

# CRITICISM REGARDING THE ROLE OF THE MIRROR NEURONS SYSTEM IN EMPATHY YET TO BE REFUTED

By: Judith Bolding (s3209725)

Date: 19<sup>th</sup> of June 2019

Basic unit: Behaviour and neurosciences

Supervisor: Eddy van der Zee

## ABSTRACT

The neuronal involvement in empathy is not well understood, although it has been studied from many perspectives. A share of cognitive neuroscience studies focused on a system of neurons with, so called, “mirror” properties. These neurons fire both when an action is performed and when that action is observed in another individual. This property allows you to understand the observed action and is proposed to underly our ability to empathize. A functional role of this mirror neuron system (MNS) in empathy received a lot of criticism over the years. Nevertheless, new investigations to prove this relationship keep popping up. In this paper I first introduce empathy and the MNS and explain the criticism that followed this mentioned theory. Four recent studies are highlighted and judged if they can refute the criticism. In conclusion, a causal link between the MNS and empathy is still not proved, but more support of this idea is delivered and new techniques for investigating the MNS are presented.

CONTENTS

- 1. Introduction .....2
- 2. What is empathy?.....2
  - 2.1. Empathy1.....3
  - 2.2. Empathy2.....3
- 3. The mirror neuron system .....3
  - 3.1. The mirror neuron system in monkeys .....4
  - 3.2. The mirror neuron system in humans.....4
- 4. The role of the mirror neuron system in empathy .....5
  - 4.1. Evidence and critical comments .....5
  - 4.2. Recent findings .....6
    - 4.2.1. *fNIRS suitable for investigation of the functional role of the MNS* .....6
    - 4.2.2. *High empathy results in stronger facial mimicry and MNS activation* .....7
    - 4.2.3. *Analysis reveals functional connections between MNS-related and empathy-related seed regions* .....7
    - 4.2.4. *Viewing of painful pictures results in greater mu suppression, which is dampened by emotional invalidation* .....7
- 5. Discussion and conclusions.....8
- 6. References.....9

## 1. INTRODUCTION

Empathy, the feeling of what others are feeling, is a complex ability that involves both innate, affective mechanisms and cognitive processes. So, empathy can be subdivided in emotional contagion and empathic understanding. In order to display empathy, one must understand others' actions and have knowledge of emotions (Heyes, 2018). It is commonly found that females empathize more than males, but according to a review by Christov-Moore et al., 2014 males seem to simply be better at controlling their empathy but are not less good at displaying it.

The neuronal involvement in empathy is not well understood, although it has been studied from many perspectives. A study by Singer et al., 2004 showed activation in overlapping areas involved with experiencing pain and empathizing with pain of others and, with that, jumpstarted the investigations into the field of social neuroscience. Since then a tremendous increase in scientific papers about the neural networks enabling empathy is documented (Lamm & Majdandžić, 2015).

From all the researches in this field, a share of cognitive neuroscience studies focused on a system of neurons with, so called, "mirror" properties. These neurons fire both when an action is performed and when that action is observed in another individual. This property allows you to understand the observed action. It has been proposed that this internal simulation of actions and emotions by the mirror neurons happens automatically and unconsciously and underlies our ability to empathize. This theory is partly based on a presumed link between imitation and empathy (Baird, Scheffer, & Wilson, 2011). This so called mirror neuron system (MNS) was first discovered in monkeys (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), and there is evidence suggesting the presence of this system in the human brain (Cook, Bird, Catmur, Press, & Heyes, 2014). To study the neural networks of empathy, one's perception of pain in others is often used as model for empathy. Using this paradigm, researchers have supported the linking of the MNS to empathy for pain (Arnett, Roach, Elzy, & Jelsone-Swain, 2019). Supporters of the theory used functional neuroimaging studies showing overlapping areas between the MNS and empathy-related brain areas and lesion studies in the MNS showing impaired empathy.

However, the theory received a lot of criticism over the years, pointing out lack of substantial evidence of a human MNS and even the absence of evidence of a causal link between the MNS and empathy. Researchers have even challenged the extent to which the MNS is involved (Baird, Scheffer, & Wilson, 2011) (Christov-Moore, et al., 2014) (Lamm & Majdandžić, 2015). Nevertheless, new investigations to prove this relationship keep popping up. But, do the new findings of these recent studies bring more clarity into the role of the MNS in empathy, and can the previous criticism on the link between both be refuted?

