Comenius University in Bratislava
Faculty of Mathematics, Physics and Informatics

The role of mirror neurons in cognition

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Supervising department:	Department of Applied Informatics
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Aim: 1. Compile a review of current findings on the topic of mirror neurons from primate and human studies.
2. Delineate the anatomy of the mirror neuron system and present a critical analysis of its putative function and origins.
3. Provide personal perspective based on the researched literature.

Annotation: Mirror neurons are a class of brain cells originally discovered in the premotor cortex of the macaque monkey that become active during the execution of monkey's own actions, and similarly during it's observation of similar actions executed by another monkey. Initially speculated to represent a neural mechanism for action understanding, in about two decades of their research, the mirror neurons grew into one of the most prominent theories in cognitive sciences today, claimed to be a simple explanation for a number of complex cognitive phenomena. But some parts of this theory might be worth reconsideration.

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Úloha zrkadliacich neurónov v kognícii

Cieľ: 1. Vypracujte prehľad aktuálnych poznatkov na tému zrkadliacich neurónov zo štúdií na primátoch i ľuďoch.
2. Popíšte anatómiu systému zrkadliacich neurónov a poskytnite kritickú analýzu jeho domnelej funkcie a pôvodu.
3. Vyjadrite vlastnú perspektívu vzhľadom na preštudovanú literatúru.

Anotácia: Zrkadliace neuróny sú typom mozgových buniek pôvodne objavených v premotorickej kôre makakov, ktoré sú aktívne počas vykonávania vlastného pohybu opice, a rovnako i pri jej pozorovaní podobného pohybu vykonávaného inou opicou. Zatiaľ čo sa pôvodne predpokladalo, že zrkadliace neuróny sa podieľajú na reprezentácii neurálnych mechanizmov pre porozumenie akciám, za približne dve dekády výskumu prerástli do jednej z najprominentnejších teórií dnešných kognitívnych vied, a považujú sa za jednoduché vysvetlenie viacerých komplexných kognitívnych javov. Avšak niektoré časti tejto teórie sa oplatí prehodnotiť.

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I hereby declare that the work presented in this thesis is original and the result of my own investigations. Formulations and ideas taken from other sources are cited as such.

. . . .

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I am deeply thankful and indebted to Igor Farkaš for his invaluable commentaries, assistance and patience. I would also like to thank Marijan Palmović and his colleagues for lending us both their laboratory and their knowledge.

Abstract

Mirror neurons are a class of brain cells fortuitously discovered in the premotor cortex of the macaque monkey that become active during both execution and observation of the same action. This straightforward property is what enabled these neurons to conquer the fields of cognitive science and become one of the most acclaimed discoveries from the turn of the century. Whether it was a result of rigorous research or a consequence of undue speculations is debatable.

With this thesis I strive to open the debate and point the reader towards a critical reconsideration of what we currently know and think about the mirror neurons. I commence my efforts by providing a thorough introduction to the neurobiological background of the primate action observation–execution network, into which the mirror neurons are embedded, and which facilitates their function. I continue with a review of the methods and results of human mirror neuron studies that laid down the foundations for further incorporation of mirror theories into their respective fields, only to then turn the tables and reveal their problems as the critics point out. In the concluding part of the thesis, I myself assume the sceptical perspective and voice my own concerns regarding the plausibility of the mirror neuron on a conceptual level. I further provide the results of an original EEG study, with the intention to illustrate the limited explanatory power of this method. Finally, I present my own vision of a resonance system that approaches the mirror neurons rather reasonably.

Keywords: mirror neurons, motor resonance, action understanding, brain

Abstrakt

Zrkadliace neuróny sú typom mozgových buniek objavených šťastnou náhodou v premotorickej kôre opice makak, ktoré sú aktívne ako počas vykonávania pohybu, tak počas jeho pozorovania. Táto jednoduchá vlastnosť umožnila týmto neurónom ovládnuť odvetvia kognitívnej vedy a stať sa jedným z najuznávanejších objavov na prelome storočí. Avšak či sa k tomu dospelo cez dôkladný výskum alebo to bolo v dôsledku prehnaných špekulácií je diskutabilné.

Touto prácou sa snažím nastoliť diskusiu a usmerniť čitateľa ku kritickému prehodnoteniu toho, čo dnes vieme, a čo si len myslíme o zrkadliacich neurónoch. Svoje úsilie zahajujem poskytnutím podrobného úvodu do neurobiológie observačno–exekučného okruhu primátov, v ktorom sú zrkadliace neuróny uložené, a ktorý sprostredkováva ich funkcie. Ďalej pokračujem prehľadom metód a objavov z oblasti výskumu na ľuďoch, ktoré položili základy pre postupné zapracovanie zrkadliacich neurónov do teórií daného odboru, iba aby som následne na to odhalil námietky vznesené ich kritikmi. V záverečnej časti práce zaujmem skeptickú pozíciu a vyjadrím svoje znepokojenie nad prijateľnosťou zrkadliacich neurónov na konceptuálnej úrovni. Ďalej poskytnem výsledky vlastnej EEG štúdie, so zámerom ilustrovať obmedzenú výpovednú hodnotu tejto metódy. V úplnom závere predstavím svoju vlastnú víziu rezonančného systému, ktorý pristupuje ku zrkadliacim neurónom s dávkou nadhľadu.

Kľúčové slová: zrkadliace neuróny, motorická rezonancia, porozumenie akciám, mozog

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Abbreviations

AIP anterior intraparietal area

CIP caudal intraparietal sulcus, sometimes cIPS

EPSP excitatory postsynaptic potential

EEG electroencephalograph

fMRI functional magnetic resonance imaging

IPSP inhibitory postsynaptic potential

IPL inferior parietal lobule

IPS intraparietal sulcus, area 7ip

IT inferotemporal cortex

LIP lateral intraparietal area

M1/F1 primary motor cortex

MIP medial intraparietal area

MDP medial dorsoparietal area

MEG magnetoencephalograph

MEP motor evoked potential

MN(s) mirror neuron(s)

MNS mirror neuron system

MST medial superior temporal area

MT middle temporal area of the STS

PE superior parietal lobule, area 5

PEa part of intraparietal sulcus, roughly MIP

PEip part of intraparietal sulcus, roughly MIP and MDP

PEci caudal part of the cingulate sulcus

PF anterior part of inferior parietal lobule, area 7b

PFG central part of inferior parietal lobule, area 7ab

PG posterior part of inferior parietal lobule, area 7a

PGm medial part of superior parietal lobule, area 7m

PMd dorsal premotor area

PMdc/F2 caudal part of dorsal premotor area

PMdr/F7 rostral part of dorsal premotor area

PMv ventral premotor area

PMvc/F4 caudal part of ventral premotor area

PMvr/F5 rostral part of ventral premotor area

PO parieto-occipital cortex, V6 and V6A

PPC posterior parietal cortex

pre-SMA/F6 pre-supplementary motor area

PRR parietal reach region

SI/S1 first somatosensory cortex

SII/S2 second somatosensory cortex

SMA/F3 supplementary motor area proper

SPL superior parietal lobule

STP superior temporal polysensory cortex

STS superior temporal sulcus

TEa and TEm areas of the lower bank of rostral STS

TMS transcranial magnetic stimulation

TPO middle area of the upper bank of STS

V6 and V6A medial areas of posterior SPL

VIP ventral intraparietal area

Introduction

The Brain. The one and a half kilogram water-and-fat personal universe, making each and every one of us so unique and alike at the same time. Without a doubt one of the biggest enigmas in science, this magnificent piece of biological machinery has kept scholars scratching their heads for the good part of the humankind's history. The beginning of the 20^{th} century proved to be a turning point, following the conception of the *neuron doctrine* that stemmed from the pioneering research of Camillo Golgi and Santiago Ramón y Cajal whose discoveries in cellular anatomy of the human brain laid down the foundations of what can today be considered the modern neuroscience (Golgi, 1906; Ramón y Cajal, 1906).

The ensuing technological progress brought in with the blossoming of information science and engineering opened new avenues of study to complement slowly ageing practices. Data provided by imaging and computational modelling methods enabled the brain to be studied in great detail and unveiled the dynamic processes underlying our conscious lives. But answers to the *really difficult* questions such as how does a thought, mind, or consciousness emerge from mere chemical interactions of cells still remained far from our reach. It was becoming clear that anatomy and physiology by themselves were not sufficient to reveal every mystery of the brain, and a larger collaboration would be needed to aid their efforts.

The questions about mind and other mentalistic aspects of our lives sparked another great change of that period. The first half of the century was largely dominated by the *behavioural psychology* with its central notion that the brain is in essence an association device, linking environmental stimuli to proper motor responses, thus driving the correct behaviour. Emphasis was given entirely on the observable-objective part of the behaviour, and the role of beliefs, expectations or mental states was disregarded. This led to tension between behaviourists and a new generation of thinkers who refused to simply leave the mind out of the equation. Many scientists, including Noam Chomsky and George Miller, argued that human behaviour is complex beyond the explanations of behaviourism, and that the mind is not a stimulus–response associator but rather a dynamic information processing device. This later became known as the *cognitive revolution*, a starting point for a paradigm shift that ultimately gave birth to the *cognitive science*, an interdisciplinary field dedicated to the mind and the brain, initially defined by George Miller as involving psychology, linguistics, neuroscience, computer science, anthropology and philosophy (Miller, 2003).

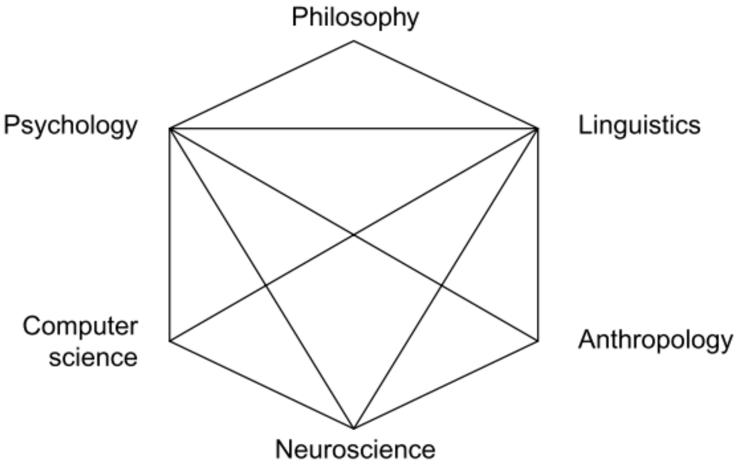


Figure A: **Miller's description of cognitive sciences in 1978.** Many had since been joined into their own "sub-fields", such as computational neuroscience or neurolinguistics. Figure adapted from Miller (2003).

Today, the cognitive sciences, or brain research as such, are seen as a frontier in life sciences, intriguing both the professionals and public. It is felt that we now need to explore the brain, to gain full understanding of ourselves, the causes of prevailing mental illnesses, to wit, depression, schizophrenia, autism, Alzheimer's disease or addictions, and to be able to counter their life-degrading symptoms. And the results of this desire can be easily seen throughout the world. Institutes such as Howard Hughes Medical Institutes *Janelia Farm Research Campus* or *Allen Institute for Brain Science* yield dozens of ground breaking findings each year. The US Government recently announced funding of a programme called *Brain Research through Advancing Innovative Neurotechnologies* (BRAIN) with a $100 million starting budget for year 2014, carrying on after the Decade of the Brain, as the 90's were designated by U.S. president George W. Bush. The *Blue Brain Project* is another ongoing and remarkable effort by researchers from École Polytechnique Fédérale de Lausanne, attempting to reverse engineer the mammalian brain and reconstruct it as a virtual model. The impact of such an accomplishment would be immense.

More and more people, experts and students alike, are beginning to support the existence of organizations dedicated to creating opportunities for collaboration and sharing of new ideas through the internet and independently organised conferences, *Society for Neuroscience* being one of the best known, uniting more than forty thousand members. And it is also the intrinsic science fiction like nature of cognitive sciences driving smart young people to join. Artificial life, human–machine hybridisation, recording of dreams, it all sounds rather exaggerated. But just looking at what we have accomplished so far leaves one wondering what will be next.

The popularity of brain research also caught the eye of mass media, which became a prominent proxy between the scientific community and general populace. This presents a problem however, as the modus operandi of majority of media is to attract attention by the means of awe rather than accuracy. Interesting new theories and speculative hypotheses therefore often get misinterpreted and misquoted through media, causing widespread misconceptions often referred to as "neuromyths". Several studies have shown that about half of the population thinks that we only use 10% of our brains (Herculano-Houzel, 2002), and that such beliefs are not exclusive to the layman but are also present amongst primary and secondary school teachers (Dekker et al., 2012).

The temptation to amaze is one that all men share though, and sometimes even a scientist can get biased and rashly jump to a conclusion that may at the first glance seem straightforward and elegant, but might be based more on trivial observation than sound data. That is after all why the geocentric model ruled the astronomy for centuries. And it is also where the story of the mirror neurons starts.

Since their discovery, the mirror neurons were met with quite the enthusiasm, showcased by the early prediction of V.S. Ramachandran who in 2000 stated that "mirror neurons will do for psychology what DNA did for biology" (Ramachandran, 2000), and later reinforced his position in his TED talk titled "The Neurons that Shaped Civilisation" (Ramachandran, 2009). Many others shared his feelings and mirror neurons quickly became a keenly discussed topic in both scientific and popular journals, ultimately earning the moniker "the most hyped concept in neuroscience" (Jarrett, 2012). The mirror neurons seemed to be a simple answer to anything from how we understand movement to how we connect with others.

It took more than a decade for the first sceptics to start publicly arguing against certain aspects of the mirror neuron theories. Multiple studies had shown that mirror neurons are not necessary or dissociate with many phenomena of which they are supposed to be the underlying mechanism. The strongest criticism to date came in from the book by Gregory Hickok (2014) named aptly “The Myth of Mirror Neurons”, in which he tried to point out the problems of the agreed upon functions of the mirror neurons and provide alternative explanations for their role in the human brain.

I myself was also impressed by the mirror neurons when I initially got acquainted with them during a lecture on embodied cognition. But as I delved deeper into the existing literature on all of their putative functions, I started to question, whether the explanatory power that was being given to a single cell type thoroughly studied only in a primate that supposedly does not imitate, empathise, use language or suffer from autism spectrum disorder, really rests on solid foundations, or is more a manifestation of our desire to have a simple model for understanding the complex in us – a modern neuroscientific parallel to the geocentric model. Thus I, too, became a “mirror sceptic” and the following sections present the results of my investigations.

Chapter 1 is fully dedicated to the overview of empirical data, definitions and descriptions of what mirror neurons are and what parts of the brain were reported to contain them. The review primarily draws upon the original experiments with macaque monkeys, supplemented by recent findings in primate brain anatomy and connectivity.

Chapter 2 continues by clarifying the difficulties of studying mirror neurons in human subjects, summarising commonly employed methods and their limitations. A portion is also dedicated to the hypothetical function of the system that the mirror neurons are supposed to subserve, mainly the understanding of motor acts and social cognitive phenomena.

A critical outlook will follow in Chapter 3, discussing the issues and inconsistencies in the published research. The chapter deals with the unclear terminology laid down in the original studies, and a bias present in many others, where the conclusions about the mirror neuron function sometimes seem to be relying on beliefs more than the results themselves. Alternative explanations by critics of the mirror neurons are provided to both the cited studies and the role of the mirror neurons in human and non-human primate brain. The chapter also briefly visits the topic of the origin of the mirror neurons and how their function might have, to use the words of Ramachandran, “shaped the civilisation”.

Chapter 4 directly builds upon the previous, consisting of my own investigations into the mirror neurons. Its first part consists of my own concerns with several aspects of the mirror neuron theory. Following is a simple EEG experiment, conducted to demonstrate the limitations and difficulties of drawing sound conclusions from human studies as discussed in Chapter 2, and show the different levels of supposed mirror neuron activation during observation of human and artificial movement with and without a goal. The closing part is then dedicated to an outline of an alternative model of action observation–execution system that does not consider the mirror neurons as its central premise.

Other than being a mystery, our brain is also a great source of inspiration. It inspires to *create*, it inspires to *explore* and it also inspires to *think*, and his thesis tries to present my part in a little bit of each.

Chapter 1

Discovery, properties and anatomy of primate mirror neuron system

One of the most intriguing developments in neuroscience in recent years has been the discovery of a system that seems to be unifying the generation of movement with its perception, owing it all to a cell called the *mirror neuron.* Mirror neurons have since been a passionately discussed topic in the scientific literature throughout the last two decades, even finding their way into many articles in the popular press, and rightfully so. Mirror neurons are a class of brain cells that exhibit changes in activity both while an individual is executing a motor act, and while the same or closely similar motor act is being observed or even imagined – hence *mirror* neurons (Gallese et al., 1996; di Pellegrino et al., 1992). This differentiates the mirror neurons from motor or sensory neurons that are active either during execution or observation but not both. All the excitement and speculations stemmed from this newly found concept that the primate brain seems to engage similar neural circuits in both action execution and action observation. An inherent relation between these two processes should therefore exist, implying that the ability to understand or interpret an action requires involvement of one's motor repertoire. This established an interesting new perspective on how the brain processes movement and how this way of processing influences other parts of cognition, as the mirror neurons appear to be the ideal underlying neural substrate for a range of phenomena and disorders in motor learning, social cognition and theory of mind (Decety and Meyer, 2008; Iacoboni, 2009b; Gallese, 2013; Ramachandran and Oberman, 2006; Rizzolatti and Fabbri-Destro, 2008; Vanderwert et al., 2013).

Mirror neurons were first discovered in the ventral premotor cortex of macaque brain (Rizzolatti et al., 1988) and have since been reported in a number of different brain areas, together forming a complex interconnected network. The goal of this chapter is to introduce the functional properties of mirror neurons and to review the literature on the location and connectivity of the brain areas where neurons with mirror properties have been reported, in order to delineate a framework through which we can further investigate their function.

1.1 Serendipity in Parma

The initial studies into mirror neurons were conducted by a group from University of Parma, whose original research interests were focused on how the brains of macaque monkeys (*Macaca nemestrina*) encode visual properties of an object into motor code for action. Their study of the rostral part of ventral prefrontal cortex, also known as area F5, indicated that neurons present in this area respond to execution of object-directed movement such as grasping, holding and tearing (di Pellegrino et al., 1992; Rizzolatti et al., 1988). A number of cells were also found to be active during passive visual or somatosensory stimulation, when no actual movement was performed by the monkey. This phenomenon was interpreted as a supporting neural mechanism for priming of grasping and feeding related motor acts from the monkeys motor "vocabulary" through sensory stimulation (Rizzolatti et al., 1988).

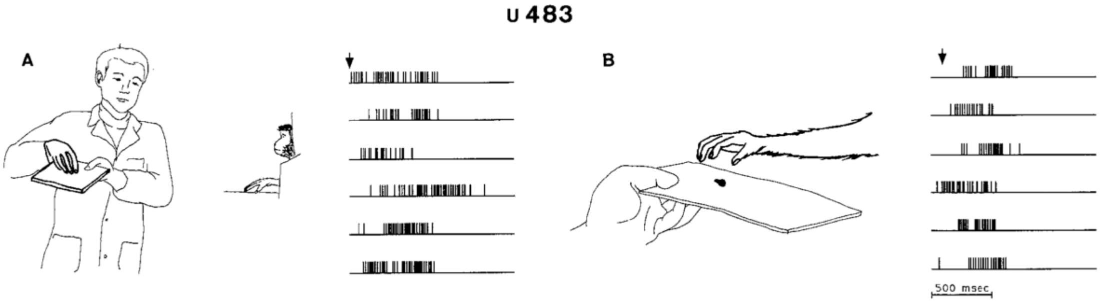


Figure 1.1: **Mirror neuron discharging** during (A) experimenter's grasping movement observed and (B) similar movement executed by a macaque monkey. The arrows indicate approximate onset of the grasping. Figure adapted from di Pellegrino et al. (1992).

In subsequent research by the same group, the cells in the F5 were fortuitously found to fire during monkey's observation of the experimenter's hand movements, and the term "mirror" neuron was coined (di Pellegrino et al., 1992). From the population of examined cells in the F5 area, 17% were found to possess the mirroring property, i.e. being active during the observation of a hand or mouth movement directed toward an object. 55% of these manifested selectivity for the type of action performed, with

75% representing the grasping movement (Gallese et al., 1996). The group proposed that this activity in essence reflects the observed movement and plays fundamental part in its understanding, by creating an inner motor representation on the neural level. Existence of a similar mechanism was later also suggested to exist in humans (Rizzolatti et al., 1996a).

1.2 Primate brain areas forming the parieto-frontal mirror network

Following their discovery in the premotor cortex, further investigations identified mirror neurons in several additional brain areas, most notably the inferior parietal lobule (Gallese et al., 2002) and the primary motor cortex (Tkach et al., 2007). Of particular interest were the regions of inferior parietal lobule that has been already known to be involved in sensory-motor transformations and for sharing rich, reciprocal connections with the premotor cortex, especially area F5. Together with the anterior part of the intraparietal sulcus, these three brain regions became known as the *mirror neuron system* (Rizzolatti and Craighero, 2004), or a more recently proposed *parieto-frontal mirror network* (Rizzolatti and Sinigaglia, 2010). The mirror neuron system (MNS) comprises a complex network of functionally distinct areas containing mirror neurons (see Kilner and Lemon, 2013; Molenberghs et al., 2012, for a review), that facilitate not only the generation of appropriate movement, but according to the earliest hypotheses also underlie its understanding (Rizzolatti, 2001) and imitation (Jeannerod, 1994). Another brain area that plays a crucial role in MNS, yet is not strictly a part of it due to being devoid of neurons with motor properties, is the superior temporal sulcus (STS). A more detailed description of both "classical" mirror neuron areas and areas extending the MNS is provided in the following sections.

