie, & Frith, 1985).

It is certain that impairments of social cognitive skills are frequent in mental disorders. Regarding current leaps made every year in research of social cognition, more results with wider extend and deeper precision are yet to come.

2.6. Critical view on mirror neuron system and its role in social cognition

From the first discovery of MN, their role in various cognitive abilities and parts of prosocial behaviour were vastly investigated. Neurobiologists from all over the world divided into two groups - those, who were very optimistic about the actual functions of MN in human behaviour and those, who stayed unpersuaded about the miraculous abilities of mirror neurons in humans.

Claus Lamm and Jansminka Majdandžič presented an article (2015), which discussed drawbacks of the current interest in mirror neurons and empathy. In recent years, many articles

present various results on activity of brain regions. Most of the results were obtained by fMRI and EEG techniques. Apart from their outstanding effectivity and possibilities, these techniques do possess certain drawbacks, the biggest one is their indirect way of measurement. As for the fMRI, its ability to unveil activated regions is not ordinary, it still does not provide the researchers with the reason for the activation. In order words, some activity in a certain emotion-processing region while observing someone´s emotions may imply the result of sharing the feeling or, at the same time, it might be the pathway how the observed feeling is processed (Lamm & Majdandžić, 2015). EEG measurements are based on neurophysiological brain response as a sign of activity in certain brain regions. Problem with EEG remains the same – results may show similar activation, though there is no explanation of what caused this activation and which pathway was undertaken (Lamm & Majdandžić, 2015). More exact techniques like neurophysiological lesion studies or neurostimulations do provide the researchers with more precise and reliable results. However, patients with lesions in only emotional regions are rather scarce. Moreover, the fact of complexity of social cognitive skills must be taken into account, as even reactions like empathy, mentalizing and compassion walk hand in hand. Distinguishing and attributing corresponding activations to their own inputs is problematic.

The fact that only a little is known about the ontogeny of the MN does not add up any clarity. A question arose - how had they obtained their mirroring qualities? Cecilia Heyes proposes (Heyes, 2010), that it is only hardly believable that these neurons would incorporate both motor and sensory abilities with no actual explanation of the reasons behind the choice. In her idea, ability of mentalization, or, if amplified, telepathy belongs to ancient Greece rather than modern world based on pragmatic knowledge. She proposes her idea of associative origin of these neurons. In this hypothesis, their sensorimotor abilities are admitted, though gained not by accident, but rather as a result of associative learning, which requires numerous repetitions. These repetitions would ensure that from previously motor neurons would after being activated by similar stimuli transform into the MN.

More controversial questions are discussed in review by Hickock (Hickok, 2009). He proposed several theories and evidence why MN do not serve the purpose of action understanding, as one action may have more than one goal and the boom around the MN is based on lack of actual studies done on action understanding and role of MN in it.

Answers or contra-arguments will never appear out of nowhere. Therefore, additional time has to pass to unveil us the different, surprising or disappointing properties of these mirror neurons.

3. Conclusion

In my bachelor thesis, I aimed to analyze available and applicable articles about mirror neuron system and social cognition, in order to provide the reader with an up-to-date review of current knowledge and organize the information into a comprehensive structure. Thanks to the advantages of modern imagining techniques, the steps made in recent years have move this field tremendously and the trend is expected to continue in the upcoming years.

Opinions about the actual role of the MNS are in continuous development, though their sensorimotor character has been widely accepted, as well as its role in learning, language and imitation, which is connected with socially applicable skills of social cognition. Topics of social cognition, empathy and theory of mind tend to cause certain level of controversy, as the hierarchy is not particularly stabilized, and authors might easily find themselves floating in terms without any hard ground underneath.

I would like to proceed with studying of mirror neurons in social cognition further in my master studies on Faculty of Science on Charles University in Prague, cooperating with the National Mental Health Institute in Prague.

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