## 2. WHAT IS EMPATHY?

Empathy has a variety of definitions. Publicly, empathy is identified as a general feeling of compassion towards others. For example, wishing someone to get well is emphatic regardless of the underlying thought or what you're feeling. On the other hand, neuroscientists and other specialists know empathy to be the matching of emotions of two people, where the "agent" adopts the emotion of the "target". Empathy is then, for example, the feeling of sadness because someone else is sad. Other scientist might define empathy as a component of mindreading, or theory of mind, the ability to attribute mental states to oneself and others. The dual system model of empathy (see **Figure 1**) proposes that empathic responses can be produced by one or both of two systems, Empathy1 and/or Empathy2. (Heyes, 2018).

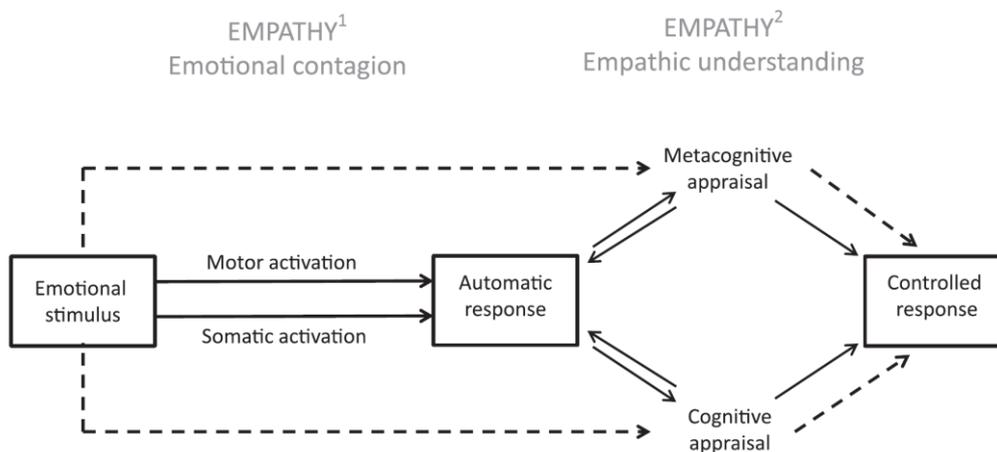


FIGURE 1 | The dual system model of empathy (Heyes, 2018).

## 2.1. Empathy1

Empathy1, or emotional contagion, acts automatically, is developed early in humans, and can be found in multiple other animals. Emotional stimuli automatically trigger various brain areas involved in motor activation and somatic activation causing a rapid change in emotional state towards the emotion of the agent. For example, the sight of someone being hurt triggering a fear-related elevation of heart rate (Heyes, 2018).

Empathy1 is widely assumed to be an innate mechanism that has emerged through evolution and that it is genetically inheritable. This is plausible since it has been found in multiple other animals besides humans, and empathy seems to be favourable. A second hypothesis, the Learned Matching hypothesis, states Empathy1 is established during development via associative learning. A sensory cue is bidirectionally connected to a motoric or somatic response. It has been suggested that Empathy1 is implemented by mirror neurons which seem to develop through associative learning (Heyes, 2018).

## 2.2. Empathy2

Empathy2, or empathic understanding, involves controlled processing, resulting in “voluntary” or “intentional” responses. Empathy2 is developed later, and likely unique to humans. It assesses the automatic response of Empathy1 alongside information about context, the agent’s relationship with the target, and current priorities. Besides this it assesses information about different outcomes of different actions. This cognitive assessment together with metacognitive assessment (awareness or analysis of one’s own and others’ emotions) can modulate the output of Empathy1 (Heyes, 2018).

## 3. THE MIRROR NEURON SYSTEM

Mirror neurons are visuomotor neurons that fire not only during the execution of a movement, but also when this movement is observed in others. Neurons with mirror properties were first discovered in 1992, in area F5 of Macaques’ ventral premotor cortex (PMC) (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Later in 1996 the term “mirror neurons” was first introduced (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996).