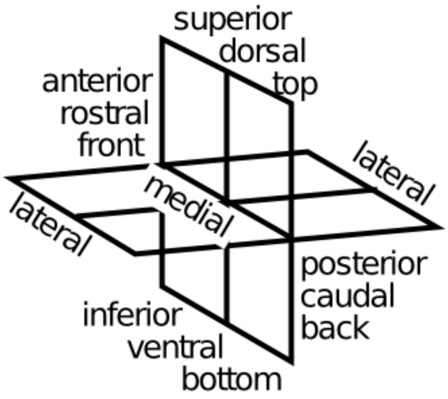


Figure 1.2: **Anatomical terms of location**

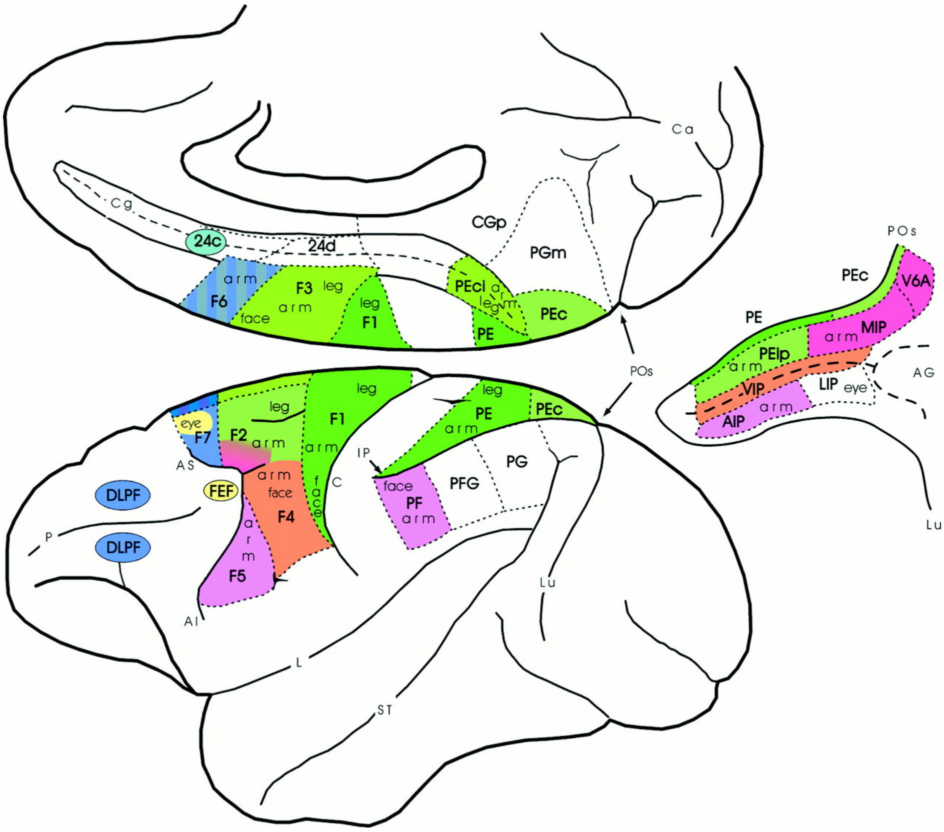


Figure 1.3: **Medial and lateral view of the macaque brain** labelled according to the cytoarchitectonic organisation proposed by Matelli et al. (1991). The small section in the right part of the picture represents the unfolded view of areas of the intraparietal sulcus. Green colours represent motor cortex that is mostly the target of somatosensory information; red colours represent motor cortex that is the target of either visual or visual and somatosensory information; blue colours represent motor cortex with predominant prefrontal and/or cingulate inputs. Adapted from Luppino and Rizzolatti (2000).

There are a number of ways of organising the brain into subdivisions. Probably the most prevalent is by using the Brodmann areas, a system based on the cytoarchitectonic organization of the cerebral cortex. Though recent functional and neuroanatomical studies show that the cortex can be organised in a much more precise manner, considering not only the architectonics of the cortical area but also the functional properties and interconnectivity with other regions of the brain. Figure 1.4 shows the two most frequently used types of organisation of the brain in the context of the mirror neuron research, in this case specifically of primate frontal cortex. The depicted cortical organisations are the contemporary functional organisation and the histochemical-cytoarchitectonic organization devised by Matelli et al. (1985, 1991) respectively, and will be used predominantly throughout the thesis. The Matelli organisation was specifically proposed for primate research and is based roughly on the organisation by von Economo and Koskinas (1925) and Pandya and Seltzer (1982).

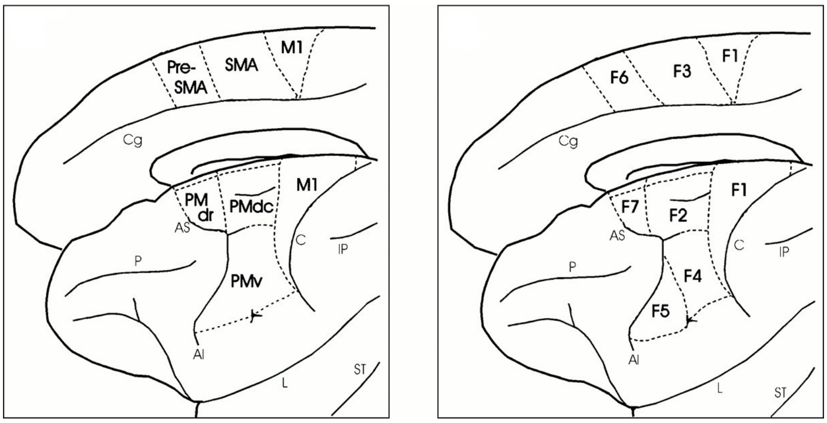


Figure 1.4: **Comparison of cortical organisations** showing the primate motor cortex divided using the modern functional organisation, and histochemical and cytoarchitectonic map proposed by Matelli et al. (1991). Figure adapted from Luppino and Rizzolatti (2000).

Given that the following sections deal heavily with macaque brain anatomy, Figure 1.3 provides a reference point for all mentioned areas except for superior temporal sulcus, which will be illustrated in its respective section, Figure 1.2 represents a visual aid for standard anatomical terms of location, and the Abbreviations (page xi) provides a list of all referenced brain areas with their respective shorthand.

1.3 Frontal areas

Functional studies of the frontal motor cortex radically changed our view on both the organisation and properties of this part of the brain. Instead of being a single large "module" exclusively responsible for everything related to movement, it was shown to consist of multiple functionally independent subdivisions with rich connections either within or outside the frontal motor cortex. These connections form an intricate circuit that plays a crucial role in sensorimotor transformation and is hypothesised to also be at the basis of an array of higher cognitive functions, such as action recognition, attentional control in motor response generation, associative motor learning and imitation (Gallese et al., 1996; Luppino and Rizzolatti, 2000; Picard and Strick, 1996).

1.3.1 Ventral premotor cortex (areas F5 and F4)

The ventral premotor cortex (PMv) is a lateral region of the frontal lobe lying roughly between the lower arm of arcuate sulcus and the primary motor cortex, formed mostly by agranular neural tissue. It can be further divided into ventral premotor cortex, rostral (PMvr) and ventral premotor cortex, caudal (PMvc) that correspond to areas F5 and F4 respectively (see Figure 1.4).

Area F5

Area F5 is a region of the ventral premotor cortex drawing most of the interest in primate studies due to its particularly complex functions that remain to be fully understood. It occupies the rostral part of the PMv, caudal to the inferior part of the arcuate sulcus (Geyer et al., 2000). The latest neuroanatomical studies identified the area itself to comprise three architectonically distinct interconnected subdivisions, designated F5 anterior, F5 posterior, and F5 convexity (F5a, F5p and F5c, respectively) (Belmalih et al., 2009).

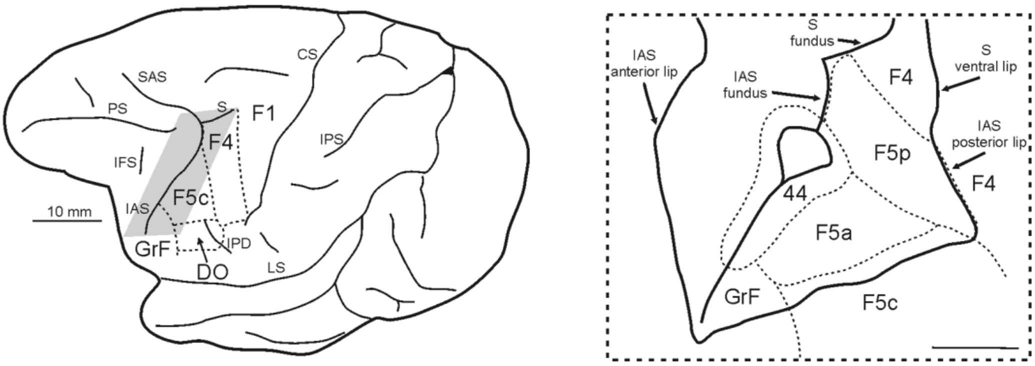


Figure 1.5: **Subdivisions of area F5** and an unfolded view of the inferior arcuate sulcus showing the areas F5a and F5p buried within. Figure adapted from Belmalih et al. (2009).

Aside from their dense intrinsic connectivity, the “sub-areas” of the F5 differ in their connections with other brain areas. F5a occupies the anterior part of the postarcuate bank and is characterized by the presence of relatively large pyramidal neurons in cortical layer III and a prominent and homogeneous layer V (Rizzolatti et al., 2014). It is mostly connected with premotor area F4 and pre-supplementary motor area F6, regions of the prefrontal cortex, namely rostral opercular area, area 46v and 12 (Gerbella et al., 2011). Its parietal connections were found to be the most robust, receiving dense input from the anterior intraparietal sulcus (AIP), inferior parietal area PFG, the entire hand/arm representation of the SII region (Fitzgerald et al., 2004; Rizzolatti et al., 1998), and a weaker input from the inferior parietal area PF and area 24. Gerbella et al. (2011) suggest that the role of F5a is predominantly the integration of parietal sensorimotor and prefrontal higher-order information, that is then routed to the adjacent F5 areas.

F5c is the premotor division in which the mirror neurons were originally discovered and it corresponds largely to hand and face/mouth representation. It is a poorly laminated area with an overall homogeneous cell population, located on the convexity of the precentral gyrus adjacent to the inferior limb of the arcuate sulcus (Rizzolatti et al., 2014). Similarly to F5a, its connected with area F4 and opercular cortex, and to a much lesser extent with areas F3, M1, 44, 46v and 12. The parietal connections consist of a heavy reciprocal circuit between the PF and PFG regions of the inferior parietal lobule, and inputs from area AIP, SII region for the hand and face, and area corresponding roughly to the temporoparietal junction (Gerbella et al., 2011; Rizzolatti et al., 1998).

Area F5p lies within the posterior part of the postarcuate bank and is quite different from F5a and F5c in that its cortical layer Vb was found to contain large pyramidal neurons similar to those in primary motor cortex that project directly to the cervical spine segments (Belmalih et al., 2009; Dum and Strick, 1991; Rizzolatti et al., 2014). Recent studies have shown that some of these cells possess classical mirror properties, and some even exhibit "inverse" mirror properties, i.e. the neuron is active during the execution of a movement, but gets suppressed during its observation (Kraskov et al., 2009, 2014). In terms of cortico-cortical connectivity, the most prominent connections are with the hand field of M1, modulating its motor output (Kraskov et al., 2011; Prabhu et al., 2009), premotor areas F2 and F4, and the parietal AIP and SII (Gerbella et al., 2011).

Noteworthy are also the subcortical connections of F5, mainly those of F5a and F5p, which receive substantial cerebellar input relayed through the thalamus (Geyer et al., 2000).

Neurons in area F5 are organized somatotopically, where arm movements are represented dorsally and orofacial movements ventrally (Geyer et al., 2000). The substantial amount of research done on F5 suggests it to be responsible for fine control of hand and mouth movements, specifically for the hand shaping during grasping and griping movements and the interaction with the mouth, representing a sort of a "motor vocabulary" (Graziano et al., 2002; Matelli et al., 1984; Rizzolatti et al., 1988, 2014). Compared to the findings regarding the neurons encoding hand movements, which have been extensively studied, less is known about functional properties of neurons representing mouth movements, though the existing data points toward similar ends (Ferrari et al., 2003). In earlier studies, the F5a and F5p were together referred to as F5ab (for arcuate bank) and due to the reciprocal connections mainly with the AIP, the AIP-F5ab circuit has been suggested to play a crucial role in visuomotor transformation for grasping (Luppino et al., 1999; Rizzolatti et al., 1998).

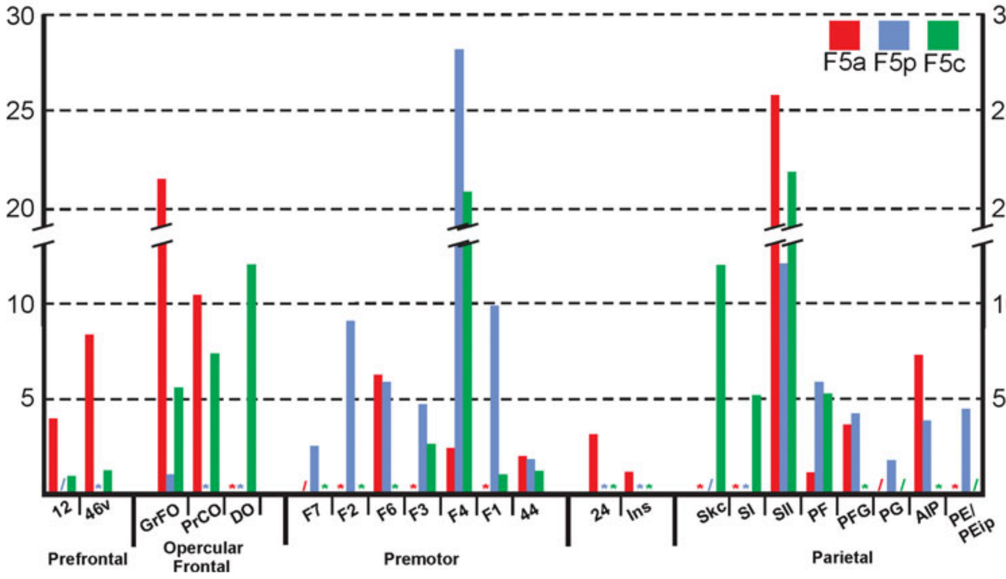


Figure 1.6: **Cortical connectivity of area F5** shown in terms of mean percentage of distribution of retrograde labelling (/ = no labelling; * = labelling <1%), representing the relative strength of the connections. Adapted from Gerbella et al. (2011). Note that the study was primarily concerned with area F5a and thus the data on F5c and F5p might not be complete.

Area F5 cell properties

Motor properties of neurons in the F5 area were originally researched by Rizzolatti and the Parma group, as already briefly mentioned in Section 1.1. Neurons linked to hand movement were found to discharge during specific object-directed movements such as grasping, tearing or holding, with a large number of neurons being specific to a certain type of hand movement (Rizzolatti et al., 1988). Later studies even found cells sensitive to grasping using a tool (Umiltà et al., 2008).

Rizzolatti's group also found that the activity of the neurons appeared to correlate more with execution of distal rather than proximal motor acts. Based on the movement during which a particular neuron was active, they divided the F5 neurons into several types. Four types of neurons were established for distal movement, namely:

- *grasping with the hand and the mouth neurons*
- *grasping with the hand neurons*
- *holding neurons*
- *tearing neurons*

and two types for the proximal movement:

- *bringing to the mouth or to the body neurons*

- *reaching neurons*

Majority of the recorded neurons belonged into the distal types. An interesting property of the distal type neurons was their specificity to the way the hand was shaped during execution of the motor act. Three recurring shape types were identified:

- *precision grip neurons*
- *finger prehension neurons*
- *whole hand prehension neurons*

The neurons in F5 did not seem to be specific to the movement of a particular hand and almost all of those recorded by Rizzolatti's group discharged during motor acts performed by either hand. Furthermore, 50% of the neurons responded to somatosensory stimulation and about 20% to visual stimulation. According to the authors, visual activation required a "motivationally meaningful stimuli" where the size of the stimulus also appeared to be critical for the neurons to be successfully triggered (Rizzolatti et al., 1988).

Sensitivity of F5 neurons to visual stimuli is admittedly the most interesting property of this premotor area. Certain F5 neurons become active during mere observation of a three-dimensional object in absence of any overt movement, and similarly during actual interaction with the object. The precondition for this phenomenon is that the actual type and shape of the grip encoded by the neuron must be congruent with the size and shape of the presented object (Jeannerod et al., 1995). Results of study by Murata et al. (1997) indicate that these neurons encode the shapes of objects in terms of the motor system, that is to say, when an object is presented to the visual system, its features are translated into an internal motor representation. This event occurs whether an actual motor response towards the object is required or not. Such neurons have been dubbed *canonical neurons* (Rizzolatti et al., 1988; di Pellegrino et al., 1992).

Canonical neurons seem to have properties very similar to those of anterior intraparietal area responsible for visual control of hand manipulation movements. Reciprocal projections between AIP and F5 have been found by several studies (Luppino et al., 1999; Matelli et al., 1994; Rizzolatti et al., 1998) indicating that the AIP-F5 circuit may indeed play a role in transformation of visual or spatial characteristics of an object into appropriate hand movements, where AIP is responsible for description of the objects features in terms of its affordances, and then transmitted to the F5, where potential interactions with the object are encoded (Fagg and Arbib, 1998; Murata et al., 1997, 2000; Sakata et al., 1995).

Many studies have also reported F5 neurons responsive to action observation, as opposed to object observation. Aptly named *mirror neurons*, this class of neurons possesses the motor properties indistinguishable from other F5 neurons, meaning they are active during execution of a certain motor act, but in addition also become active while a similar motor act is being observed (Gallese et al., 1996; di Pellegrino et al., 1992). Most of the mirror neurons of area F5 are suggested to be located in its F5c part, but this might be due to single cell recordings in arcuate bank areas being rather rare.

Mirror neurons require interaction between the observed individual and an object. The sight of the object alone nor a pantomimed movement of an interaction with such object is a sufficient stimulus for triggering mirror activity. In case of the studies with macaque monkeys, the actions are carried out by an experimenter and are often related to grasping or manipulation with food or simple objects in front of a monkey restrained in a primate chair.

Majority of mirror neurons appear to be active during observation of only a single particular motor act (Gallese et al., 1996; di Pellegrino et al., 1992; Rizzolatti et al., 1996a). Numbers from the study by Gallese et al. (1996) were briefly mentioned in Section 1.1, yet to provide further details, out of 532 neurons measured in macaque F5 area, 92 (roughly 17%) were mirror neurons, of which 51 were active during observation of only a single action, 38 responded to two or three actions, plus 3 neurons that were active when the monkey observed the experimenter grasping with his hand or mouth.

32 mirror neurons were tested alternately using the right and left hand. In case of 12 (37.5%) the hand used significantly affected the activity of the neuron. In absolute terms, 5 neurons preferred the right and 7 the left hand. It is also worth mentioning that the response of 9 neurons was stronger when the hand used in the stimulus was ipsilateral to the hemisphere containing the measured neuron, and 3 preferred the contralateral hand.

Grasping movement seemed to be the most successful in activating the mirror neurons with 60 of these responding only to grasping with hand, 9 to grasping with mouth, and 11 neurons firing for either hand and mouth grasping.

Gallese et al. (1996) also described a relationship between the visual and motor properties of mirror neurons, that is, the observed action they respond to and the motor response they encode. Based on the congruence between the effective observed action and the effective executed action measured from the monkeys in their study, they devised a classification into three classes:

- *strictly congruent*

- *broadly congruent*
- *non-congruent*

A strictly congruent mirror neuron is defined as being highly specific in both visual and motor properties. The neuron discharges when the effective observed and executed actions are identical both in terms of the general action (e.g. grasping, rotation, tearing) and in terms of the way in which the action was executed (e.g. precision grip, power grip) (Gallese et al., 1996; Rizzolatti et al., 1996a). Figure 1.7 shows an example of a strictly congruent mirror neuron, where the measured neuron responds only to a single direction of the rotation.

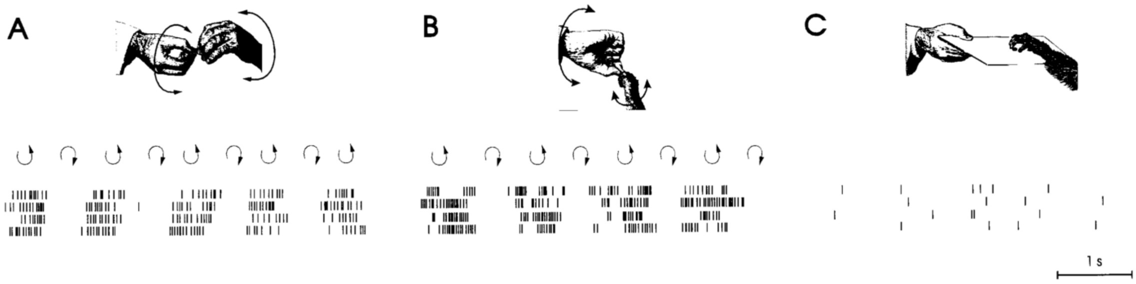


Figure 1.7: **Activity of a strictly congruent mirror neuron.** (A) a monkey observes an experimenter rotating his hands in opposite directions around a piece of food, alternating between clockwise and counter-clockwise movement, (B) the experimenter rotates a piece of food held by the monkey, opposing its wrist rotation, again in an alternating fashion, (C) the monkey picks up the piece of food as a control condition. The curved arrows indicate the direction of the rotation. Activity of four recorded neurons is pictured. Adapted from Rizzolatti et al. (1996a).

Broadly congruent mirror neurons are somewhat flexible regarding the relationship between the effective observed and effective executed actions. Gallese et al. (1996) describe it as a link, but not identity between these two actions. Furthermore, they specified three subgroups of these neurons. In early studies of the Parma group, 48.9% of measured mirror neurons were classified as broadly congruent (Kilner and Lemon, 2013).

The motor properties of the first group of broadly congruent mirror neurons are identical to those of strictly congruent neurons, discharging only to a specific type of hand action and type of grip, but they respond to observation of more than one type of grip (e.g. grasping using a precision grip and grasping using a whole hand prehension) (see Figure 1.8).

The second group comprises mirror neurons that become active during execution of a single general action (e.g. grasping), but visually respond to observation of two or more (e.g. grasping and holding). Mirror neurons from this group were found to be the most abundant from the set measured by Gallese et al. (1996).

Mirror neurons of the last broadly congruent group appear to discharge with respect to the goal of the observed action regardless of the executed movement.

Lastly, the non-congruent mirror neurons are defined as those having no apparent relationship between the effective observed and effective executed actions of the monkey (Gallese et al., 1996).