Possible functions that are proposed and researched in the years since the discovery of mirror neurons are: action understanding, imitation, language, empathy, intention-reading, and emotion recognition. It even is suggested that dysfunctions in the MNS contribute to several disorders like autism, schizophrenia, Down’s syndrome, multiple sclerosis, cigarette addiction, and obesity (Cook, Bird, Catmur, Press, & Heyes, 2014).

### 3.1. The mirror neuron system in monkeys

In a monkey's area F5 there are two classes of neurons: canonical neurons, which activate when an object is presented, and mirror neurons, which activate when an action is observed. For mirror neurons to be activated there must be interaction between an object and a biological effector like a hand or mouth. This means that the sight of an object or gesture alone does not trigger the neurons. Some mirror neurons only activate when the observed action is exactly similar in goal and means to the action the neuron encodes. These neurons are "strictly congruent" and represent one third of the F5 mirror neurons. Mirror neurons that are activated by actions somewhat like the motor response it codes are classed "broadly congruent" (Cook, Bird, Catmur, Press, & Heyes, 2014).

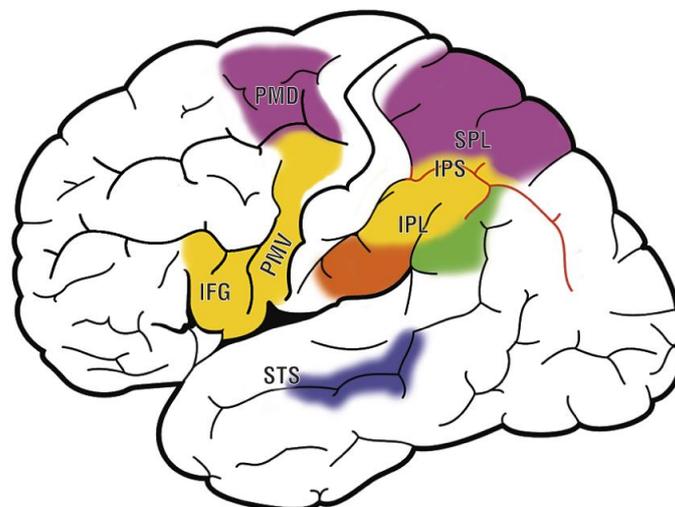
Studies researching the properties of the lateral part of area F5 found most neurons were related to mouth actions. These mouth mirror neurons were divided in two classes: ingestive and communicative mirror neurons. Ingestive mirror neurons are activated by actions related to ingestive behaviour like grasping food with the mouth, breaking it with the mouth, or sucking on food. Communicative mirror neurons respond to communicative gestures, i.e. lip smacking, lip protrusion, and tongue protrusion (Cook, Bird, Catmur, Press, & Heyes, 2014).

Besides the F5 there are other regions in the monkey's brain with mirror neuron properties. One of these is the inferior parietal lobule (IPL). However, the IPL lacks motor properties. Mirror neurons are also found in non-classical areas like the primary motor cortex and the dorsal PMC (Cook, Bird, Catmur, Press, & Heyes, 2014).

### 3.2. The mirror neuron system in humans

In 1995 researchers first attempted to locate the MNS in humans. The region homologous to area F5 in monkeys, Broca's area, was stimulated via transcranial magnetic stimulation (TMS). At the same time the subjects had to 1) observe the grasping of an object, 2) look at the same object, 3) observe geometrical figures being traced in the air and 4) detect the dimming of light. The scientists found that motor evoked potentials (MEPs) increased during observation, which reflected the patterns of muscle activity during execution of the observed actions (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995).

However, only one study reported recordings of single neurons from the supposed mirror neuron areas in humans, so no direct evidence really exists. Although data suggests there is an MNS present. Mirror neurons area's in humans (see **Figure 2**) are assumed to be the posterior regions of the inferior frontal gyrus (IFG, Broca's area), superior temporal sulcus (STS), dorsal premotor cortex (PMD), ventral premotor cortex (PMV), superior parietal lobule (SPL), inferior parietal sulcus (IPS), and inferior parietal lobule (IPL) (Cook, Bird, Catmur, Press, & Heyes, 2014) (Cattaneo & Rizzolatti, 2009).



**FIGURE 2** | Cortical areas related to the human mirror neuron system. PMD = dorsal premotor cortex, PMV = ventral premotor cortex, IFG = inferior frontal gyrus, SPL = superior parietal lobule, IPS = inferior parietal sulcus, IPL = inferior parietal lobule, STS = superior temporal sulcus (Cattaneo & Rizzolatti, 2009).

## 4. THE ROLE OF THE MIRROR NEURON SYSTEM IN EMPATHY

It has been proposed that mirror neurons implement several psychological functions including empathy.

### 4.1. Evidence and critical comments

A few years after the first mirror neuron studies, accounts of activation during processing of one's own emotion and empathizing with others started showing up in areas, which overlapped with mirror neuron areas. Seeing other people touching a hot stove or cutting their finger with a knife activates brain areas including the mid cingulate cortex (CC) and anterior insular cortex, but most important the inferior parietal cortex and ventral premotor cortex, which are associated with the MNS. Several following studies have confirmed these findings (Lamm & Majdandžić, 2015). During psychiatric surgeries, surgeons found neurons in the anterior CC that only fired during painful stimulations, but also during watching painful stimulation on someone else. Subsequently, findings showing the activation of mirror neurons driven by communicative gestures and by sounds of an action, strongly suggest the MNS could be extended to the emotional domain (Christov-Moore, et al., 2014).

However, this does not mean the MNS is the only implementor of empathy. Studies of disgust and taste show a role of the insula in empathy, and thus show the importance of other brain regions besides the MNS. Also, it is noted that the inferior frontal gyrus (triggered during empathy and part of the MSN) activates during a wide range of tasks and could reflect attention or language processing. Although, damage to the inferior frontal gyrus resulted in deficits in empathy (Baird, Scheffer, & Wilson, 2011). Research shows that the MNS is even unnecessary for empathy. Empathy is often evoked without any visual cue. For example, reading about emotions of a character in a book can evoke empathic feelings. In many situations empathy often occurs without the involvement of brain areas associated with the MNS. In addition, the MNS alone does not seem adequate for a correct empathic response. This is addressed in experiments where subjects were exposed to painful situations for themselves, but not for the observed other. This manipulation resulted in similar MNS responses to action observation, but a strongly altered emotional responses (Lamm & Majdandžić, 2015).

Lamm & Majdandžić, 2015 said the assertion of a hard-wired predisposition to act empathic through hard-wired mirror neurons is invalid. The Learned Matching hypothesis of empathy, however, suggests the MNS acquires its mirror properties through associative learning and that the properties are thus not hard-wired. Mirror neurons end up being indirectly activated by emotions of others through connection with brain areas involved in emotion perception. These connections come about through self-stimulation, synchronous emotion, and affect mirroring (Heyes, 2018). There is substantial evidence that mirror neurons in the fronto-parietal cortex acquire their mirror properties through associative learning (Cook, Bird, Catmur, Press, & Heyes, 2014).

The presumption of a relationship between imitation and empathy has contributed to the idea of the MNS as a neural network of empathy. Baird et al., 2011 separates voluntary imitation from automatic imitation. Many functional neuroscience studies use voluntary imitation as a proxy for empathy, which is, according to Baird et al., a non-viable approach since voluntary imitation requires subjects to copy an action. Such an imitation performance has already been proven to always require the activation of mirror neurons. This way researchers can always conclude an involvement of the MNS in empathy. A purer measure for empathy is automatic imitation since the involuntary movements generated by the observation of an action or expression are measured. To date of the Baird et al. article no functional neuroimaging studies made use of automatic imitation (Baird, Scheffer, & Wilson, 2011).