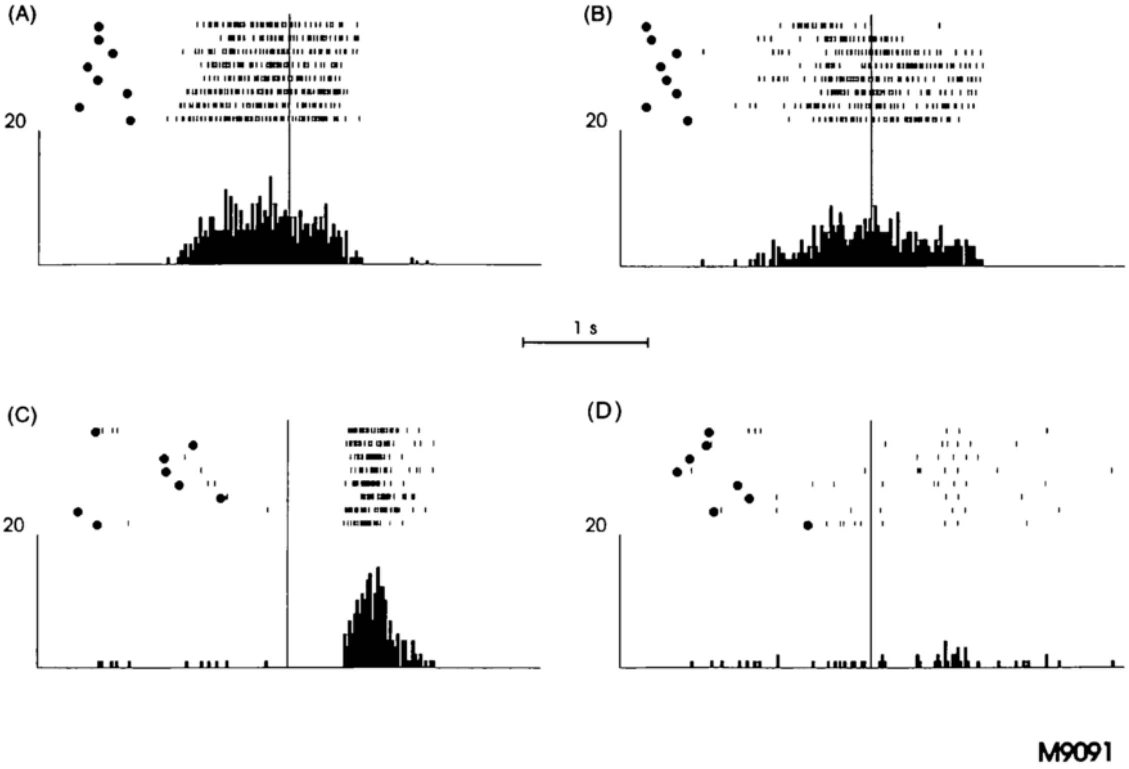


Figure 1.8: **Activity of a broadly congruent mirror neuron of the first group.** (A) a monkey observes an experimenter grasping a piece of food using precision grip, (B) the monkey observes the experimenter grasping an object with whole hand prehension, (C) the monkey grasps a piece of food using precision grip, (D) the monkey grasps an object with whole hand prehension. The neuron shows specificity for precision grip in case of active execution of the movement. Vertical lines in A and B represent the moment when the experimenter interacted with the food/object, and in C and D the moment at which the door of the monkeys testing box were opened. Adapted from Gallese et al. (1996).

Area F4

Area F4 is located caudal to the area F5 and rostral to the primary motor cortex, extending dorsomedially towards the arcuate spur. It is connected with supplementary motor areas F3 and F6, the connection to area F3 (i.e. SMA proper) being considerably stronger than that with area F6 (i.e. pre-SMA) (Geyer et al., 2000). It also receives substantial input from the inferior parietal lobule areas PF and PFG, SII, and shares a strong reciprocal connection with ventral intraparietal area (VIP), creating a parieto-frontal circuit similar to that of F5 and AIP (Lewis and Van Essen, 2000; Luppino et al., 1999; Rizzolatti and Fadiga, 1998). Unlike area F5, area F4 is devoid of any prefrontal and cerebellar input, however, receives substantial inputs from basal ganglia through ventrolateral thalamus (Geyer et al., 2000).

The main projection sites of area F4 seem to be the primary motor cortex, in case of the dorsal part of F4 responsible for hand representation the reticular formation of the brain stem and the spinal cord, and in case of the ventral part representing the face the facial nucleus (Geyer et al., 2000).

Neurons in area F4 are somatotopically organised. The area seems to contain motor representations for arm, head, mouth, and trunk movements (Gentilucci et al., 1988). The mouth field is located laterally and the hand field medially. The neurons respond to tactile and visual stimuli in peripersonal space and show no apparent representation of distal movements (Fogassi et al., 1996; Gentilucci et al., 1988). Ablations were shown to cause peripersonal neglect while extrapersonal stimuli remained to be perceived normally (Rizzolatti et al., 1983). The area is therefore considered to play crucial part in encoding the peripersonal space.

Although area F4 does not contain mirror neurons, most of its neurons fire during the execution of goal-directed motor acts, and also respond to sensory stimuli, either tactile (unimodal) or visual and tactile (bimodal). Somatosensory and visual receptive fields of its neurons seem to correlate with the direction of effective movement of the proximal arm (e.g. a neuron with visual or tactile receptive field in the facial region becomes active during arm movement toward that region) (Gentilucci et al., 1988).

Based on the rich connections and similarity with the VIP neurons that also hold bimodal receptive fields and respond congruently to movement or light touch in peripersonal space (Colby et al., 1993; Duhamel et al., 1998), it has been concluded that the VIP-F4 circuit plays a role in encoding the peripersonal space and transformation of object locations into motor codes for guided movement towards these objects (Rizzolatti and Fadiga, 1998). Fogassi et al. (1996) suggest that the visual responses of bimodal F4 neurons represent a potential motor act within the peripersonal space.

1.3.2 Dorsal premotor cortex (areas F7 and F2)

The dorsal premotor cortex (PMd) occupies the dorsolateral aspect of the frontal lobe, separated from the prefrontal cortex by the superior part of the arcuate sulcus, and from the PMv by the arcuate spur. Similarly to PMv, it is further divided into rostral part, PMdr or F7, and caudal part PMdc or F2.

Area F7

Area F7 comprises two loosely defined sectors, a dorsal sector, also called the supplementary eye field (SEF), and a ventral sector. SEF receives inputs from the lateral intraparietal area (LIP) responsible for attentional eye position and encoding saccadic memory, and might represent an oculomotor circuit (Matelli et al., 1996) that may play a role in complex saccade control during head or body movements (Geyer et al., 2000). The projections from SEF to superior colliculus only further affirm this notion.

The ventral sector is the predominant target of the medial part of superior parietal lobule, area PGm (or 7m) and the dorsolateral prefrontal cortex. The neurons in this sector become active in relation to both arm and eye movements (Fujii et al., 2000). Lesion studies suggest a crucial role of this area in stimulus–response associations and in motor learning, as lesioned monkeys showed impairment in the performance of previously learned motor association tasks with no visible motor deficits, and were incapable of novel learning (Rizzolatti et al., 2014). The projections from the ventral sector terminate mostly in the reticular formation.

Area F2

Area F2 is roughly somatotopically organised, with leg movements represented dorsally and arm movements ventrally relative to the superior precentral dimple. Separation of proximal and distal movements is rather poor (Geyer et al., 2000).

It again receives strong parietal inputs that differ based on the precise location of the projection. The F2 region around the superior precentral dimple (F2prcd) receives strong somatosensory input from areas PEip and PEc, while the ventrorostral (F2vr) part is a target of visual areas MIP and V6A (Geyer et al., 2000). Both of these circuits were studied by Rizzolatti et al. (1998) and suggested to be involved in monitoring and control of the limb position during object- directed movement using somatosensory information in case of the "PEip/PEc–F2prcd" circuit, and visual information in case of the "MIP/V6A–F2vr" circuit. Furthermore, Hoshi and Tanji (2000) stressed its role in integrating information about target location and arm to be used in action planning.

F2 projects mainly to primary motor cortex and surrounding motor areas. The

F2prcd is unique in that it also gets subcortical inputs from basal ganglia and cerebellum, and also projects down the corticospinal tract.

The cells in F2 are quite interesting as well. Wise et al. (1997) distinguished three types of neurons in this area, namely:

- *signal-related neurons*
- *set-related neurons*
- *movement-related neurons*

This classification is based on the activity of neurons during the delay period between the instruction signal and the movement trigger signal of a reach-to-grasp task that conveys information necessary for correctly reaching an object and controlling the direction of the arm movement (Rizzolatti et al., 2014). The first group of neurons exhibit a visually driven phasic response immediately after the instruction signal. The second group discharges during the whole delay period before the trigger signal. The third group discharges in association with the movement onset.

1.3.3 Supplementary motor areas (F6 and F3)

The supplementary motor area occupies the medial aspect of the frontal lobe, just anterior to the primary motor cortex, superior to cingulate cortex, and dorsally to the PMd. It comprises two regions, the supplementary motor area proper (SMA proper, or simply SMA), and the pre-supplementary motor area (pre-SMA) (Rizzolatti et al., 1996c). Although they differ in terms of functional properties, cytoarchitectonics, and connection to other brain areas, they are both roughly somatotopically organised and hypothesised to contribute to postural control, bimanual coordination, and temporal organisation of movement (Rizzolatti et al., 2014).

Both regions are also a part of different subcortical motor loops, as both receive input from different sources, relayed through different thalamic nuclei. SMA proper is targeted mostly by the pallidum and putamen, while pre-SMA receives input from the caudate nucleus and the cerebellum (Geyer et al., 2000).

Area F6

Area F6 represents the more anteriorly located pre-SMA, extending 5 to 6 millimetres caudally from the prefrontal cortex. It is predominantly connected with rostral premotor areas F5 and F7, rather fairly with prefrontal and cingulate cortex, and also receives weak projections from the IPL and STS. Descending projections from F6 mostly terminate in the brain stem (Rizzolatti et al., 1996c).

Area F6 is weakly excitable to electrical stimulation. The movements observed using high intensity currents were either fast and short-lasting, or slow, complex, and mainly engaged the forelimbs in movements resembling natural movements or postural adjustments of the animal (Luppino et al., 1991). Representation of proximal movements exceeds that of distal movements.

Neurons in area F6 were found to fire in response to visual stimuli, and rarely also to somatosensory stimuli (Alexander and Crutcher, 1990). They also fire well before the initiation of the movement. According to Tanji and Shima (1994), F6 neurons typically discharge during the interval between two particular motor acts (e.g. during the preparation of a push following a pull), or to a motor act having a particular rank inside a sequence (e.g. the third act in a sequence). These results indicate that F6 neurons must be contributing to the organization of complex motor sequences. Such assertion corresponds with the fact that unlike other motor areas, F6 receives most of its input from the prefrontal cortex, which is well known to be involved in planning. Rizzolatti et al. (1998) denoted the pre-SMA as the "supramotor" area, controlling movement based upon motivational factors and external contingencies.

Area F3

Area F3, the SMA proper, is located caudally to pre-SMA and rostrally to M1. Cortical afferents to this area come basically from all motor areas, mainly F2 and F4, slightly less so areas F5, F6, F7 and even M1. Similarly strong afferents also come from the primary and secondary somatosensory cortex, the cingulate cortex, and the posterior parietal areas PE and PEci. Descending projections target both the brain stem and the spinal cord (Geyer et al., 2000).

F3 contains a complete somatotopic representation of body movements (Luppino et al., 1991), with the leg field located caudally, the arm field rostrally, and a much smaller face field located at the rostral end of the arm field. Inversely to the pre-SMA neurons, those in SMA proper respond to somatosensory stimuli, mostly proprioceptive input, with only a few also to visual stimuli (Rizzolatti et al., 1998). Most F3 neurons phasicly discharge in association with active movements, typically time-locked onto the movement onset. Some neurons fire exclusively in relation to specific sequences of movements (Tanji et al., 1996).

The area F3 is electrically excitable with low-intensity currents, eliciting limb displacements involving two or more joints. Proximal movements are represented more than the distal ones, although without visible anatomical segregation (Rizzolatti et al., 2014).

1.3.4 Primary motor cortex (area F1/M1)

The primary motor cortex (F1 or M1) represents a convergence point for most of the cortical areas concerned with generation and control of movement, and plays a major role in movement execution. Located on the precentral gyrus, M1 is a poorly laminated cortical area characterised by the absence of cortical layer IV and prominent giant pyramidal cells, known as Betz cells, in layer V (Geyer et al., 2000). Descending axons of the Betz cells form a significant amount of the corticospinal tract, the main efferent motor pathway in the spine, forming synapses with lower motor neurons that directly innervate muscles primarily of the distal limb. The output from M1 represents roughly 30–50% of the corticospinal fibres, since the numbers in the literature tend to vary (Dum and Strick, 1991; Guyton and Hall, 2006; Toyoshima and Sakai, 1982).

SMA dominates the cortical afferents into M1, closely followed by lateral premotor cortex and parietal somatosensory areas 1, 2 and 5 (PE, part of superior parietal lobule). Thalamic connections also constitute a considerable part of the M1 input (Geyer et al., 2000).

M1 exhibits somatotopic organization; the leg field is located on the medial surface and extends on the dorsolateral convexity, the arm field lies in the intermediate position, and the face field occupies the ventrolateral position. The proximal and distal movements of the arm field are anatomically segregated. Proximal movements tend to be represented rostrally and distal movements caudally, in the anterior bank of the central sulcus (Rizzolatti et al., 2014). The organization of M1 reflects movements or motor acts, not just muscle and joint activations as previously thought. Geyer et al. (2000) interprets the influence of M1 on voluntary movements in three assertions: that much of the motor cortex is active during every movement, that the activity of each cell figuratively represents a "vote" for a particular direction of movement, and that the actual direction of the movement is determined by a sum and averaging of the votes within the cell population.

In the early Parma studies, Gallese et al. (1996) considered the absence of mirror activity in M1 as a control that the studied monkey did not engage in any covert movement during the measurement. But recent studies have proven their premise wrong, when mirror neurons were identified directly in M1 (Dushanova and Donoghue, 2010; Tkach et al., 2007; Vigneswaran et al., 2013). Similarly to the F5 corticospinal mirror neurons described by Kraskov et al. (2009), both classical MNs and a subset of neurons with inverse properties, i.e. suppression during action observation, were described in M1 (see Figure 1.9). The purpose of this mechanism in M1 remains to be fully understood, the current hypotheses generally corresponds with that for F5 MNs,

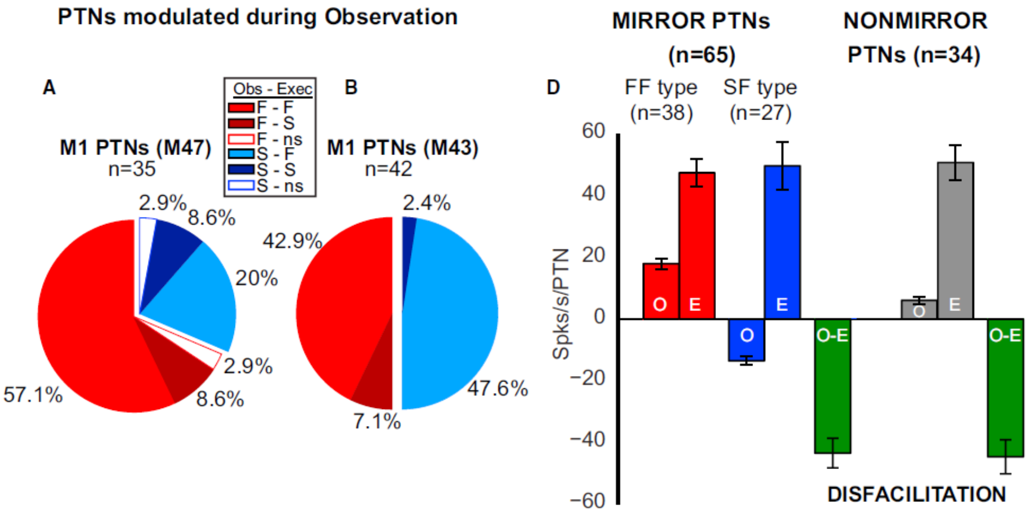


Figure 1.9: **Activity of M1 mirror neurons** recorded in two macaque monkeys plotted as pie charts showing different types of facilitation (red, F) and suppression (blue, S). Lighter shades of both colours indicate proportions of these neurons whose discharge was facilitated during execution, darker shades indicate proportions showing suppression during execution. The graph on the right shows the maximum firing rates of MNs during observation and execution trials, expressed as raw firing rates from the pooled results from both monkeys. Figure adapted from Vigneswaran et al. (2013).

and M1 has become considered as being a part of a larger action observation–execution matching network, aiding in recognition and understanding of observed actions (Hari et al., 1998).

1.4 Parietal Areas

The parietal areas that contribute to the action execution-observation network lie in the posterior parietal cortex (PPC), located posterior to the postcentral gyrus, superior to the temporal lobe and anterior to the occipital lobe. PPC comprises two lobules – the superior parietal lobule and the inferior parietal lobule – separated by the intraparietal sulcus. PPC plays a major role in establishing and maintaining a spatial reference system constructed through integration of inputs from the adjacent visual, auditory and somatosensory areas, in order to guide eye, limb, and body movements (Lewis and Van Essen, 2000). The nomenclature of these areas usually follows the cytoarchitectonic maps of Pandya and Seltzer (1982) (e.g. PF, PFG, PG) or Cavada and Goldman-Rakic (1989) (e.g. 7a, 7b), despite the latter being today considered rather inaccurate. Their approximate relation is noted in the Abbreviations (page xi) for a reference.

1.4.1 Inferior parietal lobule (PF, PFG and PG)

The inferior parietal lobule (IPL) represents a multimodal area concerned with the processing of visual, auditory, and somatosensory information in order to guide reaching and grasping movements of the hand and finger. IPL neurons are somatotopically organized, with the mouth field located rostrally in area PF, the hand field intermediately in area PFG, and the arm and eye fields caudally in area PG (see Figure 1.3). Neurons in this area were found to discharge in association with goal-directed movements alone, as well as to mirror such grasping movements similarly to F5 mirror neurons (Rozzi et al., 2008).

Area PF

Area PF represents the IPL mouth field. It is characteristic by the predominant responsiveness to somatosensory stimulation of the mouth and face. Motor responses of this area represent biting, licking, and grasping with the mouth. Visual responses are rather scarce, essentially non-existent (Rozzi et al., 2008). All of this suggests the role of PF mostly in organising eating behaviour and food-related motor acts.

The connectivity of PF corresponds with its responsiveness. The strongest connections comprise those with somatosensory cortices SI and SII, followed by the anterior areas of IPS, namely AIP and VIP, and PMv areas F5 and F4. PF also shares strong connections with adjacent PFG, PFop and PO, and weaker ones with insular and cingulate cortex (Pandya and Seltzer, 1982; Rozzi et al., 2006).

Area PFG

Area PFG contains a large population of cells associated with motor and somatosensory responses, primarily encoding hand motor acts such as grasping. Neurons with responses to mouth stimulation are also present, presumed to play a role in linking hand and mouth motor acts to enable fluent movements of bringing food to mouth (Rozzi et al., 2008).

The area additionally houses cells responsive to peripersonal and object directed visual stimuli, many of which also respond to tactile stimuli and active movement, in the sense of mirror neurons. Similarly, a large number of neurons were found to respond to visual presentation of objects, and again, also possess motor properties. This suggests the role of PFG in organising manipulative hand movements according to object properties (Rozzi et al., 2008).

The connections of PFG are similar to those of PF, however, the strong somatosensory interconnectivity is replaced by connections with visual areas, namely MST and superior temporal polymodal area (STP). The primary connections consist of those with AIP, VIP, F5 and insula, to a lesser extent with F4 and F2. Again, a large part of the connectivity is local with PF, PG, PEa and PO (Pandya and Seltzer, 1982; Rozzi et al., 2006).

Area PG

Area PG neurons mostly represent the arm reaching and the related eye movement. Motor and visual responses are therefore widely represented, while somatosensory responses are quite rare. The possible role of PG might be the organization and control of visually guided arm reaching (Rozzi et al., 2008).

PG mostly connects with caudal parietal and cingulate areas, including the parietal reach region (PRR), areas MIP, V6A, PEc, PEci and 23. It also shares strong connections with MST and STS, and rather weak ones with F2 and F5 (Pandya and Seltzer, 1982; Rozzi et al., 2006).

1.4.2 Intraparietal sulcus

The intraparietal sulcus (IPS) is formed by a set of interconnected, anatomically and functionally diverse sectors (see Figure 1.10) that process visual and sensory information as a part of neural circuits comprising frontal motor cortex and occipital visual cortex. Depending on the connectivity of the respective IPS area, each provides the motor cortex with specific information such as spatial coordinates of objects and body parts, eye movement parameters, or geometrical properties of objects such as shape, size and orientation (Grefkes and Fink, 2005; Rizzolatti et al., 1998).

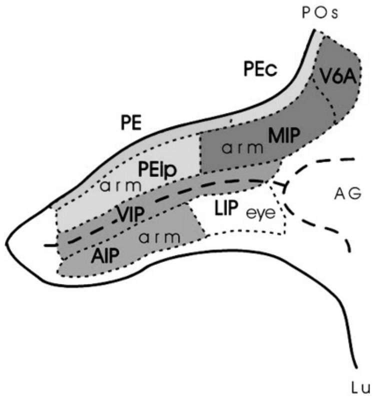


Figure 1.10: **Subdivisions of the intraparietal sulcus.** Figure adapted from Luppino and Rizzolatti (2000).

Anterior intraparietal area

Anterior intraparietal area (AIP) is located on the anterior lateral bank of the IPS. Neurons in this area were found to discharge during fixation and manipulation with objects, and exhibit high levels of selectivity for the shape, size, and orientation of objects (Murata et al., 2000). AIP is reciprocally connected to PMv, especially area F5, and receives further inputs from SII and the ventral stream areas TEa, TEm, and MT (Davare et al., 2011).

According to Sakata et al. (1995), AIP comprises three groups of neurons based on their visuomotor discharge properties, namely the *motor-dominant neurons* that strongly respond to movement regardless of the visual conditions, the *visual-motor neurons* that respond to movement differently in the light and the dark, and the *visual-dominant neurons* that do not discharge in response to movement in the dark. Furthermore, some of the latter two types discharge even when no object manipulation is performed, termed *object-type neurons*. Murata et al. (2000) hypothesised that AIP in combination with area F5 constitute a visual control circuit, in which the visual responses of object-type neurons represent the shape, size, and orientation of 3D objects, whereas those of the non-object-type represent the shape of the hand grip, grip size, or hand orientation.

Ventral intraparietal area

Ventral intraparietal area (VIP) is located in the fundus of the IPS, and constitutes a multimodal association zone responsive to visual, tactile, vestibular and auditory stimuli, involved in the construction of head-centred representations of near extrapersonal space (Duhamel et al., 1998). VIP receives majority of its connections from visual areas MST and MT, and somatosensory projections from areas PEc and PFG (Rizzolatti et al., 1998).

VIP constitutes a circuit with area F4, supposed to play a role in the encoding of the peripersonal space and in the transformation of object locations into appropriate movements toward the objects (Rizzolatti et al., 1998).

Lateral intraparietal area

Lateral intraparietal area (LIP) is found in the lateral wall of the IPS. LIP is interconnected with the frontal eye field (FEF) and a part of a circuit with the supplementary eye field (SEF) of area F7, and thus is involved primarily in the control of eye movements and mediating saccades (Grefkes and Fink, 2005; Rizzolatti et al., 1998).

Medial intraparietal area

Medial intraparietal area (MIP) is a part of the parietal reaching region (PPR), together with areas V6A, PEc and PEip. The whole PPR is supposed to mediate planning, execution and monitoring of reaching movements, and constitutes a circuit with area F2 (Grefkes and Fink, 2005; Rizzolatti et al., 1998).

Caudal intraparietal area

Caudal intraparietal area (CIP) rests in the lateral bank of the caudal IPS, posterior to area LIP. CIP receives massive projections from visual areas V3, V3A and V4 (Cavada and Goldman-Rakic, 1989) and is involved in analysis of 3D object features, especially to axis and surface orientations of objects in space (Grefkes and Fink, 2005). Unlike the other IPS areas, CIP does not project into any motor area. However, according to Sakata et al. (1997), it might contribute to the visual adjustment of the shape of the hand grip and orientation indirectly through projections to AIP.