## 4.2. Recent findings

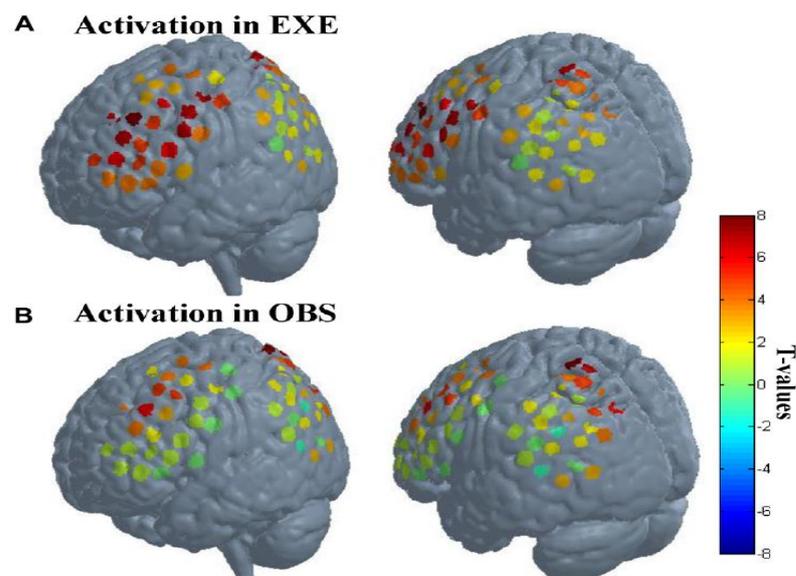
### 4.2.1. fNIRS suitable for investigation of the functional role of the MNS

Sun et al. investigated in 2018 the feasibility of functional Near-Infrared Spectroscopy (fNIRS), a non-invasive neuroimaging technique, to explore the functional role of the MNS, like social interaction. fNIRS seems to be better than previously used functional Magnetic Resonance Imaging (fMRI) because its ecological validity is higher. fNIRS is namely portable, cost-effective, and sturdy against body movements, making it an excellent technique for measurements during real-life situations in natural environments. This contrasts with fMRI where subjects are required to lie in a narrow scanner that restricts movements in unnatural surroundings. Only few studies investigated the feasibility of fNIRS before, but, without any significant evidence of MNS activity. Additionally, they investigated gender differences in neural synchronization.

30 healthy, right-handed volunteers (15 males and 15 females) were recruited to produce a table-setting task. The subject sat face to face to the experimenter at a table with at their right side a placemat with tableware (plate, fork, knife, soup spoon, and dessert spoon) and a placemat in front of them. In the execution condition the participants were cued to move the tableware to their appropriate position on the placemat in front of them with their right hand. The execution condition was repeated seven times. During the observation condition the experimenter executed the assignment while the subject observed.

Changes in oxyhemoglobin (HbO) and deoxyhemoglobin (HbR) concentrations in each channel of the fNIRS were measured by two standard probe sets. The sets were attached to a swimming cap at the left hemisphere since this is dominant when performing right-handed actions and covered mostly regions of the MNS. Two group analyses were done: traditional Channel-Based group analysis, which assumes that anatomical locations are homologous among subjects, and ROI-Based group analysis, which achieves better spatial consistency, but at the cost of spatial scale.

In both analyses Sun et al. were able to find significant activation of the MNS in both execution condition and observation condition (see **Figure 3**). Areas of the MNS where activation was found included the premotor cortex, inferior frontal gyrus, superior posterior lobe, and rostral inferior posterior lobe. The execution condition showed a significant greater activity than the observation condition. No significant difference was found between gender. Thus, they proved the feasibility of fNIRS in further research exploring the functional role of the MNS, for example in empathy.



**FIGURE 3** | Activation when using the traditional channel-based group analysis. (A) Activation in execution condition. (B) Activation in observation condition. The probe sets were projected on the brain template-Colin 27. The left images in (A) and (B) mainly represent probe 1, and the right images mainly represent probe 2. Each circle represents one channel. The assorted colours represent the t-values at group level. EXE, execution condition; OBS, observation condition (Sun, et al., 2018).

#### 4.2.2. High empathy results in stronger facial mimicry and MNS activation

A study by Rymarczyk et al., 2019 investigated the relation between facial muscle responses, brain activity and empathy. It was predicted that MNS structures would be involved in the perception of emotional facial expressions and that dynamic facial expressions trigger a greater activity than static expressions. Secondly, greater activation of MNS areas in correlation with stronger facial mimicry (FM) in highly empathic people was hypothesized.

46 healthy subjects (25 males, 21 females) participated in this study. Their empathy scores were measured using the Questionnaire Measure of Emotional Empathy (QMEE). Herein empathy is defined as followed: “*vicarious emotional response to the perceived emotional experiences of others*”. They were divided over a High Empathy (HE) and Low Empathy (LE) group based on the median score on the QMEE. As stimuli, facial expressions of disgust and fear were taken from The Amsterdam Dynamic Facial Expression Set, and the neutral conditions of the same actors were used. As static condition, stills were used from the dynamic clip. Each stimulus (static, dynamic and neutral) was repeated once for the six presentations within an expression type. During display presentation, fMRI images were collected as well as muscle reactions, measured with EMG, of the facial corrugator supercilia (CS) and levator labii (LL) were recorded.