1.5 Superior temporal sulcus

The superior temporal sulcus (STS) represents a major landmark of the temporal lobe, spanning its length from the temporal proisocortex up to the angular gyrus of the IPL. It is the first sulcus located inferior to the lateral fissure, dividing the lobe into superior and inferior temporal gyri (superior and middle in the human brain). Decades of research have revealed STS to be a highly diverse area. It comprises several distinct subregions (see Figure 1.11) that differ considerably in terms of architectonics, connectivity and function (Hein and Knight, 2008). Mirror neuron literature only rarely explicitly refers to any particular STS area and usually uses general terms of location such as “lower bank” or “ventral bank”, which roughly correspond to areas TPO, TEa and TEm, thus only these three will be described in more detail.

STS is considered to be a higher-order sensory area and the target of the ventral visual stream through inferotemporal (IT) areas TE and TEO. Given the adjacent visual and auditory cortices, limbic structures, and adding in the dense connections with prefrontal and parietal areas, it is not surprising that STS is supposed to subserve a spectrum of complex cognitive functions, including audiovisual integration, biological motion and face perception, social interaction and visual tasks on theory of mind (Beauchamp et al., 2004; Hein and Knight, 2008; Pavlova et al., 2010). According to Hein and Knight (2008), the functional distribution in STS is largely determined by the functional characteristics of co-activated brain regions, rather than simply by its proposed subdivision, implying that STS is essentially a multifunctional area.

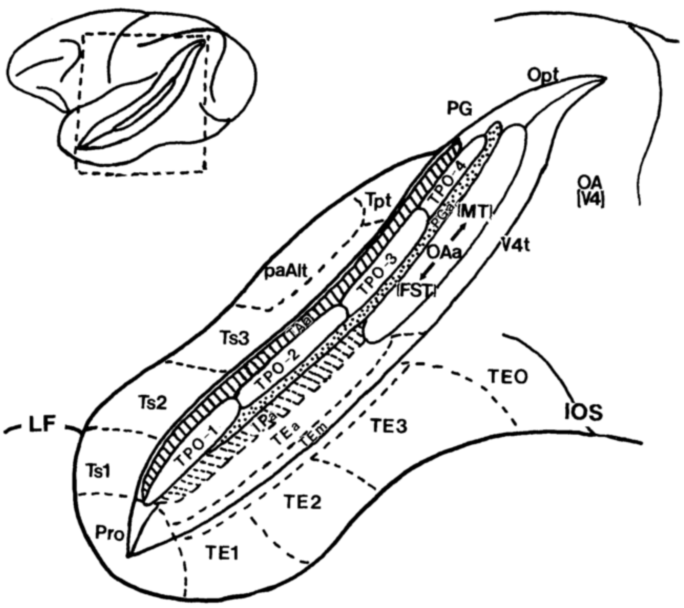


Figure 1.11: **Subdivisions of STS** according to Seltzer and Pandya (1989b).

It is also worth noting that several subregions of STS project through several different pathways to Broca's area (Petrides and Pandya, 2009), and that STS also communicates reciprocally with the cerebellum (Sokolov et al., 2012).

1.5.1 Areas TEa and TEm

TEa and TEm are located in the rostral lower bank of STS and based on their unimodal visual inputs represent predominantly visual association areas. Most of their connections comprise regions of the inferior temporal cortex (IT), V4, AIP, LIP, and parahippocampal gyrus (Davare et al., 2011; Seltzer and Pandya, 1994). They share reciprocal connections with TPO and several other STS areas, and project into frontal areas 11, 12, 46 and 8 (Seltzer and Pandya, 1989a).

TEa and TEm possess several interesting properties. They contain neurons sensitive to different kinds of simple visual stimuli (e.g. sine-wave gratings, colours, shapes) and complex visual stimuli, but also an especially high proportion (19%) of visual neurons selective for faces (Baylis et al., 1987).

1.5.2 Area TPO

TPO occupies the upper bank of STS. It represents the main part of what is often referred to as the superior temporal polysensory cortex (STP). TPO is a multimodal area with diverse connections, based on which Seltzer and Pandya (1978, 1989b) further divide it into four distinct regions TPO-1, TPO-2, TPO-3 and TPO-4. A later study by Cusick et al. (1995) instead proposed three areas designated in rostral-to-caudal manner, namely TPOr, TPOi and TPOc that do not include TPO-1 and represent a slightly different sectional distribution for the other three areas. As there is not a set consensus on their borders, I will mostly refer to them using the anatomical terms of location, which combined with Figure 1.11, should be descriptive enough to accommodate either approaches to TPO division.

The connectivity of TPO is quite astonishing. Afferent projections coming from the prefrontal cortex target mostly the rostral and intermediate regions, while parietal, cingulate and temporal projections primarily target the intermediate and caudal part. The whole TPO receives afferents from regions of lateral fissure and ventral temporal lobe, but interestingly only indirectly from IT through areas TEa and TEm. Of special interest are the connections with IPL, namely area 7a (PFG and PG), which is to a variable extent reciprocally connected with the whole TPO, more strongly with the intermediate and caudal parts, and area LIP that projects to its caudal part (Cusick et al., 1995; Seltzer and Pandya, 1994). Figure 1.12 provides a diagram of these connections.

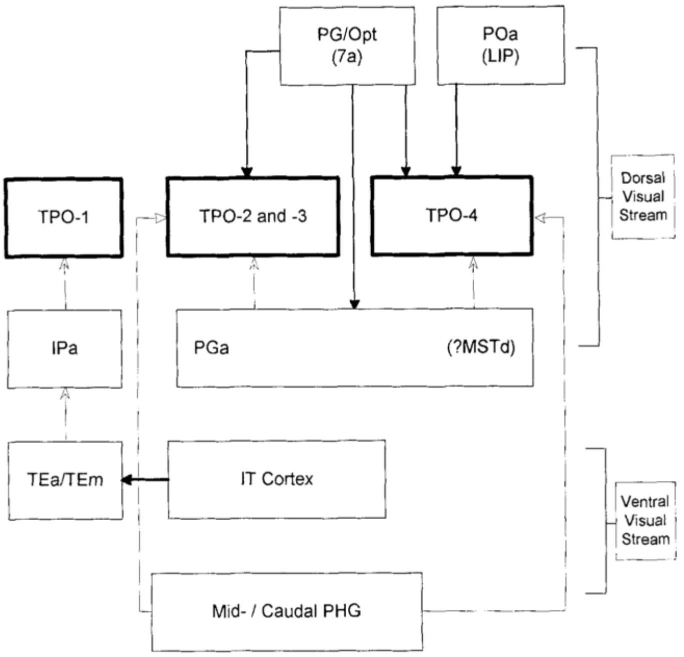


Figure 1.12: **Diagram of cortical inputs to TPO**. Feed-forward projections are drawn in boldface, lateral projections are indicated by thin lines and open arrows. Adapted from Seltzer and Pandya (1994).

TPO connections with the frontal lobe are organized in line with the rostral-to-caudal topography of the sulcus. The rostral parts project to the ventral (areas 13, 12, 11, and 14), medial (areas 24, 32, 14, and 9), and lateral (areas 10, 12, and 46) frontal regions, the intermediate parts project to the rostral region of the lateral prefrontal cortex (dorsal area 46, areas 9 and 10), and the caudal part to the caudal region of the lateral prefrontal cortex (areas 46, 8, and 6) (Seltzer and Pandya, 1989a). A majority of these connections is reciprocal in nature. Figure 1.13 roughly illustrates these connections.

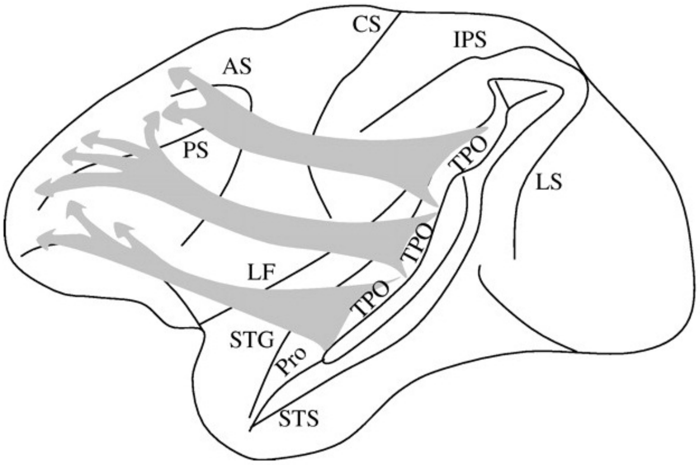


Figure 1.13: **TPO projections to the frontal lobe**. Adapted from Seltzer and Pandya (1989a).

TPO is considered an area near the highest levels of cortical processing, particularly the caudal parts, as the information "flow" is hypothesised to follow the rostral-to-caudal manner, leaving the TPO-4 / TPOc as the terminal area in the hierarchy (Cusick et al., 1995).

Unlike TEa and TEm, TPO contains cells responsive to visual, auditory and even tactile stimuli (Baylis et al., 1987; Beauchamp, 2005; Hein and Knight, 2008). Amongst the cells selective to visual responses, 30% are tuned to moving stimuli, 18% to faces, 6% to other complex stimuli, and 14% to relatively simple stimuli (Baylis et al., 1987).

1.5.3 STS and mirror neurons

STS contains neurons very similar to those in the premotor cortex, especially F5. Both areas contain populations of neurons that appear to encode actions with a certain level of generalisation. Movements that were reported to elicit activity in STS are walking, turning the head, bending the torso, moving the arms, and even responses to implied movement were reported (Jellema and Perrett, 2003). STS neurons also respond to the observation of goal-directed hand movements (Perrett et al., 1990; Rizzolatti and Craighero, 2004), and a large number of cells use an object-centred frame of reference to encode actions with animate objects (Jellema and Perrett, 2006).

The major difference is that unlike premotor neurons, the neurons in STS do not respond to self-executed movement. For that matter, STS is not considered a part of the mirror neuron system. However, due to the fact that STS constitutes the origin of high-order input projected to parietal areas, Gallese et al. (1996) hypothesised that STS might embody the semantic aspect of movement representations, while the F5 would take on the pragmatic aspect. Rizzolatti and Fogassi (2014) later proclaimed STS as the “likely origin of the higher-order visual input necessary for the genesis of mirror neurons in the parieto-frontal circuit”, thus cementing the position of the parieto-frontal mirror network in the centre of their theory and regarding STS as a mere input.

Chapter 2

Mirror neurons in human brain

With the discovery of the mirror neurons in macaques and enunciating them the underlying mechanism of action understanding and imitation, it was only a matter of time before the attention shifted to the human brain. The mirror neurons had introduced new possibilities to answering old questions, and the development during the subsequent years reflected the enthusiasm accordingly, with many scientists fully embracing the mirror mechanism and gradually forming it into one the most prominent theories today.

This chapter presents the mirror neuron system in the context of human research. The first part presents the methods used to study mirror neurons in human subjects and tries to explicate their relevance and limitations. The second part is concerned with the development of the mirror neuron theory after the integration of the results from human studies. I provide a review of the most influential hypotheses together with studies from which they emerged or further provide data in their favour.

2.1 Methods and limitations of human studies

The mirror neurons were discovered in macaques using single-cell or single-unit recordings, a method for measuring the activity of individual neurons that requires a set of special microelectrodes to be implanted directly into the brain. It is therefore not surprising that the research with human subjects had to tackle the problem of finding a different experimental approach that would be suitable for studying the activity of the mirror neurons non-invasively. The first attempt was carried out by Fadiga et al. (1995) who used transcranial magnetic stimulation (TMS) coupled with the recording of motor evoked potentials from the hand, and to their success demonstrated the matching of action execution with observation in human participants. This procedure, together with a few others employing different facilities, is used to this day and this section provides an overview of their use in MNS research.

2.1.1 Transcranial magnetic stimulation

Transcranial magnetic stimulation (TMS) is a non-invasive method of stimulating the brain and the peripheral nervous system by using strong transient magnetic fields to induce currents in the nervous tissue. This method enables painless stimulation of the human brain, both to elicit responses directly and to modify excitability and plasticity of stimulated area, or to even “turn off” a studied area altogether by interfering with its activity to simulate a lesion. Common applications of TMS today aside from research are as a diagnostic or therapeutic tool in various mental or motor system disorders (Barker and Freeston, 2007).

Mechanism of action in MNS research

The TMS uses a coil to generate a magnetic field pulse to in some way influence the activity of a desired area. Although the mechanism is rather straightforward and can be summed up in a sentence, there are several different stimulation protocols that can be exploited by TMS, using magnetic fields of different strength (max. $\sim$1 T), different pulse lengths, or complementing TMS with another device.

In MNS experiments, such as that by Fadiga et al. (1995), TMS is used to excite neural activity in regions of primary motor cortex that control the hand and arm movements. Stimulation of these areas induces a current resulting in involuntary twitches of the hand and arm muscles, amplitude of which can be recorded with electrodes attached over these muscles in the form of motor-evoked potentials (MEP). The MEPs were found being larger when people are observing hand and arm movements, especially object-directed grasping actions, compared to when they observe objects alone. This is thought to arise from mirror neuron activity increasing the excitability of the primary motor cortex.

2.1.2 Functional magnetic resonance imaging

Functional magnetic resonance imaging (fMRI) is a modality used for functional imaging of brain activity based on changes in MRI signal. It is a hemodynamic method that does not require radioisotopes to detect the changes in activity, but instead relies on changes in concentration of oxygenated hemoglobin, arterial tissue perfusion, or blood volume in a target area (Kherlopian et al., 2008; Pan et al., 2011). Functional brain imaging can also be carried out by employing methods of the nuclear medicine, such as positron emission tomography (PET) or single photon-emission computed tomography (SPECT), but due to the need of using a radioactive tracer in measurements, fMRI tends to be favoured for the use in research.

Nature of the measured activity

Blood Oxygenation Level Dependent (BOLD) imaging is the most widely used technique in fMRI imaging. The BOLD signal results from changes in the concentration of deoxyhemoglobin caused by alterations in local blood flow and oxygen consumption, mostly in small capillaries downstream to large draining veins. These changes correlate with increased neural activity in the target brain area (Pan et al., 2011). The MRI detects this activity due to different spin states of oxygen-bound hemoglobin and deoxyhemoglobin, which cause a distinct resonance spectrum to be recorded. Statistical methods can then be employed to construct a parametric image showing higher contrast (1–5% increase in image intensity) in areas activated by a stimulus presentation (Kherlopian et al., 2008).

Drawback of the functional aspect of the measurement using BOLD technique is the limited spatial resolution due to veins draining the sites of activation and large surface vessels also contributing to the recorded signal, causing contamination. Another disadvantage is the slow response time, generally on the order of seconds. Other methods capable of detecting fast dynamics of the brain such as MEG and EEG are therefore often employed in tandem to measure the latency of an evoked response (Ogawa and Sung, 2007).

Relevance for mirror neuron research

Functional imaging is used to explore brain activations for some desired task the subject performs during the scan. It is therefore mostly used to find regional correlations between observing and executing movement, but also cognitive phenomena, such as emotions, empathy, or even sensing a touch (e.g. Keysers et al., 2004; Wicker et al., 2003). The data is then used to make implications between observing and acting, such as that neural mechanisms enabling our own movement or sensations may also underlie their comprehension.

2.1.3 Electroencephalography and magnetoencephalography

Magnetoencephalography (MEG) and electroencephalography (EEG) are non-invasive methods that both measure activity of the same cortical sources employing two different approaches of electromagnetism. While MEG measures the magnetic fields generated by neural activity, EEG measures electrical potentials recorded from the scalp. Unlike PET or fMRI, MEG and EEG do not rely on measuring indirect markers of changes in brain activity, but instead the measured signal directly reflects the fluctuations in postsynaptic currents generated by large populations of cortical neurons (Braeutigam, 2013). Graphical representation of this signal is a waveform representing the changes plotted over time.

Magnetoencephalograph

MEG uses an array of very sensitive magnetometers to measure the subtle magnetic fields (10^{-15}–10^{-12} T) generated by synchronous activity of large cortical neurons from the outside of the head. Magnetometers used in most modern MEG are so called SQUIDs, superconducting quantum interference devices that convert the sub-quanta changes in magnetic flux into voltage changes (Barnes et al., 2010). Depending on the quality of the MEG, up to several hundred SQUID sensors can be mounted in a helmet-shaped recess for simultaneous recording of activity from the whole scalp (Braeutigam, 2013).

Because of high sensitivity of these magnetometers, the MEG is required to be housed in a magnetically shielded room to prevent noise caused by ambient magnetic fields. SQUIDs also require to be cooled by liquid helium to temperatures below -269 degrees Celsius for the measurement not to suffer from thermal noise (Hari and Salmelin, 2012). This causes the operation costs of MEG to vastly exceed those of EEG. The sensors are also sensitive mostly to the sources located tangentially relative to the skull.

On the other hand, magnetic fields are able to pass through the tissue and the skull undistorted, enabling better location of underlying sources. Modern whole-scalp MEG is capable of recording with spatial resolution as low as few millimetres depending on the signal quality and the source model, with temporal resolution of less than 1 ms (Braeutigam, 2013). This enables the MEG to track and relatively accurately localise even the fastest neural processes, making it a very desirable device for research of cognitive functions, such as memory, speech etc.

Electroencephalograph

EEG is recorded using electrodes placed onto the subject's scalp. The electrodes are attached to the scalp directly by the use of adhesive pastes or mounted into a specialised EEG cap worn by the subject. The number of electrodes depends on the EEG system used and ranges between 20 to 256 electrodes (Nunez and Srinivasan, 2007).

EEG recording is usually referential, meaning that the recorded signal represents a potential difference measured between a recording electrode and a reference electrode. The reference electrode essentially represents a "baseline voltage" and its placement might differ with respect to the purpose of the recording. Some of the common placements are ear lobes and mastoids (Niedermeyer and da Silva, 2005).

From technical standpoint, the only advantage of using EEG over MEG is that EEG is sensitive to both tangential and radial sources. Electrical potentials measured from the scalp get attenuated by passing through tissue, meninges, and the skull, lowering the spatial resolution of EEG and the possibility of pinpointing the location of the source. The impedance between the scalp and electrodes also needs to be remedied prior to the measurement to reduce noise.

On the other hand, electrical potentials are relatively easy to detect, thus do not require sensors nearly as expensive to be accurately measured as in the case of MEG. EEG devices are also generally more practical, that is, they do not restrain movement, are relatively portable, and do not need a shielded room to prevent ambient noise (Niedermeyer and da Silva, 2005).

Sources of MEG and EEG signal

An magneto- or electroencephalogram provides a graphic representation of the voltage difference between two cerebral locations plotted over time. The obtained signal is often mistakenly thought to be the sum of action potentials of neurons from a measured area, which is not the case per se.

Action potentials are the result of a depolarisation of a neuron, a violation of its resting state membrane potential of about -70 mV, during which the membrane potential of the neuron rapidly rises, falls, and returns to its resting state. These three events usually happen in no more than couple of milliseconds (Niedermeyer and da Silva, 2005). This time period is too short for active contribution to the recorded signal.

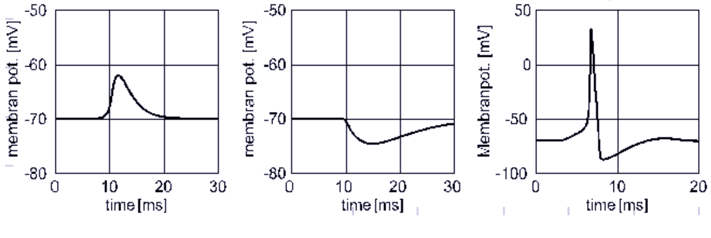


Figure 2.1: **Postsynaptic potentials and action potential.** The change in membrane potential over time following a stimulus. Figure adapted from Natschläger (1998).

When an action potential reaches the axon terminal, it triggers a neurotransmitter release into the synaptic cleft. This, depending on the type of the synapse, induces an excitatory postsynaptic potential (EPSP) or an inhibitory postsynaptic potential (IPSP) on the receiving neuron.

Postsynaptic potentials have a very different character compared to action potentials. Firstly, they last for a significantly longer time periods than action potentials do. When an action potential crosses a synapse, it causes the part of the dendrite on the postsynaptic neuron, where the synapse is located, to become temporarily depolarised or hyperpolarised, depending on whether the synapse is excitatory or inhibitory. This change in polarisation peaks for 1 to 3 milliseconds and then decays exponentially in time for the next 5 to 10 milliseconds (Freeman, 1992). This allows the postsynaptic potentials to appear in a mutually overlapping time, that is, if another action potential arrives to the same synapse, the newly induced postsynaptic potential is summed up with the existing one, resulting in stronger net change in polarisation.

Secondly, postsynaptic potentials involve a rather large membrane surface, considering that the number of synapses on a single neuron reaches hundreds or even thousands (Niedermeyer and da Silva, 2005). The neuron has to integrate the inputs coming through all of its synapses into one value, by summing all EPSPs and IPSPs induced throughout its whole dendritic tree. This causes the neuron to become a dipole with an electrical field. Due to the nature of organisation of neurons in the cerebral cortex, neurons in a single cortical column often share similar receptive fields and are very probable to exhibit similar potentiation. The whole column therefore seemingly creates one large dipole that can then be rather easily measured (Olejniczak, 2006). According to Boutros et al. (2011), about 6 cm^2 of neural tissue is needed to produce a recordable EEG signal.

μ-rhythm as an indicator of the mirror neuron activity

One of the characteristics of the neural tissue is that through the influence of various mechanisms, large populations of neurons are often driven to fire in synchrony, giving rise to neural oscillations, the so called "brain waves". One such oscillatory activity, amongst others, is the μ-rhythm (mu-rhythm), an EEG oscillation typically occurring in 8–13 Hz and 15–25 Hz bands. The μ-rhythm originates in the sensorimotor cortex and is strongest in the absence of movement, for which it is considered to be reflecting the "idling" state of the area (Pineda, 2005). Known since the 1950s without receiving much attention (Gastaut and Bert, 1954), it has recently been revisited by several researchers (Muthukumaraswamy and Johnson, 2004; Oberman et al., 2005; Pineda, 2005) implying its suppression during execution and observation of movement as manifestation of the mirror neuron activity.

2.2 Direct evidence for mirror neurons in human brain

So far all the mentioned methods employed in human studies relied on measurements of large populations of neurons, leaving the conclusions to be drawn only from correlations with what is known from primate studies.

At last, the first and to this day the only direct evidence for existence of mirror neurons in humans was provided by Mukamel et al. (2010). During surgery of 21 patients suffering from pharmacologically intractable epilepsy, the researchers exploited the clinical procedure, in which electrodes needed to be implanted in the patients' brains to identify the source of the seizures, and conducted a single-cell level study not unlike those done with macaques. Because of the criteria of the procedure, the examined cells were not from brain areas normally associated with mirror neuron activity. Instead, areas of the medial frontal and temporal cortex were examined, including supplementary motor area, anterior cingulate gyrus, and the areas of the limbic system.

The patients were shown video clips of hand grasping actions and facial emotional expressions, and were also asked to perform these actions and expressions themselves. Substantial proportions of cells were found to respond to execution (∼23%), observation (∼17%), and execution-observation matching (∼8%) in all examined areas. Due to their functional diversity, it was concluded that the precise role of the mirror neurons varies according to their location, encompassing movement initiation and sequencing, memory recollection, and emotions such as fear and disgust.

2.3 Functions of the human mirror neuron system

The introduction of experimental paradigms for human MNS research led to an exponential increase in publications concerned with mirror neurons throughout the first decade of this century, most of them utilising methods described in previous sections. The same essentially happened with hypotheses of their putative function. The extrapolation on the human brain with its advanced cognitive capabilities led to the coining of several influential theories, which sparked new discussions and rekindled old ones among fields ranging from neuroscience, through linguistics, to philosophy. An overview of the most prominent theories will be the topic of this section.

2.3.1 Action, goal and intention understanding

In accordance with the findings in macaques, the role of mirror neurons in goal-oriented action understanding was also implied in humans, but under the influence of the accumulating data, the theory became more elaborate. Imaging studies have localised the human MNS to brain regions of the parieto-frontal system corresponding to those in macaques (Decety et al., 1997; Rizzolatti et al., 1996b; Grafton et al., 1996). However, unlike in monkeys, numerous studies reported human MNS sensitive to observation of individual, intransitive movements (Fadiga et al., 1995; Lui et al., 2008; Maeda et al., 2002; Oberman et al., 2007b).

This led to the proposition of the *direct-matching hypothesis* by Rizzolatti (2001) that holding that we *understand actions of others* by mapping the visual representation of the observed action onto *our motor representation* of the same action. The coupling of a perceptual representation to a motor representation is not mediated by higher cognitive functions, and takes place in form of the *motor resonance.* This view puts the motor system into a central role in perception, unlike the rivalling visual hypothesis, stating that understanding is based on a visual analysis of the elements that form an action.

Rizzolatti (2001) tried to prove his point through the study by Umiltà et al. (2001), who tested whether hand/object interaction is necessary to evoke a response of mirror neurons in macaques. The monkeys observed an action in two conditions, full view and hidden view. In full view, the monkey observed an object-directed motor act. In hidden view however, the crucial part of the act, the interaction with the object, was hidden from the monkey. Nevertheless, mirror neurons were found firing in both conditions, and it was concluded that the monkey can infer the goal of an action, even when the visual information about it is incomplete, thus understands the action through motor resonance.

The direct-matching hypothesis was further developed as to reflect a so-called *understanding from the inside* (Rizzolatti and Sinigaglia, 2010; Sinigaglia and Rizzolatti, 2011), to account for theoretical problems with understanding actions not in one's motor repertoire. The concept is based on assumption that understanding of any action is possible through the visual analysis, but only having a motor representation of an action can lead to "deeper" understanding.

Evidence supporting this reportedly comes from a functional study by Buccino et al. (2004a), in which participants were presented with video clips of actions that did or did not belong into their motor repertoire, such as dog biting and dog barking, respectively. The study found out that actions from the human repertoire engaged principally the parieto-frontal network, while those outside it caused activity in superior temporal sulcus.

Another line of evidence is provided by a study examining the ability of expert basketball players to predict the outcome of an observed "free throw" (Aglioti et al., 2008), reporting that their predictions were superior to that of both novices and expert watchers, even being able to predict the outcome before the ball left the observed shooter's hands. A different approach was taken in a study by Casile and Giese (2006), who reported that non-visual motor training, i.e. learning a novel movement while blindfolded and relying only on verbal and haptic feedback, leads to improved visual recognition of this movement from a point-light display stimulus, promoting the notion that the recognition comes from the inner understanding of the movement.

The capability of mirror neurons to not only subserve understanding of an action, but also its intention, stemmed from an fMRI study by Iacoboni et al. (2005). In their experiment, participants observed three scenes representing three conditions – a hand grasping a mug without a context (action condition), a scene containing "afternoon tea" objects (context condition), and a grasping hand actions performed in two different contexts, either to drink or to clean up (intention condition). What they found was that the intention condition induced stronger activations in right caudal inferior frontal gyrus and ventral premotor cortex than the other two conditions, and concluded that the regions must reflect the intention of the otherwise identical action. Several subsequent studies cemented this position (Cattaneo et al., 2007; Hamilton and Grafton, 2008).

2.3.2 Imitation

Jeannerod (1994) was amongst the first to hint the role of mirror neurons in imitation, however imitation is a rather broad term that can in itself encompass several behaviours. Moreover, it is not regarded as equal in humans and monkeys, some even go as far as to say that monkeys do not imitate (Iacoboni, 2009a; Rizzolatti and Craighero, 2004). With this in mind, the approach taken by Rizzolatti (2001) in one of the earlier reviews was by referring to the *response facilitation*, which in his words is an "automatic tendency to reproduce an observed movement", and can take place with or without understanding. Hence the response facilitation with understanding is exemplified by imitative behaviour of an adult human, and without understanding concerns most other species.

The involvement of the MNS in imitation was examined by Iacoboni et al. (1999) using an fMRI experiment, in which participants were tasked to observe and imitate a finger movement presented in a video. The movements were indicated either by an actual finger movement of a model actor or a visual cue presented in the video (for clarity see Figure 2.2). Of principal interest was the comparison between brain activity elicited during trials where the participant imitated the movement as a response to observing it and those where it was indicated by the cue. The results showed that imitating a movement upon seeing it causes significantly higher activation in inferior frontal gyrus, the right anterior parietal area, the right parietal operculum, all of them being putative mirror areas.

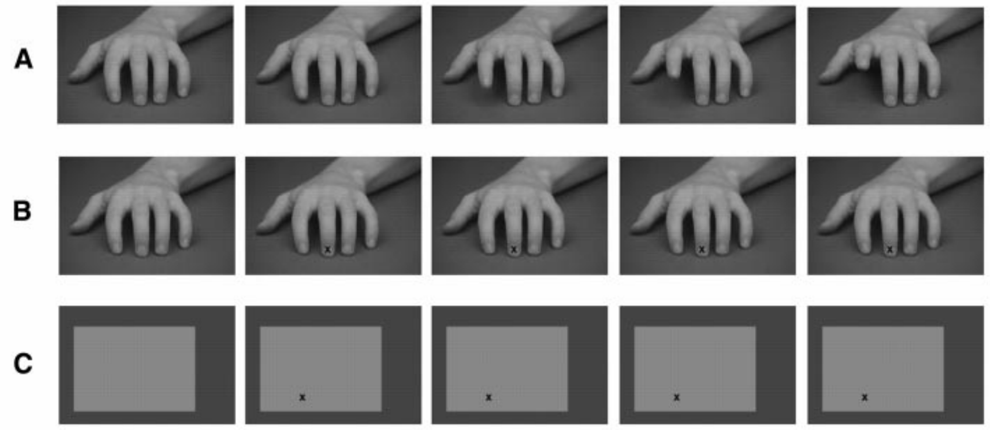


Figure 2.2: **Stimuli used in the fMRI study by Iacoboni et al. (1999)**. (A) a video of a finger movement executed by an actor, (B) motionless hand of an actor with the appropriate finger movement indicated by a cross cue on the middle finger, (C) image of a grey rectangle with only the cue present, indicating the movement based on its position - left for index, right for middle finger.

Similar results were replicated by subsequent studies, however, whether the activity is lateralised to certain hemisphere or exhibited bilaterally is a matter of a discussion. A meta-analysis of 139 fMRI studies (Caspers et al., 2010) on this topic revealed multiple reports of conflicting evidence. However, the authors argue that the data seem to favour bilateral activation.

A related subject to imitation is the observational, or the imitation learning, rooted in the early social learning theories of Bandura (1963), for which the mirror neurons seemingly provide the ideal neural substrate. A study by Buccino et al. (2004b) addressed this by means of an fMRI experiment that involved teaching participants with no prior experience playing the guitar to play a chord by imitating an expert player. Similarly to the results of Iacoboni et al., their data indicated the correspondence of brain areas responsible for new motor pattern formation with mirror neuron regions.

2.3.3 Language

Involvement of the mirror neurons in evolution and production of language is mostly based on the assumption that the Broca's area, the speech production centre of a human brain, is a putative homologue of monkey F5 area (Rizzolatti and Arbib, 1998). The exact idea varies from author to author, but the general notion posits that language evolved by exploiting the multi-modal character of the sensorimotor system, driving a progressive transition of simple goal-directed movements and mouth ingestive actions to patterns of communicative gestures, which ultimately developed into vocal expressions carrying abstract meaning (Arbib, 2005; Gallese and Lakoff, 2005; Rizzolatti and Arbib, 1998; Rizzolatti et al., 2014).

Research into involvement of motor and, for that matter, mirror areas in language comprehension is quite extensive and a subject to heated discussions. Several lines of evidence seem to support the motor-centric views.

In a TMS study, Meister et al. (2003) found out that the excitability of left hemisphere motor areas corresponding to hands is increased while reading and speaking. No speech-related change in excitability was reported in areas corresponding to legs.

Similar results came from numerous fMRI studies demonstrating that reading (Hauk et al., 2004; Pulvermüller, 2005) and hearing (Raposo et al., 2009) action words elicits a roughly somatotopically organized activity in premotor and primary motor areas.

Last but not least, even studies employing EEG or MEG confirmed these findings, reporting onset of very early somatotopic activations in the motor cortex in response to spoken verbs and nouns (Dalla Volta et al., 2014; Shtyrov et al., 2014).

2.3.4 Empathy, theory of mind and social cognition

A homologous mechanism to that found for motor resonance was also uncovered for emotional displays, sometimes referred to as limbic or emotional resonance (Decety and Meyer, 2008). Functional studies have revealed several brain areas, in particular the anterior cingulate cortex, anterior insula, and inferior frontal gyrus, to be congruently activated while observing feelings of others, especially pain, fear and disgust (Avenanti et al., 2009; Botvinick et al., 2005; Wicker et al., 2003), but also in secondary somatosensory area representing "sensing" of an observed touch (Ebisch et al., 2008; Keysers et al., 2004). This corroborated the views of several authors suggesting that the mirror matching mechanism bridges the gap between motor cognition and theory of mind through simulation, and thus underlies humans ability to understand, empathise and infer other peoples' mental states (Decety and Jackson, 2004; Gallese and Goldman, 1998; Gallese et al., 2004; Iacoboni, 2009b; Rizzolatti and Fabbri-Destro, 2008).

A fascinating case for emotional resonance is one of a disorder called *mirror touch synaesthesia* (MTS) (Ward and Banissy, 2015). People suffering from MTS *consciously experience* tactile and emotional displays of other people. They are essentially an living *embodiment* of what the emotional resonance researchers are preaching. The disorder hypothesised to stem from anomalies in brain regions responsible for sense of agency or self-identity, such as the temporo-parietal junction (Cioffi et al., 2014; Maistera et al., 2013), banishes the person into a "chameleon-like" personality, causing their mental state to fully reflect the state of peers they are interacting with. At the same time, several social aspects of everyday life become unbearable, such as attending social/sport events or even eating with other people, as the person *feels* as if the tongues of those around were moving in their mouth. A prime example of how empathy can be a double-edged sword.

An exactly opposite problem is believed to be the cause of autism spectrum disorders (ASD). The "*broken mirrors theory*" was proposed by Ramachandran and Oberman (2006) based on their EEG studies (Oberman et al., 2005, 2007b), in which the μ-rhythm of participants suffering from autism was found to get significantly suppressed only during self-performed movement, but not to its observation. The follow-up research further provided support to the notion of dysfunctional mirror neuron system in individuals with ASD (Cattaneo et al., 2007; Iacoboni and Dapretto, 2006; Minio-Paluello et al., 2009).

2.4 Mirrors everywhere

During the last few years, the mirror neurons were also implied as a neural substrate for several less illustrious, nonetheless interesting phenomena. To name a few noteworthy, smoking (Pineda and Oberman, 2006), therapeutic hypnosis (Rossi and Rossi, 2006), contagious yawning (Cooper et al., 2008), predicting the degree of an erection (Mouras et al., 2008), and a personal favourite, self-awareness and sense of agency in dolphins (Herman, 2012), demonstrating dolphins' capability for motor imitation of self-produced and others' behaviours, including that of humans.

Evidently, the mirror neurons have became the missing piece that everyone was looking for. It is quite impossible to mention every single development the mirror neurons have led to, yet it must be obvious that their influence on many fields was profound. And the influence reaches even farther. A quick search on the internet rather nicely illustrates how successful they were in crossing the expert–layman barrier, as evidenced by the sheer number of blogs, talks and news reports telling their story. Even whole books, such as "*Mirrors in the brain*" by Rizzolatti and Sinigaglia (2008) or "*The Empathic Brain*" by Christian Keysers (2011), are now being dedicated exclusively to revealing their importance for life as we know it to everyone.

However, as it always is, there are two sides to every coin. The next chapter takes on discussing the other side, the problems and counterarguments that the mirror neurons face, and which only seldom reach a reader beyond the scientific circle.

Chapter 3

Problems of the mirror theories

Incorporating the data obtained from the human studies with what had already been known from the primate research led to a small theoretical revolution. The new findings have suddenly been dictating the progress in many fields as much as influencing the thinking of many scientists. Most, obviously, embraced the mirror neurons with keen enthusiasm. However, there were also individuals who did not entirely share these feelings and retained a healthy dose of scepticism. Going against the stream is always difficult, but some aspects of the mirror theories did not seem entirely right, and so they started to quibble. Soon, more began to realise that under the glamour of the new discovery there are holes that might undermine the validity of the mirror neurons in several aspects, thus quibbling turned into counterarguments and individuals into an "opposition", which has been leading heated discussions with the mirror neuron proponents to this day.

In this chapter, I present the views of this hypothetical "opposition" that challenge the ingrained claims of the mirror theorists and advocate a different approach to the mirror neurons. I provide a review of the most controversial aspects of the mirror theories, primarily the action understanding and the origin of mirror neurons, and the alternative explanations proposed by their critics.

3.1 Mesmerising mirror neurons

The mirror neurons admittedly possess some "intrinsic charm" that makes them so appealing. Heyes (2010a) called them *mesmerising*, Hickok (2014) chose the word *myth*, but whatever artistic label we use, the simplicity of the mirror neurons essentially allows them to fit into any system in the brain. The state of their research supports this claim quite aptly.

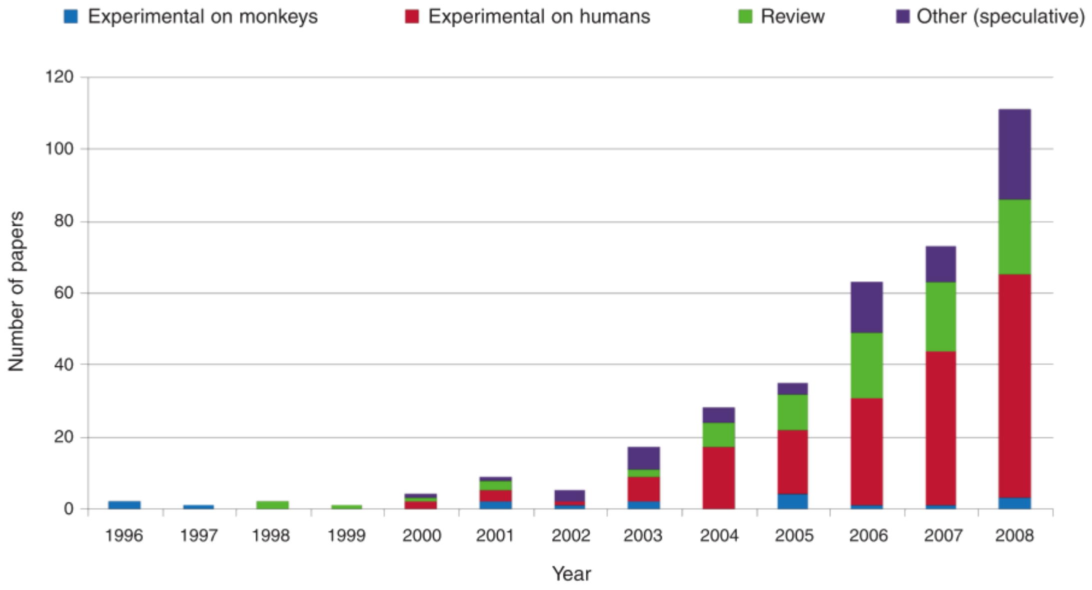


Figure 3.1: **Graph of the growing mirror neuron literature** in years following the pioneering studies of the Parma group. Adapted from Pascolo et al. (2013).

Despite the early and speculative stages of the research, many claims regarding the function of the mirror neurons were rather bold. Bold meant more impact and more impact meant more interest and research. On the one hand, this does not seem like a detriment. On the other, however, an atmosphere full of expectations was created, in which everyone wanted to contribute with a ground-breaking discovery, while most of the existing data rested on the validity and conclusions of only a few pioneering studies. And that reliance on such limited evidence is quite disconcerting. Figure 3.1 presents a graph of the published research on the topic of mirror neurons during the decade or so after their discovery, in which the reliance of the exponentially growing human research on the few original primate studies is quite evident.

Such an argument was posed by Pascolo et al. (2009), who objected that the conclusions of the original Parma studies were not consistent with the measured data. They argued that the responses of the proposed mirror neurons reported in their early studies (di Pellegrino et al., 1992; Rizzolatti et al., 1996a) did not "mirror" the experimenter as much as anticipated his actions, and the measured activity was not a cell-defining property but an epiphenomenon of the activity of a group of neurons observed in a certain time frame. Dinstein et al. (2008) expressed similar concern, stating that the studies were unconvincing because of their qualitative nature, and that they provide little support to the variety of speculative functions attributed to the MNs. In a later essay, Pascolo et al. (2013) even went so far as to doubt the employed experimental methods and criticised the authors for their, and I quote, "over-eagerness to construct a mind theory, even from the earliest experiments".

However, the most shocking claim addresses the integrity of the researchers more than the theory itself. Pascolo et al. (2013) points out a series of figures in the book by Rizzolatti and Sinigaglia (2008), which were adapted from an fMRI study by Buccino et al. (2004a). The figures differ from those in the original study in that the fMRI activation images have had the apparent mirror activity edited and exaggerated in a way that better supports the cause of the authors (see Figure 3.2). Even though the book is basically a one-sided review of MN research aimed at a "casual" reader of scientific literature, such behaviour drastically undermines the credibility of the authors. That is at least my opinion.

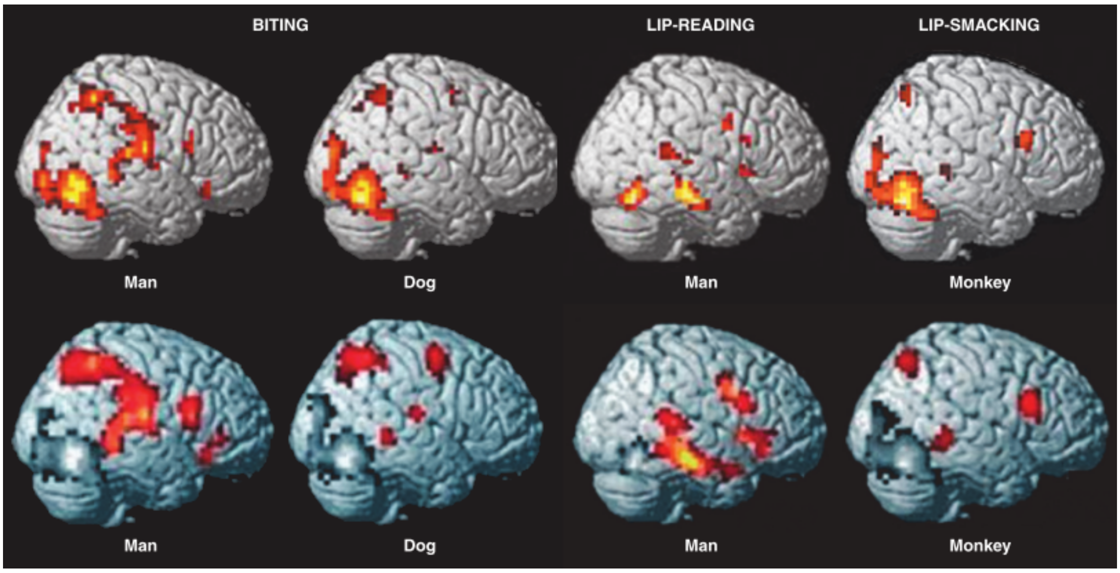


Figure 3.2: **The dishonest fMRI results**. The first row shows the results from the original study by Buccino et al. (2004a), the second row shows corresponding images from the book by Rizzolatti and Sinigaglia (2008). Modified from Pascolo et al. (2013).

The criticism by Pascolo et al. (2009, 2013) is probably the most direct and disapproving amongst all present in this chapter. However, even if they were wrong about the conclusions and methodology of the Parma group, pointing out the rather dishonest attitude of Rizzolatti and Sinigaglia would still remain worth consideration.

3.2 Biases and fallacies

The quote about the over-eagerness from the previous section indirectly raises the topic of biased decisions. The desire to prove a point can sometimes lead to conclusions based more on expectations or an established consensus rather than a rigorous interpretation of data. Such imprudence is not admissible in the scientific method, though it is quite evidently to a certain degree present in numerous MN studies, particularly in the form of confirmation bias – the tendency to interpret one's data based on one's aspirations.

A prime example would be the study by Ferrari et al. (2005), which described a "new type" of premotor MNs termed *tool-responding mirror neurons*. The study was conducted in line with the original macaque experiments and involved a two month period during which two monkeys were trained in execution and observation of goal-directed movements using a tool – either a stick or a pair of pliers. Out of 209 neurons recorded from area F5, about 20% was found to fire in a mirror fashion to the observation of a tool action, with majority preferring the stick. The authors concluded that their findings represent a new population of neurons capable of extending the action understanding ability to actions that are not part of one's motor representation.

There are several lines of evidence, however, pointing towards a different explanation. Hickok (2014) argues that the original studies regarded the unresponsiveness of the F5 mirror neurons to abstract and tool actions as the evidence for their specificity to the monkey's motor repertoire. Furthermore, the large percentage of neurons found responding to the tool use could not have been simply overlooked before, indicating that the extended period of training must have been the principal cause of their emergence. The authors admit that the training formed associations between the hand and the tool, ultimately making the tool an "extension" of the monkey's hand. However they regard this as the inherent function of the F5 neurons that from evolutionary perspective led to the onset of tool use through generalisation of actions such as grasping with a hand to actions employing a tool such as grasping using a pair of pliers. And yet, from what they have reported in the study, it is not clear whether the monkey understood either the tool or the action. After the experiment, one of the monkeys was placed in a cage with a platform that contained a food morsel and a stick, which would enable the monkey to reach the food. An hour-long observation of the monkey's behaviour led to the following statement:

> "During this brief test, the monkey never attempted to use the tool for reaching food, although in the first minutes after the stick was available, the monkey grasped it and bit it. After few minutes, the monkey ignored the stick, trying to take the food by moving the platform."