Activity in the CS was measured during observation of both fear and disgust. Activity in the LL was only measured during viewing of disgust. A larger response was shown in the HE group in comparison to the LE group, indicating a relationship between FM intensity and empathy. There was no difference between static or dynamic stimuli, while this was observed in previous studies for happiness and anger. Brain activity was found in namely the inferior frontal gyrus and the inferior posterior lobe, areas implicated in the MNS. Activity in the inferior frontal gyrus was greater during dynamic stimuli than static stimuli and greater in the HE group compared to the LE group, indicating it plays a role in understanding of intentions and others' mental states. In line with this, there was a correlation between facial mimicry and brain activity suggesting that the MNS could constitute the neural correlates of involuntary facial mimicry for fear and disgust.

#### 4.2.3. Analysis reveals functional connections between MNS-related and empathy-related seed regions

The next study by Alcalá-López et al., 2018 tried to come to a systematic agreement about the interaction between neural processing levels resulting in social cognition. By summarizing the numerous previous brain-imaging studies covering social cognitions in humans, the researchers made a social brain atlas with 36 seed regions. This atlas was the basis for all further analysis steps: 1) meta-analytic connectivity modelling (MACM) to determine a coactivation map for each seed region, 2) resting-state functional connectivity (RSFC) to define a map of correlated fluctuation for each seed region, and 3) network clustering of both analyses to determine functional groups in the atlas.

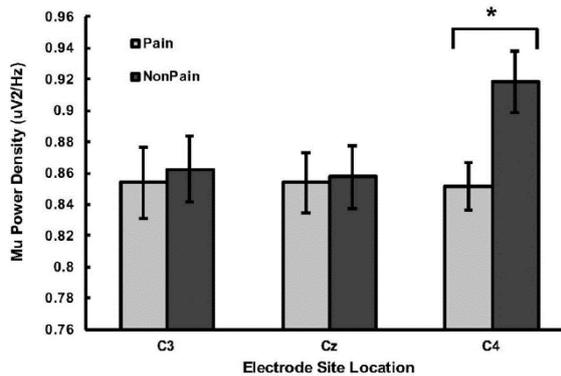
Important for this paper are their findings on the MNS. They found functional connections between seed regions of the MNS and empathy-related seed regions. So much so that these seed regions gathered in the same functional group, the intermediate-level cluster, within the social brain hierarchy.

#### 4.2.4. Viewing of painful pictures results in greater mu suppression, which is dampened by emotional invalidation

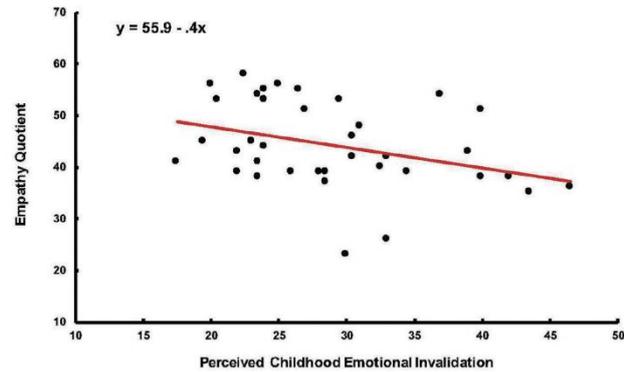
Arnett et al., 2018 sought to examine mu suppression as a model for the MNS and the role of MNS in empathy. Secondly, their goal was to examine the relationship between emotional invalidation during childhood and empathy, and lastly, they investigated possible influence of emotional invalidation on mu suppression. Mu rhythm occurs within the same EEG frequency as alpha rhythm (8-13 Hz), however, alpha rhythm desynchronizes during visual stimuli and changes in attention, while mu rhythm is desynchronized during motor activity and action observation, which makes it a good proxy for MNS activity. There has even been found a link between mu suppression and action understanding and between mu suppression and observing pain in others.

40 healthy, right-handed college students were asked to fill in two questionnaires: the empathy quotient and the invalidating childhood environment scale. Afterwards, during EEG recordings, they were shown pictures of right hands and feet in painful situations and pictures involving no pain. Subsequently, after each picture they were to rate it as painful or non-painful using keys on a keyboard.

The researchers found greater mu suppression during the observation of pictures depicting painful situations in comparison to neutral pictures (see **Figure 4**). Subjects with higher empathy showed the biggest mu suppression. Participants that perceived emotional invalidation during childhood appeared to have less mu suppression and to be less empathic (see **Figure 5**). Concluding, perceived emotional invalidation during childhood appears to be able to influence MNS activity during pain observation and those who experienced more emotional invalidation show less empathy.



**FIGURE 4** | Average mu power suppression (calculated from mu power density of trial-type/baseline) for each condition at each electrode site. Raw means and standard errors are displayed (Arnett, Roach, Elzy, & Jelsone-Swain, 2019).



**FIGURE 5** | Scatterplot showing the negative relationship between perceived childhood emotional invalidation and empathy (Arnett, Roach, Elzy, & Jelsone-Swain, 2019).

## 5. DISCUSSION AND CONCLUSIONS

In this paper I tried to find answers to the question if the new findings of recent studies into the relationship between the MNS and empathy bring more clarity into this topic, and if the previous criticism on the link between both can be refuted. Ever since the first studies tried to find evidence of a role of the MNS in empathy there has been a lot of criticism, but more recent studies are still not able to deliver hard evidence.

Sun et al.'s investigation into fNIRS as a viable technique to research the functional role of the MNS was according to them a success. fNIRS is indeed ecologically more viable than the previously often used fMRIs, seeing it can extend research to real-life social situations rather than it being restricted to laboratories. However, they lacked a control condition. Without the control the activation they related to the MNS could be caused by other factors like attention or visual information. fNIRS is, however, not precise enough to measure the response of single neurons and is thus not capable to pinpoint mirror neurons in the human brain. Therefore, Sun et al. did not provide the empirical evidence of a human MNS. In their study they made use of automatic imitation, which is not the best measure for empathy as concluded (Baird, Scheffer, & Wilson, 2011). However, this did not influence their results since they did not use imitation as measure for empathy, but only for activation of the MNS.

In Rymarczyk et al.'s investigation into the relations among facial mimicry, brain activity, and empathy traits, they measured muscle activity in the CS and LL during reaction to fear and disgust. However, activity of these facial muscles is not distinct to single emotions. For example, an increase in activity of the CS is recorded during perception of various negative emotions. Increased activity of the LL is also seen in pain expression. Due to this non-specificity of the CS and LL it is not completely fair to

label their activity as indicator of facial mimicry for fear and disgust (Rymarczyk, Żurawski, Jankowiak-Siuda, & Szatkowska, 2019). They did, however, use automatic imitation and not voluntary imitation as proxy for empathy, which is a better measure (Baird, Scheffer, & Wilson, 2011). Rymarczyk et al.'s research is one of few neuroimaging studies who used an automatic imitation task.

Alcalá-López et al. combined many neuroimaging studies to find an agreement about interaction between neural processing levels resulting in social cognition. This results in an unavoidable dependence on the technical limitations of technology used like fMRI, which can suffer from signal dropouts (Alcalá-López, et al., 2018) and the ecological invalidation due to restriction to experiments feasible within the scanners (Sun, et al., 2018).

Lamm & Majdandžić focussed in their criticism on the suggestion that the function of the MNS is hard-wired and we are predispositioned to resonate with others' emotions. They did not agree, and I comply as well. The suggestion the MNS acquires it's mirror properties through associative learning is much more believable (Heyes, 2018) (Cook, Bird, Catmur, Press, & Heyes, 2014). The fact that Arnett et al. found that MNS activity is influenced by emotional invalidation during childhood supports the idea of a mouldable MNS and not of a hard-wired system. However, there is need for research with a longitudinal design in order to determine the direction of the relationship.