. Thus despite the fact that the tool-responding mirror neurons were recorded in the monkey's motor repertoire, the post-training behaviour provided no indication that the monkey could apply or understand any aspect of the exercise, ipso facto suggesting quite the opposite. The more cogent explanation would stress the sensorimotor associations trained into the monkey's brain as the prime cause of the observed activity, as pointed out by Hickok (2014).

Another example involves the study by Casile and Giese (2006) mentioned in Chapter 2 that supposedly provides evidence to support understanding from the inside. The objective was to investigate, whether established motor representations influence action perception. To test their hypothesis, they devised an experiment consisting of three phases: a pre-test, a non-visual motor training procedure, and a post-test. The training procedure aimed to teach blindfolded participants a novel motor act by providing them with only verbal and haptic feedback. The pre-test and post-test phases consisted of a discrimination task, in which the participants were presented with video clips of two point-light walkers and had to assess whether their movements were identical. They found out that the participants were better at identifying point-light motor acts they were taught compared to related movements. Here is the conclusion of their study:

> "Our study shows, for the first time, a direct and highly selective influence of novel acquired motor programs on visual action recognition that is independent of visual learning. Moreover, our experiment demonstrates that motor learning, even when it is mediated exclusively by non-visual sensory feedback, seems to influence visual action recognition in a very similar way as motor programs that have been acquired in the presence of visual feedback."

There are several problems with this conclusion. Even though the authors briefly consider other factors, such as motor imagery, they quickly turn to the motor representation as the prime cause of the improvement in recognition. Hickok (2015) again comments, that not only did the authors not give enough attention to the proprioceptive input, they also failed to control the response bias, rendering the finding inexplicable. Furthermore, I would argue that their findings in fact favour the visual theory more than the understanding from the inside. Myriad of studies have investigated recognition of biological, abstract and even point-light movement in association with the STS (Beauchamp, 2005; Grossman et al., 2005; Wurm and Lingnau, 2015). In fact, given the multimodality of STS and its access to tactile stimuli, the results would not even be that surprising. This however, is not considered by the authors and their conclusion is quite apparently based on their beliefs, again illustrating the confirmation bias to the letter.

Many others can be considered making similar mistakes, Aglioti et al. (2008), Fogassi et al. (2005), Michael et al. (2014) and Umiltà et al. (2001), to name a few. Though the point is not to provide an exhaustive list as much as to point out how the results can easily *change* based on one's perspective.

3.3 The meaning of "understanding"

An often mentioned problem surrounding the mirror neurons is the rather arbitrary definition of the term "*understanding*". The early studies *tried* to specify the concept, which they had envisioned to be represented by term "action understanding", as evidenced by the explanation provided by Gallese et al. (1996): "the capacity to recognize that an individual is performing an action, to differentiate this action from others analogous to it, and to use this information in order to act appropriately". However, the authors themselves started to deviate away from this explanation, until it became used interchangeably with recognition, intention or perception amongst other authors, reflecting each author's own interpretation of the term.

Cook et al. (2014) pointed out that the lack of consensus about the exact meaning of action understanding as a concept lead to a prevailing empirical problem that prevents proper examination of its validity. In other words, it is difficult to design an experimental protocol when the concept is only vaguely defined.

The later definitions provided throughout various reviews were often only poetic renditions of the neurophysiological data that simply describe a mirror neuron as a cell that fires both when an individual executes and observes a more or less congruent action, that failed to explain how or why the mirror neurons themselves give rise to understanding. Yet they were already presumed being the basis of it (Rizzolatti, 2001; Rizzolatti and Craighero, 2004). The situation did not change with the introduction of "understanding from the inside" (Rizzolatti and Sinigaglia, 2010; Sinigaglia and Rizzolatti, 2011), which Hickok (2015, 2014) considered a weakening of the original theory, proposed as a workaround for the problem of understanding actions outside of one's motor vocabulary. The difference is in that unfamiliar actions are supposedly "understood" primarily visually, engaging the temporal areas, while the parieto-frontal motor resonance is what "understands" existing motor representations (see Buccino et al., 2004a). This however opens a question why would such duality be needed, which is further discussed in the following section.

3.4 Doubts about the mirror neurons

The mirror neuron theories remained virtually unopposed until the late 2000s when Hickok (2009) published his "Eight problems for the mirror neuron theory of action understanding in monkeys and humans". The paper became one of the most downloaded publications from the *Journal of Cognitive Neuroscience* and essentially triggered the wave of discussions and criticism of the mirror neurons and their function that remain topical to this day. This section briefly reviews the counterarguments of the mirror neuron opponents and the research that supports their claims.

3.4.1 Action understanding

Action understanding is without a doubt the most controversial of all putative mirror neuron functions. A part of the controversy is credited to the already mentioned lack of consensus on what the term even signifies, the other rests on the fact that the motor resonance is built upon the activity engaging vast neural populations from several parts of the brain, thus making it easy for the proponents to ascribe it to the mirror neurons and difficult to the opponents to disprove or examine it through lesion studies.

However, reviews (Csibra, 2008; Hickok, 2009, 2014; Kilner, 2011; Mahon and Caramazza, 2008) of the limited data provided by the empirical studies examining the MNS contribution to action understanding indicate only a minor, if any, role instead of a primary one as proposed by Rizzolatti and Craighero (2004).

According to Csibra (2008), understanding cannot be achieved merely by the means of motor resonance. The understanding therefore does not represent the output of the MNs, but instead their input, which they only reflect. The following statement aptly sums up his logic:

> “All these findings reflect a tension between two conflicting claims about action mirroring implied by the direct-matching hypothesis: the claim that action mirroring reflects low-level resonance mechanisms, and the claim that it reflects high-level action understanding. The tension arises from the fact that the more it seems that mirroring is nothing else but faithful duplication of observed actions, the less evidence it provides for action understanding; and the more mirroring represents high-level interpretation of the observed actions, the less evidence it provides that this interpretation is generated by low-level motor duplication.”

Hickok (2009) similarly argues that there is no sound evidence supporting the claim that the MNs enable action understanding neither in monkeys nor humans. In fact, the data suggest quite the opposite. Several studies (Catmur et al., 2007; Press et al., 2012) reported success in “reprogramming” the mirror activity, thus indicating that the MNs not only dissociate from understanding, but are quite malleable. Hickok (2009) further points out that even Rizzolatti and Craighero (2004) admit that the MNs might not be the only mechanism underlying action understanding, which paradoxically diminishes their own view of their evolutionary importance. Instead, Hickok and Hauser (2010) provide an alternative view, in which they claim the MNs to represent a general mechanism aiding in action selection, and propose the action understanding to take place in temporal areas. Centralising the understanding to the areas such as STS and MT is becoming quite strongly supported by recent findings (Sokolov et al., 2012; Suzuki et al., 2013; Wurm and Lingnau, 2015; Wyk et al., 2009).

Hickok (2015, 2014) also argues against the understanding from the inside, as having essentially no real impact on comprehension. Using the data from a study by Michael et al. (2014), who reported disruption in comprehension of hand or lip movements in response to hand or lip area TMS, he plotted the change in comprehension that is supposed to signify the understanding from the inside (see Figure 3.3). Numerically, the effect represented 1–2%, a value only hardly compatible with "understanding".

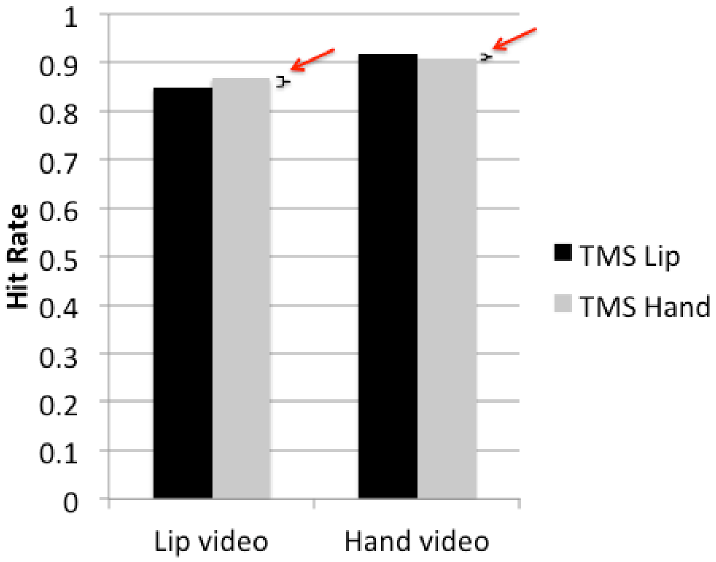


Figure 3.3: **Understanding from the inside** as reported by Michael et al. (2014). Adapted from Hickok (2015).

3.4.2 Speech perception

The function of mirror neurons in speech perception proposed by Rizzolatti and Arbib (1998) is loosely based on the motor theory of speech perception by Liberman et al. (1967), which was for a long time abandoned and revisited only because of the MNs. Hickok (2014) provides a heated critique of this theory throughout his book and in several publications (Gallese et al., 2011; Hickok, 2009), discussing at length the invalidity and strong evidence against it.

3.4.3 Other problems

Many other implications of the mirror neurons are criticised, often for similar trespasses as in the case of action understanding. The first lines from an article by Spaulding (2013) basically reflect what was already said: “Mirror neurons are widely regarded as an important key to social cognition. Despite such wide agreement, there is very little consensus on how or why they are important”. Though in this case the lack of consensus does not concern understanding, but social cognition. Others criticise the over-simplicity and inconsistency of the broken mirror hypothesis of autism (Fan et al., 2010; Hamilton, 2009) and call for its revision.

3.5 Origin of mirror neurons

How did the mirror neurons come to be? That is yet another topic of heated discussions. The two principal accounts are the *adaptation hypothesis* and *association hypothesis*, complemented with several hybrid opinions attempting to reconcile these two accounts.

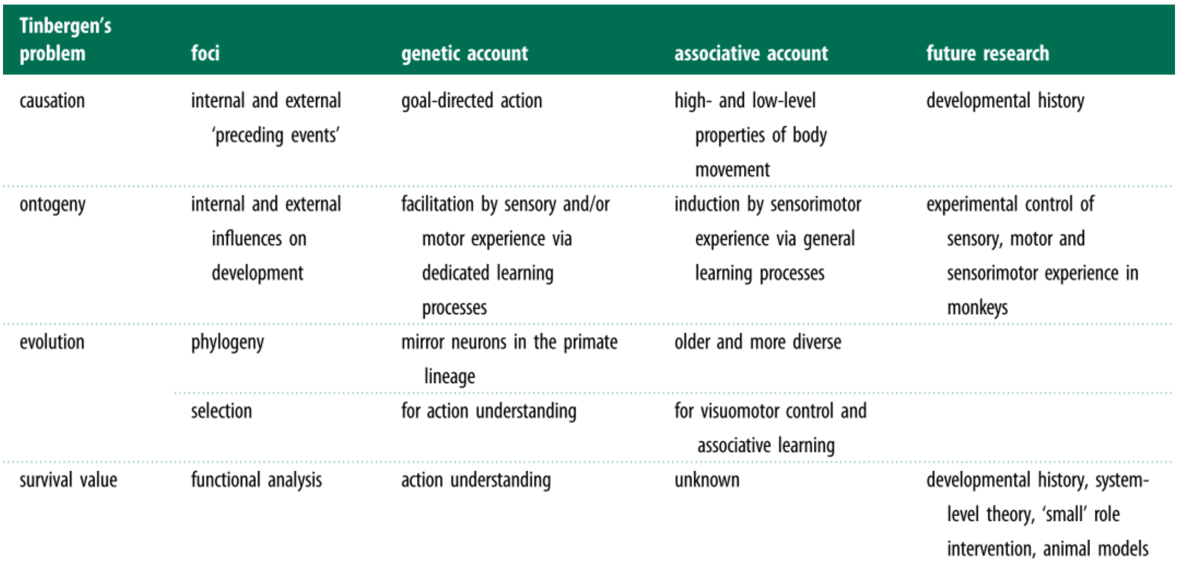
3.5.1 Adaptation hypothesis

The adaptation hypothesis stemmed implicitly from the functional properties attributed to the mirror neurons. Their proponents considered the MNs to be genetically predisposed to match perceived and executed actions, and thus give rise to their understanding (Rizzolatti and Arbib, 1998; Rizzolatti and Craighero, 2004). The adaptation hypothesis suggests that the MNs became genetically universal through natural selection, and that experience plays a relatively minor, tuning or facilitative role in their development (Heyes, 2014).

3.5.2 Association hypothesis

The association hypothesis renounces the evolutionary significance of mirror neurons and identifies them as motor neurons endowed with matching properties forged through correlated experience of observing and executing the same action. The neurons are not predetermined to any specific purpose but instead acquire and adapt their mirror properties through the process of associative learning during the course of individual development. Thus the mirroring reflects the past experience of the individual (Cook et al., 2014; Heyes, 2001).

The MNs are therefore not a genetic adaptation for action understanding or, for that matter, any other social cognitive function. However, they may enable a variety of beneficial effects. Evidence in favour of the associative hypothesis comes from a series of experiments showing that sensorimotor experience can enhance, abolish or reverse MN activation in human subjects (Heyes, 2010b). Press et al. (2012) were even able to "train" the hand area MNs to respond to observation of arbitrary geometric shapes.



Tinbergen's problem	foci	genetic account	associative account	future research
causation	internal and external 'preceding events'	goal-directed action	high- and low-level properties of body movement	developmental history
ontogeny	internal and external influences on development	facilitation by sensory and/or motor experience via dedicated learning processes	induction by sensorimotor experience via general learning processes	experimental control of sensory, motor and sensorimotor experience in monkeys
evolution	phylogeny	mirror neurons in the primate lineage	older and more diverse	
	selection	for action understanding	for visuomotor control and associative learning	
survival value	functional analysis	action understanding	unknown	developmental history, system-level theory, 'small' role intervention, animal models

Figure 3.4: **Comparison of adaptive and associative accounts** of mirror neuron development posed against Tinbergen's four problems. Adapted from Heyes (2014).

3.5.3 Hybrid accounts

Keysers and Perrett (2004) proposed the mirror neurons to arise from the interconnectivity of the "major mirror areas", i.e. F5, PF and STS, shaped by virtue of Hebbian learning, and *canalized* by genetically predisposed features of this system, such as including the tendency of infants to look at their own hands during motion (Giudice et al., 2009). Cook et al. (2014) consider this view in essence identical to their association hypothesis, given that the Hebbian learning entails both contiguity – the closer the two events occur in time, the stronger the association – and contingency – the correlation or predictive relationship between the two events.

A different approach by Arbib (2005) named *exaptation* is based on "some" special kind of sensorimotor learning, which receives input from self-observation of hand motion. It evolved from a more domain–general mechanism to promote action understanding through the production of mirror neurons. It suggests that some extra structure is required that enables the coding of goals or hand–object associations.

3.6 Remedies for the situation

In a fairly recent paper, Heyes (2013) proposed three changes in approach to the MNs that might lead to solid progress regarding their origin as well as function. Firstly, she suggests that researchers should report the developmental history of their subjects, that is experience with the actions for which MNs are being tested. If the MNs after all were a genetic adaptation, their properties should remain relatively invariant across developmental environments, making it possible to infer species-typical properties of the MNs. However, if MNs were a product of associative learning instead, this kind of inference would not be valid as all will primarily depend on the sensorimotor experience received by the individual in the course of their development.

Secondly, she calls for a system-level theory that would specify what and how do the MNs do, to enable a clear distinction from other components of the mechanism they are a part of, and dispose of the ambiguous terminology that stemmed from years of speculations.

Lastly, she advocates conducting intervention experiments, focused not only on recording the immediate properties of the MNs, but also examining their relevance to behavioural competence. In other words, testing whether animals with MNs for certain actions are better than other animals of the same species at discrimination or at imitating these actions.

Such studies have been previously dismissed as impractical, however, she suggests that it may be possible remedy this by establishing a rodent model, which is according to Takano and Ukezono (2014) already forthcoming.

Chapter 4

A different look at the mirror neurons

The main objective of the preceding chapters was to review the data published in both recent and original Parma studies, whether regarding the structure of the primate action observation–execution network, its parts involved in the mirror neuron system, or its features and problems. The goal of this chapter is to dedicate the few paragraphs to providing an outlook I acquired while working through the literature and spending some time reflecting on the ideas I had encountered.

I derive my ideas from reinterpretations of other studies, combined with my experience from human EEG experiments, and entwined into my own concepts for architecture of an action observation–execution system. I therefore do not claim to be the bearer of ultimate truth, but instead intend to provide an alternative to the mainstream view that does not place the mirror neurons into the centre of all things, and shows appreciation for the complexity of the brain. Although more complicated, it might be capable to rather simply embody everything the mirror neuron theorists are claiming the mirror neuron system to be.

The first part of this chapter mostly reflects my concerns and frustrations regarding the vagueness and bias that surrounds the mirror neurons. Following that, I provide a brief overview of an original EEG study, and describe the different approaches to the interpretation of neuropsychological results both in favour and against the MNS. The concluding part of the chapter presents my explanations for the roles of the parieto-frontal circuits and resonance mechanisms.

4.1 What are the mirror neurons?

The functional properties of the mirror neurons have been described at length throughout the previous chapters. What was not is the “cellular identity” of these cells. I was very interested in learning what kind of cells the mirror neurons are, which cortical layers usually contain them, if they belong to cortical interneurons or pyramidals, whether they share connections mainly inside a cortical column or rather project to, or receive from, other cortical areas, and so forth. Answers to these questions, to my disappointment, were not easy to find.

I cannot say, whether that is because of the presumption that the MNs are simply dispersed throughout the cortex and intermingled amongst "common" neurons, but for me it means that we basically do not know exactly what we are dealing with and consider any motor neuron that fires during execution and observation of a movement a mirror neuron. Is it a problem for the mirror theory? Probably not. But it shows us that the theory is willing to accept and expand based only on this simple condition, the same way as it did with the primary motor cortex, which was originally a control method against covert movement, and now is a part of an "extended" MNS (Kraskov et al., 2014). This raises several questions.

4.1.1 Functional equivalence

First off all, are all mirror neurons functionally equivalent regardless of their location? The studies by the UCL Institute of Neurology that found pyramidal tract mirror neurons in both F5 and M1 (Kraskov et al., 2009, 2014; Vigneswaran et al., 2013) reported roughly half of MNs in both areas to be projecting to the spine. That is half of the "understanding from the inside" going down the corticospinal tract to ultimately end by failing to excite a lower motor neuron. On one hand, this might explain what is causing the change in TMS induced MEPs usually measured in human experiments. Instead of the activation of premotor mirror neurons raising the excitability of the motor cortex as hypothesised by Fadiga et al. (1995), the change happens directly at the spinal motor neurons. On the other hand, this clearly deviates from common explanations for the MN activity. Even if we were to consider this as a demonstration of die-hard embodiment, explanations such as motor priming might be more plausible.

The UCL researchers also reported a subgroup of "suppression mirror neurons" that were mentioned on several occasions in Chapter 1. They hypothesised that these MNs are involved in the withholding of unwanted movement during action observation, which in my opinion makes little sense. The cells they measured were the large pyramidal neurons located in cortical layer V. These cells are one of the largest neurons in the cerebral cortex, in case of M1 *the* largest also known as Betz cells. These neurons possess large, heavily myelinated axons that send collaterals into the surrounding cortex, inhibiting the adjacent cells and thus "sharpening" their own excitatory influence on the lower motor neurons (Guyton and Hall, 2006). This feature might by itself provide a plausible explanation for the behaviour of suppression MNs. Here is a simplified example how: during actual movement, two neighbouring Betz cells receive enough cortical and subcortical excitation to overcome each other's collateral suppression and fire, but during observation, the excitatory signal is weaker probably because of milder subcortical input, and sufficient to excite only one of the cells, inadvertently causing the inhibition of the other. The fact that suppression MNs have not yet been seen amongst neurons without projections to the corticospinal tract further adds to the credibility of this explanation.

4.1.2 Mirrors everywhere

Secondly, if the mirror neurons are indistinguishable from any other neuron without the observation of their activity, how can we confidently tell that not all neurons in classical MNS areas are in fact mirror neurons? Figure 4.1 contains a table taken from the review by Kilner and Lemon (2013) showing that in 14 studies of the F5 MNs, the reported number of MNs varied approximately from 10 to 50%. Is such variance a consequence of each monkey possessing different amount of MNs in its brain, unfortunate choice of neurons to measure, or the parameters of each experiment? Probably a bit of each, but I would argue that it is mostly the mix of the latter two.

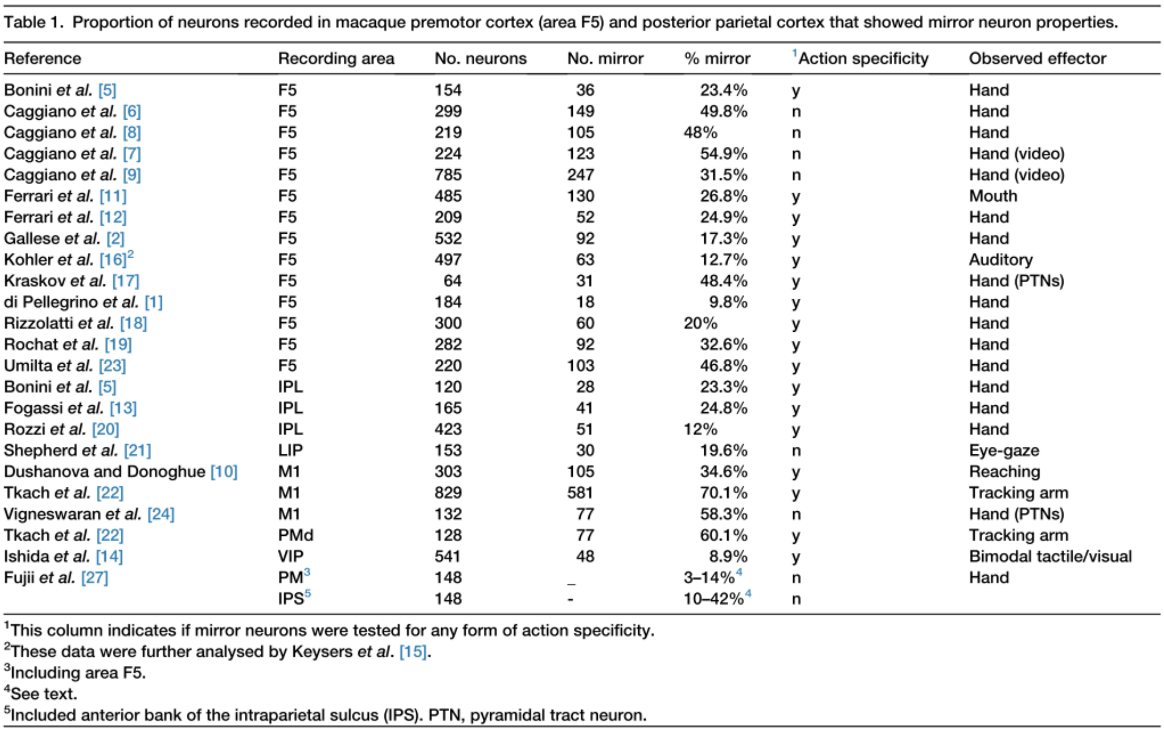


Table 1. Proportion of neurons recorded in macaque premotor cortex (area F5) and posterior parietal cortex that showed mirror neuron properties.