The use of the Invalidating Childhood Environment Scale (ICES) during Arnett et al.'s study has its limitations. Its items focus on parental behaviour rather than on how this behaviour was experienced by the subject. Also, ICES does not specifically evaluate invalidation of emotions. Lastly, findings on the psychometric properties in nonclinical samples are mixed (Zielinski & Veilleux, 2018). Mu suppression as proxy for the MNS is also not completely backed up. It is warranted that further research into the connection is needed (Hobson & Bishop, 2017). However, Arnett et al. believes their research supports the idea of mu suppression as indicator for MNS function.

So, the role of the MNS in empathy can be set as the reproduction of affective experiences of others in your own repertoire, but there is still not enough empirical evidence to conclude a causal link between the MNS and empathy. However, the new studies like Alcalá-López et al.'s and Rymarczyk et al.'s support the idea of a functional role of the MNS in empathy. Sun et al. brought a new technique to light to investigate the functional role and Arnett et al. suggested the MNS is mouldable and that mu suppression is the right measure for MNS. But even if a functional link exists, the MNS cannot be the only neural mechanism underlying empathy. Nevertheless, fundamental evidence of a MNS in the human brain must first be found, before chasing hard evidence for the MNS-empathy link.

## 6. REFERENCES

- Alcalá-López, D., Smallwood, J., Jefferies, E., Van Overwalle, F., Vogeley, K., Mars, R. B., . . . Bzdok, D. (2018). Computing the Social Brain Connectome Across Systems and States. *Cerebral Cortex*, 28(7), 2207-2232.
- Arnett, K., Roach, A., Elzy, M., & Jelsone-Swain, L. (2019). Childhood emotional invalidation and right hemispheric mu suppression during pain empathy task: An EEG study. *Social Neuroscience*, 14(2), 236-250.
- Baird, A. D., Scheffer, I. E., & Wilson, S. J. (2011). Mirror neuron system involvement in empathy: A critical look at the evidence. *Social Neuroscience*, 6(4), 327-335.
- Cattaneo, L., & Rizzolatti, G. (2009). The Mirror Neuron System. *Archives of Neurology*, 66(5), 557-560.
- Christov-Moore, L., Simpson, E. A., Coudé, G., Grigaityte, K., Iacoboni, M., & Ferrari, P. F. (2014). Empathy: Gender effects in brain and behavior. *Neuroscience and Biobehavioral Reviews*, 46, 604-627.

- Cook, R., Bird, G., Catmur, C., Press, C., & Heyes, C. (2014). Mirror neurons: Form origin to function. *Behavioral and Brain Sciences*, 37(2), 177-192.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding Motor Events: A Neuropsychological Study. *Experimental Brain Research*, 91(1), 176-180.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor Facilitation during Action Observation: A Magnetic Stimulation Study. *Journal of Neurophysiology*, 73(6), 2608-2611.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action Recognition in the Premotor Cortex. *Brain*, 119(2), 593-609.
- Heyes, C. (2018). Empathy is not in our genes. *Neuroscience & Biobehavioral Reviews*, 95, 499-507.
- Hobson, H. M., & Bishop, D. V. (2017). The interpretation of mu suppression as an index of mirror neuron activity: past, present and future. *Royal Society Open Science*, 4(3).
- Lamm, C., & Majdandžić, J. (2015). The role of shared neural activations, mirror neurons, and morality in empathy - A critical comment. *Neuroscience Research*, 90, 15-24.
- Rymarczyk, K., Żurawski, Ł., Jankowiak-Siuda, K., & Szatkowska, I. (2019). Empathy in Facial Mimicry of Fear and Disgust: Simultaneous EMG-fMRI Recordings During Observation of Static and Dynamic Facial Expressions. *Frontiers in Psychology*, 10, 701.
- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. J., & Frith, C. D. (2004). Empathy for pain involves the affective but not the sensory components of pain. *Science*, 303(5661), 1157-1161.
- Sun, P. P., Tan, F. L., Zhang, Z., Jiang, Y. H., Zhao, Y., & Zhu, C. Z. (2018). Feasibility of Functional Near-Infrared Spectroscopy (fNIRS) to Investigate the Mirror Neuron System: An Experimental Study in a Real-Life Situation. *Frontiers of Human Neuroscience*, 12, 86.
- Zielinski, M. J., & Veilleux, J. C. (2018). The Perceived Invalidation of Emotion Scale (PIES): Development and psychometric properties of a novel measure of current emotion invalidation. *Psychological Assessment*, 30(11), 1454-1467.