Reference	Recording area	No. neurons	No. mirror	% mirror	[1]Action specificity	Observed effector
Bonini *et al.* [5]	F5	154	36	23.4%	y	Hand
Caggiano *et al.* [6]	F5	299	149	49.8%	n	Hand
Caggiano *et al.* [8]	F5	219	105	48%	n	Hand
Caggiano *et al.* [7]	F5	224	123	54.9%	n	Hand (video)
Caggiano *et al.* [9]	F5	785	247	31.5%	n	Hand (video)
Ferrari *et al.* [11]	F5	485	130	26.8%	y	Mouth
Ferrari *et al.* [12]	F5	209	52	24.9%	y	Hand
Gallese *et al.* [2]	F5	532	92	17.3%	y	Hand
Kohler *et al.* [16][2]	F5	497	63	12.7%	y	Auditory
Kraskov *et al.* [17]	F5	64	31	48.4%	y	Hand (PTNs)
di Pellegrino *et al.* [1]	F5	184	18	9.8%	y	Hand
Rizzolatti *et al.* [18]	F5	300	60	20%	y	Hand
Rochat *et al.* [19]	F5	282	92	32.6%	y	Hand
Umilta *et al.* [23]	F5	220	103	46.8%	y	Hand
Bonini *et al.* [5]	IPL	120	28	23.3%	y	Hand
Fogassi *et al.* [13]	IPL	165	41	24.8%	y	Hand
Rozzi *et al.* [20]	IPL	423	51	12%	y	Hand
Shepherd *et al.* [21]	LIP	153	30	19.6%	n	Eye-gaze
Dushanova and Donoghue [10]	M1	303	105	34.6%	y	Reaching
Tkach *et al.* [22]	M1	829	581	70.1%	y	Tracking arm
Vigneswaran *et al.* [24]	M1	132	77	58.3%	n	Hand (PTNs)
Tkach *et al.* [22]	PMd	128	77	60.1%	y	Tracking arm
Ishida *et al.* [14]	VIP	541	48	8.9%	y	Bimodal tactile/visual
Fujii *et al.* [27]	PM[3]	148	_	3–14%[4]	n	Hand
	IPS[5]	148	-	10–42%[4]	n	

[1] This column indicates if mirror neurons were tested for any form of action specificity.
[2] These data were further analysed by Keysers *et al.* [15].
[3] Including area F5.
[4] See text.
[5] Included anterior bank of the intraparietal sulcus (IPS). PTN, pyramidal tract neuron.

Figure 4.1: **Proportions of mirror neurons** recorded in macaque brain. Table adapted from Kilner and Lemon (2013).

Consider an experiment, where based on the somatotopy of the area F5, we choose such a location for the insertion of electrodes that half of the cells represent hand movements and the other half mouth movements. Now if we were to explore the effects of different hand grips on the neural activity, half of the neurons in our population could not be MNs right away, as they only become active during mouth movements. In a less exaggerated scenario, let us choose a location representing only the hand and study four different hand grips. This time we report 50% of the neurons as MNs and proclaim majority of them as broadly congruent. This is much closer to real data, but the problem from the first instance persists – just because our four grip types did not activate half of the neurons, we cannot conclusively proclaim them non-mirror. In fact, I doubt there is a way to exhaustively test for all possible movements that F5 cells might code. However, if the mirror neurons are to subserve action understanding, recognition, or to reflect our intentions, then as a result even the most obscure motor behaviour should be represented by a mirror representation, and by the virtue of "use it or lose it" every neuron should participate in coding of at least one motor act.

This all subtly points to the conclusion that what we observe as mirror neuron activity might be less about the neurons and more about the activity. The neurons themselves are in no way different or specialised to be causal in any higher cognitive function, and their existence is nothing more than an epiphenomenon caused by the information flow between cortical areas of different modalities. I therefore argue that the concept of mirror neurons is irrelevant to the whole framework and poses an unnecessary restriction by inherently rendering any non-motor area an outsider, a mere contributor to the mirror system. My point is not to cynically diminish or reject any role of motor resonance in the brain, quite the opposite, but unfortunately that is exactly what the mirror neurons are doing to other brain mechanisms, while at the same time, they provide no tangible answers to any of the functions they are proclaimed to underlie.

A clear answer to my first question can actually be found in a review of Greg Hickok's book by Rizzolatti and Sinigaglia (2015). Their description of the mirror neuron system is as follows:

> *The mirror mechanism is a very general, widespread mechanism transforming sensory information into a motor format. According to where neurons endowed with this mechanism are located, their functions change.*

So in other words, the mirror neurons are everywhere, can do everything, and their principal feature is that of a translator. This basically describes the purpose of the whole brain, which is exactly my point. We observe the mirror neurons because a part of the brain is resonating with the observed experience, not the other way around.

The neuron therefore is the consequence, not the cause, and cannot possibly be the explanation for the phenomenon it is partaking in. At most, it can stay true to its name and *reflect* what is being sent to it.

4.2 Is mirroring really that special?

From a theoretical standpoint, the mirror neurons are considered to be a possible neural implementation of the *common coding theory* (Prinz, 1997). The central idea of this theory claims that perception and action share a common representational domain. Actions are coded in terms of perceptual effects they should produce upon being carried out and are thus directly linked to perception of them. Moreover, because of this link, perceiving an action automatically activates its representation, given that one is able to perform this action.

This provides a theoretical framework into which motor resonance fits almost perfectly, both in terms of intrapersonal and interpersonal resonance (Uithol et al., 2011). The more closely an observed action maps onto one's own motor representations, the more deeper and accurate will his recognition, understanding and prediction of the course and the goal of the action be. The ambiguity of the definitions surrounding this concept were discussed in Chapter 3. The motor resonance therefore stands on the details. A crude representation will resonate, but a better matching representation will resonate more. When reduced to the notion that the MNs are the cause of the resonance, an inconsistency emerges.

The spectacle of the mirror neurons comes largely from the fact that they reflect the most apparent part of an observed motor behaviour, that is the motion itself. Unlike other parieto-frontal circuits that seem to be providing less evident, nonetheless equally important details to the motor cortex as described in Chapter 1, the mirror neurons are the heralds of something easily identifiable happening right in front of us, such as "he is picking up a cup!" or maybe "he is smiling!". The finer details of such action are of lesser concern to the mirror neurons – after all, the broadly congruent MNs are the most numerous (Kilner and Lemon, 2013). To claim then that the MNs provide the ground for the motor resonance, and in doing so preserve the "depth" of the direct matching onto one's motor vocabulary, the activity of all parieto-frontal circuits partaking in this visuomotor transformation has to be generalised to the notion of mirror neuron activity.

Again, I have no quarrel with the resonance, even though my opinion on what it signifies differs from the one described, however, I find the oversimplification of the involved mechanisms bothersome. The mirror neurons more resemble a theory, not a neural substrate to instantiate one. This in my opinion unwittingly creates an illusion of mirror neurons taking precedence over other cortical mechanisms, a bias based on the overall semblance of the movement or its goal as representing a feat of higher significance, which the other cortical circuits only further refine. It is then easy to succumb to speculations that overlook the contributions from outside of the MNS and entitle the mirror neurons with praises such as "*the basis of*", "*fundamental in*" or "*crucial for*", followed by a number of complex cognitive functions.

This is especially unsettling in the case of distinguished scientists such as Rizzolatti and Ramachandran, whose claims of the mirror neurons being cells "*of great evolutionary importance*" (Rizzolatti and Craighero, 2004) that had "*shaped the civilisation*" (Ramachandran, 2009), are without any sound evidence for *how* they accomplished that blatantly fuelling the hype surrounding them. We must not be oblivious to the fact that mirror neurons were discovered in Old world monkeys, and were additionally reported in marmosets (Suzuki et al., 2013), birds (Keller and Hahnloser, 2009), with rats most probably following in the close future (Takano and Ukezono, 2014). Furthermore, the behaviour and functions they supposedly enable simply through motor resonance, are by no means as uncommon in animal kingdom, as is generally thought.

Hickok (2014, Chapter 8) provides a list of several species in which social imitative behaviour was observed, amongst others dogs, bats or bottlenose dolphins. He also describes a case of Kyoto macaques that have developed "*stone-play behaviours*", a set of behaviours ranging from gathering, piling, or clacking stones, to cuddling or rolling in them in hands. At the time the behaviour was "invented" by a single juvenile female, it initially only spread across her peers, but later after having their own offspring was passed down to these young members of the group.

A fairly recent study by Bartal et al. (2011) has provided some intriguing data on "empathetic" behaviour in rats. In their experiment two rats were placed in an arena, one rat was being restrained in a cage placed in the middle of the arena that could be opened from the outside, the other rat was free to wander around. After a few sessions, the free rat learned to open the cage for the restrained companion and kept doing so in decreasing time periods in the following sessions. Moreover, if posed with a choice between releasing the other rat or opening a cage full of treats, the free rat prioritised releasing the restrained companion and even shared the treats with the released rat afterwards. In control conditions, the free rat did not open empty or object-containing cages in any significant manner. I have had the pleasure to briefly discuss this experiment with professor Mason during one of her courses, and have seen a number of videos from this and several other experiments of their group. I must say, that in a stressful situation like this, the rats were not only helping each other on purpose, but the free rats seemed to have been repeatedly "*comforting*" the caged companions. I am willing to go as far as to say that there are human individuals that would rather keep the food for themselves or dissociate from the situation and ignore the caged compatriot in accord with the Bystander effect (Darley and Latané, 1968).

These examples in my opinion oppose Rizzolatti's and Ramachandran's claims, because either the mirror neurons are not at all an uncommon sight in the mammals and are therefore an unlikely cause for "evolutionary leaps", or the social and empathetic-like behaviour in other animals are underpinned by some other mechanism, which might then also hold for humans. If I were to answer my own question whether the mirror mechanism, or resonance, is special, I would answer both yes and no. No because I believe that it is something that brains of most mammals share, and yes because to resonate with others' actions or feelings can be a beneficial mechanism, not only to humans.

On several occasions I have tried to impugn various seemingly innocent claims about the mirror neurons presented in this chapter. However, I feel that the most serious shortcoming of the whole mirror neuron theory is not in the theory itself, but in its vagueness and exaggeration. The problems surrounding the misuse of terms such as "action understanding" and the empirical issues they have caused have been elaborated in Chapter 3. The extension of these problems is embodied in bold claims such as those by the Parma group, Ramachandran, Iacoboni and others that skew the opinion of readers in favour of the mirror theory prior to them being able to delve into its details, only to find that their claims do not rest on solid data. The omnipotence of the subject also leads to certain level of confirmation bias – the suppression mirror neurons would exactly make my point, if it indeed was a several decades known mechanism that causes their behaviour.

I would argue that attributing the mirror neurons with more and more functions, while even the originally proposed are being a subject of a controversy, is not helping neither the field nor the progress. From a more modest point of view, the mirror neurons only seem to be a by-product of a general brain activity that cannot be described in an atomic fashion. Instead, the authors should, in line with the conclusion of Chapter 3, establish their clear, unified view and provide a sound system-level definitions for *what* the system does and *how* is it accomplished.

With this I am putting my theoretical concerns aside and in the following section aim to illustrate the riskiness of drawing definite conclusions from EEG in favour of the mirror neuron system.

4.3 μ-rhythm suppression during observation of human and artificial hand movement

To test the explanatory power of electrophysiological evidence for the mirror neuron system in humans, I devised a simple experiment that was carried out with the help of my colleagues in POLIN laboratory for psycholinguistic research at the Faculty of Education and Rehabilitation Sciences of University of Zagreb.

The objective of the study was to explore the differences in μ-rhythm suppression during observation of a human and robotic hand performing grasping movements, either by employing a precision grip to pick up a pen, or performing a pantomime of the same movement. The inspiration for our study stemmed from research of Oberman et al. (2007a), Pineda (2005), and Muthukumaraswamy et al. (2004).

4.3.1 Hypothesis

The experiment was designed to examine the changes in μ-rhythm suppression during observation of experimental conditions, denoted as follows:

- Object directed human movement
- Non-object directed human movement
- Object directed artificial movement
- Non-object directed artificial movement
- Baseline

We constructed our hypotheses in accord with the existing data presented in researched literature (Oberman et al., 2007a; Muthukumaraswamy et al., 2004), and expected to achieve the following results:

- A significant level of μ-rhythm suppression was expected to be observed in both object directed and non-object directed human and artificial movement conditions, relative to the μ-rhythm in the baseline condition.
- Differences in suppression were expected, with the object directed human movement eliciting the highest level of μ-rhythm suppression and the non-object directed artificial movement possibly the lowest level.

4.3.2 Methods

Participants

Our sample consisted of mostly university students studying masters or doctoral programmes at University of Zagreb, University of Ljubljana or Comenius University in Bratislava. During the course of the experimentation, we were able to record data from fourteen participants. Two participants had to be excluded from the final analysis, one due to technical problems, and the other because of very strong alpha oscillations that flawed the recorded data, presumed to be falling asleep.

The data taken into account in the analysis was recorded from 6 male and 6 female participants with average age of 23.6 years (22–26 range). All participants were right handed (self assessed). Five participants had previous experience with EEG procedures, only one roughly knew what μ-rhythm or mirror neurons are. None had any knowledge about our experimental design prior to the experiment itself.

Procedure

Participants were seated into a chair roughly 60 to 70 centimetres away from a 22” LCD screen, and asked not to move or blink excessively during the experiment if possible.

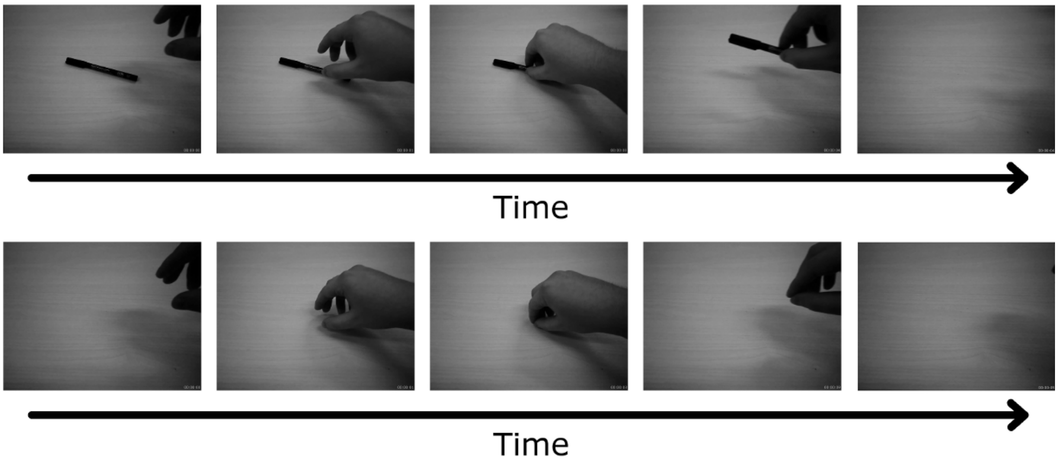


Figure 4.2: **Human hand** picking up a pen (top) and performing a corresponding pantomime (bottom).

Participants then viewed short video clips of either a human or robotic arm entering the scene and reaching into its centre to either perform a precision grip to pick up a pen, or pantomime the same movement (Figures 4.2 and 4.3). The movement was presented from a natural, first-person perspective with the scene set on a white table devoid of any distractors. Special care was taken to perform the robotic arm movement in a way that preserved the kinematics of the human hand. Depending on the condition, a black pen was prepared in the centre of the scene. A video clip of white noise (TV static) was used for the baseline condition.

The duration of a single trial was 15 seconds. Each trial consisted of a block of three consecutive plays of the respective video stimulus. The trials were separated by a one second pause. The conditions were presented in random order, with each condition being presented 8 times total.

A subtle distractor in form of a visual distortion was also introduced to several video clips to ensure that the participant was attending to the stimuli throughout the whole experiment by engaging in a continuous performance task.

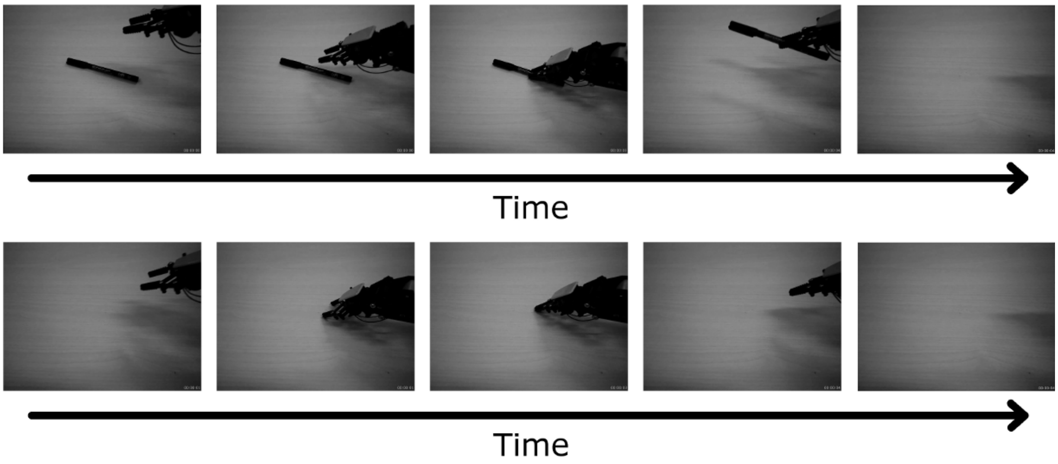


Figure 4.3: **Robot hand** picking up a pen (top) and performing a corresponding pantomime(bottom).

Data acquisition

The experiment took place in an electrically shielded room. The EEG was recorded using QuickAmp 136 amplifier at the sampling rate of 250 Hz, manufactured by Brain Products, GmbH. Data were collected from 32 active Ag/AgCl electrodes with integrated noise subtraction circuits placed according to the extended 10–20 system, with impedance on all electrodes measured as <25 kΩ. Two additional bipolar electrooculogram (EOG) electrodes were placed on the left and right sphenoid bone (horizontal), and above and under the right eye (vertical). Standard practices in the use of electroconductive and abrasive gel were employed as necessary.

Data analysis

Recorded EEG was analysed using BrainVision Analyzer. Filtering was applied, the high-pass filter set to 0.1 Hz and low-pass filter to 40 Hz. Ocular artefacts were marked, repaired or removed using semi-automatic artefact rejection algorithm employing independent component analysis (ICA) guided by data from EOG electrodes. Filtered and artefact free data was segmented according to the stimuli onset triggers.

The result was a set of eight, 15-second long segments of EEG data for each one of the five conditions. Segments for each condition were averaged, creating one final segment of EEG data representing the mean EEG activity recorded during the experiment for that respective condition. A pooled pseudo-channel containing averaged data from two contralateral electrodes C3 and C4 was created. The electrodes were picked according to their position above the sensorimotor cortex. The averaging was used to prevent bias in case of laterality differences between participants.

Fast Fourier Transform (FFT) was used on the C3–C4 pooled channel (1024 points) to create the power spectrum density (PSD) data for each condition. A cosine window was used to control for artefacts resulting from data splicing. Highest peaks in μ specific frequencies were manually identified and a ±1.5 Hz interval around the peak marked for export. These steps were applied to all recorded EEG channels.

We decided not to statistically analyse a fixed interval of the power spectrum, but rather manually pick the most characteristic part, as the locations of the peaks varied across the participants. Average μ peak in alpha band was found at 10.4 Hz, in 8.5–12.5 Hz range, and in beta band at 21.8 Hz, in 19–23 Hz range. A 3 Hz wide interval of the spectrum was exported from the data to be used in statistical analysis.

Statistical analysis

To assess the validity of our hypotheses, statistical analysis of the prepared power spectrum (PSD) density values was carried out. The μ power in both alpha and beta bands measured during each movement observation condition was compared to the μ power measured during the baseline condition by calculating the logarithmic ratio of these values. Using the ratio countered the variability in absolute power values resulting from individual differences, but since ratio data are inherently non-normal, a logarithmic transform was used in the analysis, described by the formula:

$$\mu'_{cond} = \ln(\frac{\mu_{cond}}{b})$$

where μ_{cond} represents the average PSD measured during the respective condition *cond*, compared to the PSD of the baseline condition *b*. The μ'_{cond} then represents the mean logarithmic ratio for the condition *cond*, with values smaller than zero indicating suppression, greater than zero enhancement, and 0 indicating no difference in PSD (Oberman et al., 2007a).

T-tests comparing the mean logarithmic ratio of each experimental condition to zero were performed to examine whether the observation of each stimulus caused a significant suppression of the μ-rhythm, and a two-way repeated measures analysis of variance (ANOVA) was used to evaluate the effect of the type of movement and presence of an object on the μ-rhythm suppression.

4.3.3 Results

The total performance of participants regarding the continuous performance task was roughly 96%, with three participants missing one instance of the distortion effect and one participant missing two. We considered this sufficient enough to deem the differences in measured μ-rhythm values as not being a result of not attending to the stimuli.

For the purpose of analysis, all conditions were given an easier to read label according to template "*Movement-type.Goal-orientation*", namely "Human.Object" for object directed human movement, "Human.Empty" for non-object directed human movement, "Artificial.Object" for object directed artificial movement, and "Artificial.Empty" for non-object directed artificial movement.

The t-tests of mean logarithmic ratios measured in alpha band compared to zero showed significant levels of μ-rhythm suppression in each experimental condition (Figure 4.4). That is, in case of Human.Object, ($t(11)$ = -14.2865, $p < 0.001$), Human.Empty, ($t(11)$ = -13.0436, $p < 0.001$), Artificial.Object, ($t(11)$ = -11.386, $p < 0.001$), and Artificial.Empty, ($t(11)$ = -8.3355, $p < 0.001$).

The results of data measured in beta band adequately corresponded with those measured in alpha. The t-tests of mean logarithmic ratios compared to zero also showed significant levels of μ-rhythm suppression in each experimental condition (Figure 4.5). Human.Object, ($t(11)$ = -7.8778, $p < 0.001$), Human.Empty, ($t(11)$ = -7.9099, $p < 0.001$), Artificial.Object, ($t(11)$ = -10.9862, $p < 0.001$), and Artificial.Empty, ($t(11)$ = -6.9421, $p < 0.001$).Note that the p values of all t-tests were substantially lower than values needed for statistical significance (between 10^{-8} and 10^{-5}) and are therefore reported as $p < 0.001$.

A two-way (type of movement by object presence) ANOVA performed with alpha band data revealed a slightly significant results for the main effect of movement type, ($F(1, 44) = 5.2379$, $p < 0.027$), however no significant effect in case of the object presence, ($F(1, 44) = 0.6283$, $p > 0.432$). There was no significant effect of interaction either, ($F(1, 44) = 0.8692$, $p > 0.356$).

The same ANOVA performed with beta band data showed practically identical results as in alpha band. Again, slightly significant results for the main effect of

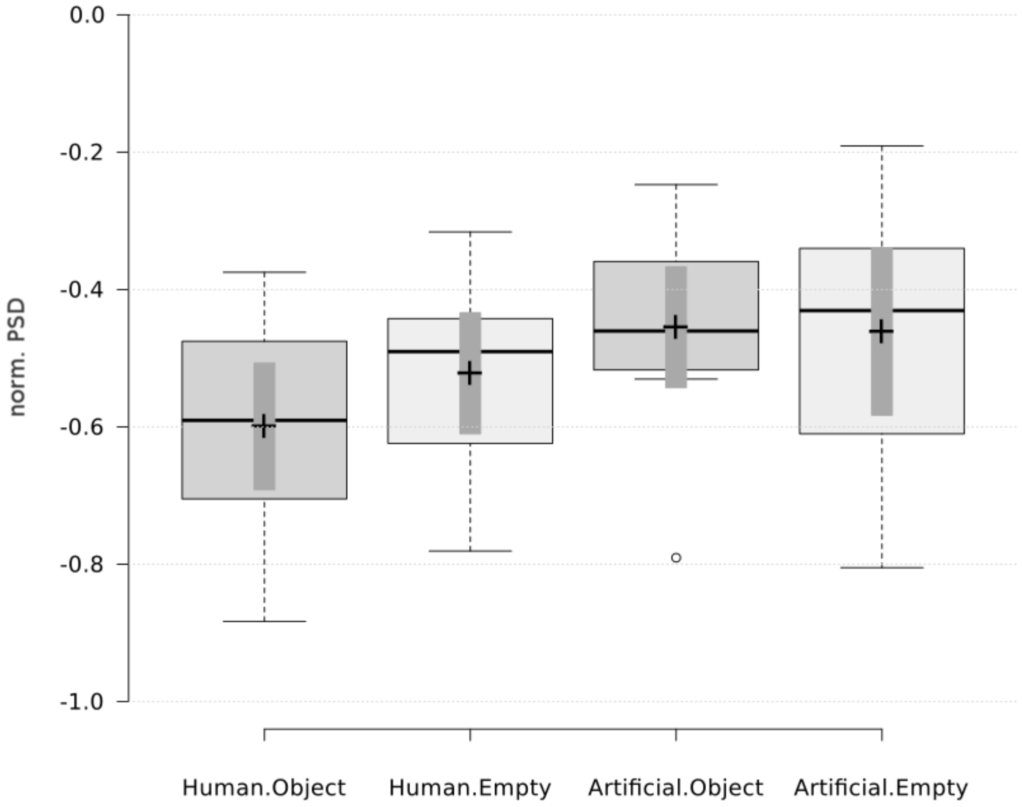


Figure 4.4: μ**-rhythm suppression** during all movement observation conditions measured in alpha band. Distribution of measured logarithmic ratios of the μ power is shown using Tukey's box and whisker plot. The plus sign denotes the sample mean with the dark grey bar indicating the confidence interval (95%).

movement type, ($F(1, 44) = 5.7211$, $p < 0.021$), no significant effect in case of the object presence, ($F(1, 44) = 1.3468$, $p > 0.252$), and no significant effect of interaction either, ($F(1, 44) = 0.8159$, $p > 0.371$).

Post-hoc testing of alpha band data based on the type of observed movement showed significant difference between human and artificial conditions in case of object directed movement, ($t(11) = -4.5359$, $p < 0.001$), but not in case of non-object directed movement, ($t(11) = -1.4186$, $p > 0.184$).

Outcome of beta band tests showed the same pattern, significant difference in case of the object directed movement, ($t(11) = -2.6719$, $p < 0.022$), but not in the case of non-object directed movement, ($t(11) = -1.8842$, $p > 0.086$).

An interesting result was found in additional test of μ power difference between Human.Object and Human.Empty conditions. Whereas in alpha band the resulting t-test did not show a significant difference ($t(11) = -1.71$, $p > 0.115$), the result for beta band was highly significant ($t(11) = -3.6073$, $p < 0.005$).

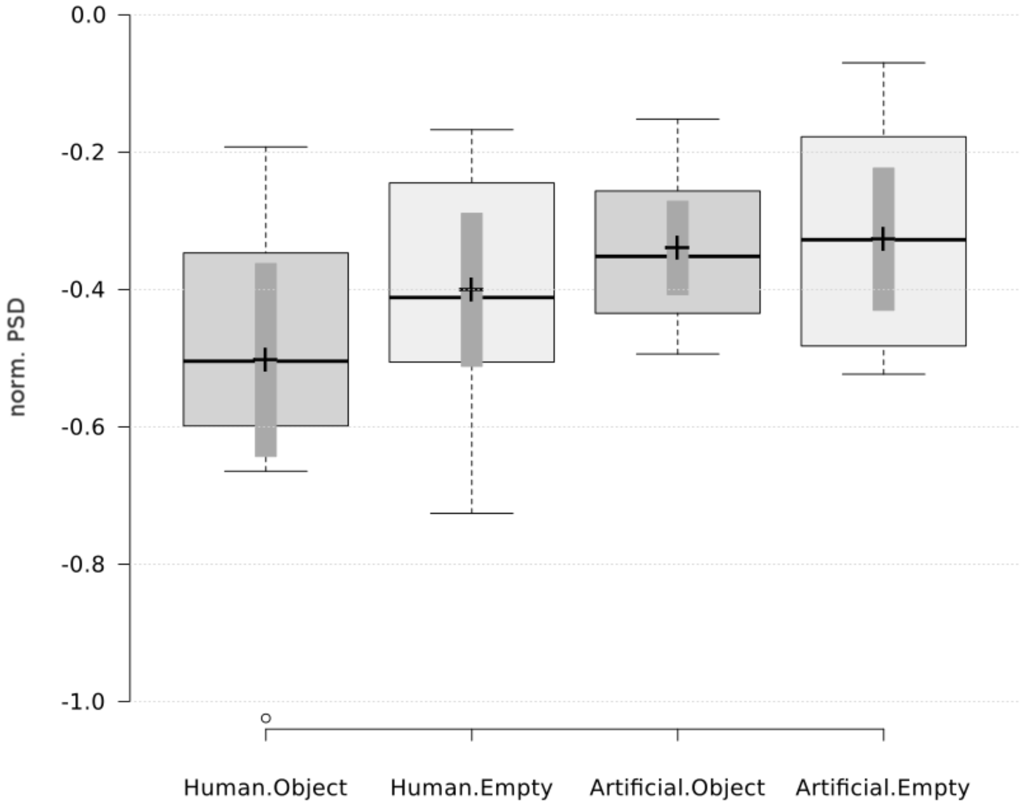


Figure 4.5: μ**-rhythm suppression** during all movement observation conditions measured in beta band. Distribution of measured logarithmic ratios of the μ power is shown using Tukey's box and whisker plot. The plus sign denotes the sample mean with the dark grey bar indicating the confidence interval (95%).

4.3.4 Discussion

Our study strove to examine the differences in suppression of electroencephalographic μ-rhythm during the observation of human and artificial movement in both object directed and non-object directed settings. As hypothesised, each condition caused significant μ suppression when compared to the baseline. Moreover, the results suggest that the μ-rhythm is to a noticeable degree sensitive to the difference between human and artificial movement, showing stronger suppression during observation of human movement, whereas the actual goal of the action seems to only cause a minor effect in case of the human movement, with practically no effect in case of the artificial.

This seemingly weak influence of the goal orientation to some extent disagrees with early findings described by Muthukumaraswamy et al. (2004), however, it seems to correspond to the data provided by Oberman et al. (2007a). One plausible, though overly simplified explanation might be the difference in somatosensory resonance between the precision grip and pantomime conditions. When there is nothing to pick up, there is

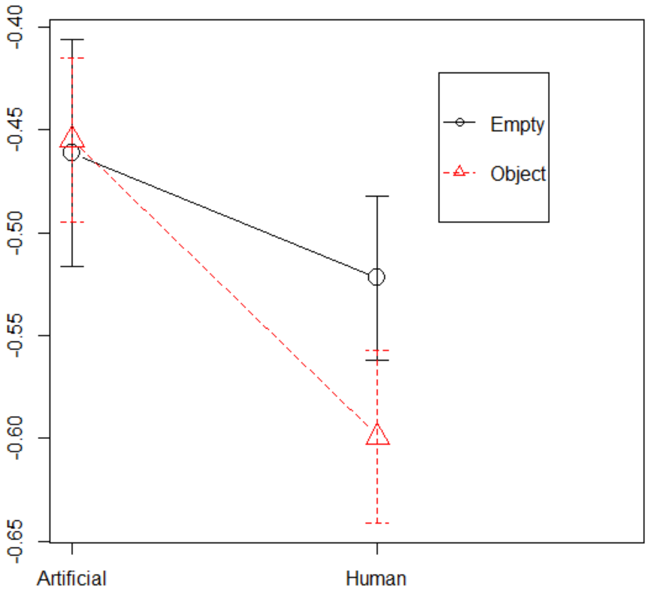


Figure 4.6: **Comparison of the mean μ suppression in the alpha band**. Error bars represent the standard error of the mean.

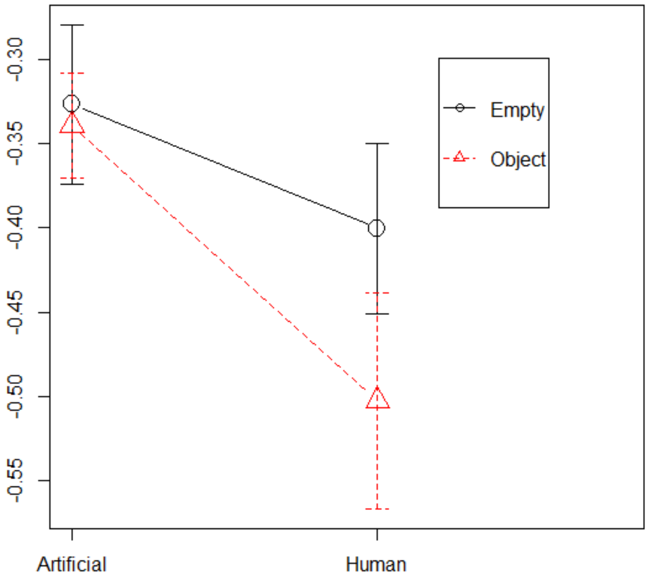


Figure 4.7: **Comparison of the mean μ suppression in the beta band**. Error bars represent the standard error of the mean.

also nothing to elicit resonance of something being picked up. Conversely, when a pen is being picked up, the projections from secondary somatosensory area to frontal areas might resonate with the tactile sensations of such an action, leading to a stronger μ suppression. Yet only in case of human movement as association of such sensations to a robot hand might be represented less or not at all in our brain. Additionally, such an explanation would also account for the lack of any significant difference between robot object and non-object directed movements, as the only aspect of the condition that resonated was the movement itself. This notion had also been considered by Muthukumaraswamy et al. (2004), only to be dismissed on account of study by Nishitani and Hari (2000), who did not find any involvement of somatosensory cortex.

A different approach might suggest a role of experience. The effect of experience on μ-rhythm suppression has been examined in several studies. Orgs et al. (2008) examined dancers and non-dancers and found stronger μ suppression in dancers watching familiar dance movements than in non-dancers watching the same movements. No such difference between the groups was found during watching of everyday movements. A similar fMRI study compared male and female ballet dancers watching videos of gender specific ballet moves (Calvo-Merino et al., 2006). Greater activation in premotor, parietal, and cerebellar areas was found during viewing of moves of one's own gender (i.e. own motor repertoire) than during viewing the moves of the opposite gender. Experience in tool use was also shown to elicit greater μ-rhythm suppression than observational experience with the tool or no experience with the tool, during observation of an action involving the use of that tool (Cannon et al., 2014).

Similar results were even found in infant studies. van Elk et al. (2008) recorded EEG of 14–16 month old infants while they watched videos of other infants crawling and walking. They found stronger μ and beta suppression for the crawling, with the measured effect correlating with the infant's own crawling experience. An exhaustive discussion can be found in a review by Marshall and Meltzoff (2014).

Using experience to account for the strongest μ-rhythm suppression in case of human object directed movement would be plausible, since the movement of picking up a pen using precision grip is no doubt a familiar and "trained" action compared to the other three. However, this does not clearly address the question why is it so, and might imply involvement of other areas or mechanisms, such as the cerebellum reported by Calvo-Merino et al. (2006).

A more elaborate explanation to be considered then might be the participation of a larger network of brain areas. Results of a fairly recent fMRI study examining neural correlates of the μ rhythm report activations in the inferior parietal lobule and premotor cortex, inferior and middle frontal gyri, right temporal lobe, cerebellum and thalamus (Braadbaart et al., 2013). Most of these findings correspond to earlier studies by Kessler et al. (2006) and **?**, who additionally provided a detailed description of interactions and differences in the timing, pattern and location of activations.

Providing a conclusive answer to what causes the differences in the μ-rhythm suppression thus becomes rather complicated. Even though "traditional" mirror areas are no doubt involved, reducing such orchestrated activity of the brain into a claim that it is a result of mirror neuron activity is an implication based on *a priori* knowledge that does not provide any tenable explanations. The only valid assertion would be to say that observation of a movement employs areas similar to its execution.

From our standpoint, we can only conclude that observing an action elicits brain activity that leads to suppression of the μ-rhythm, but does not seem to reliably reflect goals or intentions of the movement, as the presence of the object was found to influence only the movement of the human hand, and only on the threshold of statistical significance.

4.4 Dynamic Competitive Priming

I would like to conclude this chapter, and the thesis, by providing an outline of an alternative model to the mirror neuron system, based on the voiced opinions and cited literature. The model presents a conceptual framework named Dynamic Competitive Priming, in which many of the proposed MNS functions can be realised, but at this stage it concentrates solely on motor resonance and omits emotional resonance, which in my opinion differs substantially and would require addition of several more components that would unnecessarily impair clarity. Firstly, I explain the fundamentals of the framework and how it relates to the current views on the MNS, and then I proceed to delineate the principles and interactions of its respective components.

4.4.1 Fundamentals

The central idea of the model rests on the assertion that higher-order sensory areas continuously prime the motor cortex with predictions of actions that would result in appropriate behaviour for a certain situation. Each percept can elicit multiple activations, which then compete to be either executed, or in case of observation, fed back and serve as an input for further predictions. The selection of a *winning* action relies on executive control achieved through top-down attentional and intentional modulation of rostral motor cortex by prefrontal areas.

The approach to mirror (and canonical) neurons is founded on the premise that the functional role of a neuron within a cortical circuit should largely be defined by that neuron's synaptic inputs. In line with this statement, the *true* mirror neurons represent the input layers of motor and sensory areas and facilitate *sensory-motor coupling* of the projections. Subsequent neurons are not considered as being truly mirror, even though if observed, their activity would correlate with the inputs. From a broader perspective, these *collateral* mirror neurons in motor and sensory areas are *all* considered to possibly represent both execution and observation, but their role differs as it primarily corresponds with the role of the respective area in which they are located. The true MNs are therefore the part of the system that enables the brain to establish a relation between sensory (or cognitive) goals, represented elsewhere in the brain, and mediates the activation and selection of possible motor solutions for achieving these goals.

To a certain degree, the model agrees with the common coding theory, as the domain between perception and action is shared and representations elicited automatically, but due to the possibility of one perceptual representation being linked to multiple motor representations that differ based on internal states, the agreement might only hold in a less strict sense.

The specific circuits inside the model comply with their biological counterparts as described in Chapter 1 and perform their respective function. For the purpose of the explanation, I will be drawing a parallel to the F5-PF/AIP circuit, supposed to be the principal part of the MNS, and briefly discuss its implementation. An outline of the circuit can be seen in Figure 4.8.

4.4.2 Specifics

The microcircuit logistics of the model would be rather simple. Even though we traditionally see parietal and motor areas as two separate modalities, conceptually operating upon both sensory and motor representations, in reality their intricate connections essentially make them into one single mechanism which, I would argue, represents an influenced continuum of one shared representation. The apparent difference stems from the motor areas being a target of mostly prefrontal and subcortical structures, while parietal rely on sensory inputs. But they produce one joint output, as evidenced by the fact that even though we do not currently understand why, posterior sensory areas comprise about 40% of the corticospinal tract, the main descendent motor pathway of our body (Guyton and Hall, 2006).

The two parts of the circuit rely on reciprocal connections between two sparsely coded neural clusters (Olshausen and Field, 2004), that exchange information through my version of the mirror neurons. The sparsity enables an easy implementation of a competitive mechanism. The neurons coding details are located further away from the centre of the cluster that encodes the basis of the representation. Lateral inhibition can therefore easily inhibit their firing and fine tune the movement during its execution. Moreover, if a certain feature of a movement or an object is represented by a steady

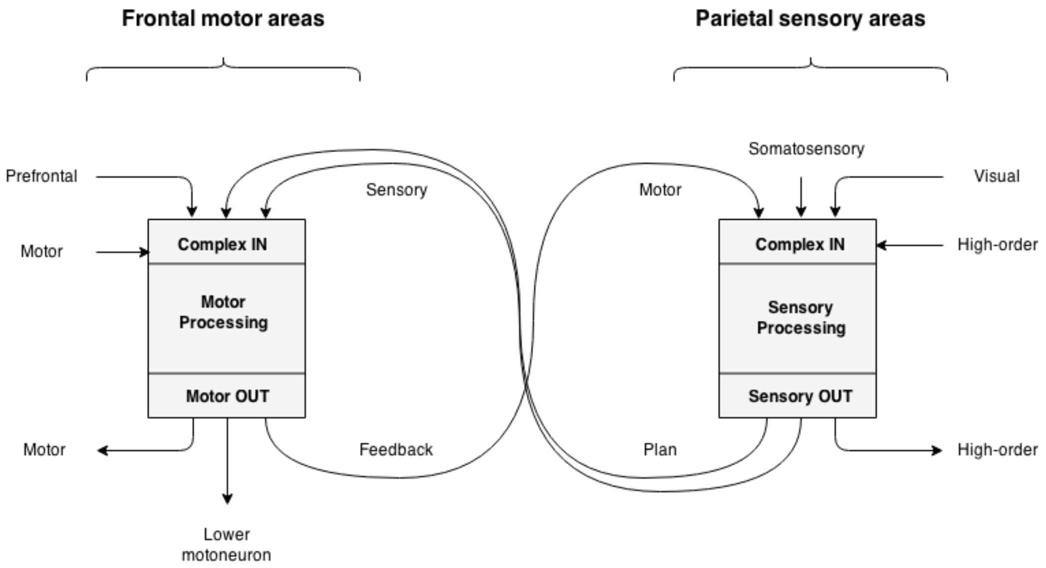


Figure 4.8: **Interaction of premotor cortex with parietal areas** according to the DCP model. The mirror neurons might be considered as inhabiting the Complex IN layers of both areas, "translating" the manifold inputs into one composite signal.

"core", reverberation would enable a certain level of motor short-term memory that might represent the currently established prime (Johnson et al., 2013).

The activation of parietal areas causes an automatic construction of a motor plan caused by the projections on the motor areas. Reversely, if control areas bias the motor activation and drive an action, the activity is fed back and confirmed with the parietal plan, strengthening the connection and essentially resulting in learning. Multiple co-activations then lead to emergence of association that might enable for shorter reaction times in recognising and executing appropriate actions.

The answer to the question of how such a mechanism develops in the brain might then be hybrid. The "mirror neurons" integrating the complex inputs into their respective areas must be present in the system from the start, probably representing some default connection in line with primitive reflexes, but their precise function gradually develops through associative learning.

From a broader perspective, far more than the interaction inside the parieto-frontal circuit is required for correct behaviour. Both dorsal and ventral streams (Ungerleider and Mishkin, 1982) play an important role in determining the winning action, only the influence of the ventral stream is more prominent for prefrontal areas and IPL, what can be interpreted as more *semantic*, less *parametric*.

The information processing then takes place in the following cycle: Retinal stimulation reaches visual cortex, climbs its hierarchy, proceeding across the parietal lobe and transforming visual information into representations of potential actions directly

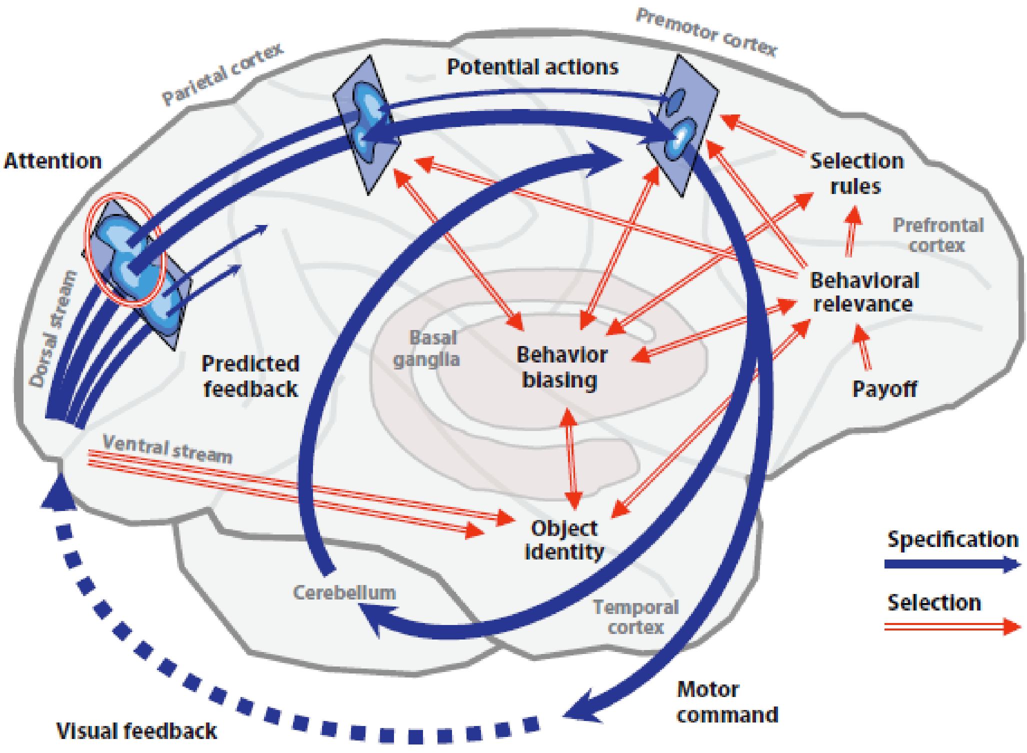


Figure 4.9: **Diagram of interactions in the brain** during visually driven movement. The bold blue arrows show the gradual generation of the appropriate possibilities to act, with the red arrows representing how the semantic information and control areas of the brain influence the voluntary decision to act. Figure adapted from Cisek and Kalaska (2010).

in the motor areas. Concurrently the same visual information flows through temporal areas to gather semantic “meta data”, which are then submitted to the prefrontal cortex. Both processes stimulate the basal ganglia that directly bias the activations in respective areas. The voluntary movement then stems from the drive elicited by the combined influence of the prefrontal and basal regions on the motor cortex. If no movement needs to be executed or the activity was caused by observation, the representation simply gets dynamically overridden by new inputs or if no change is present, returns it to a resting state. A diagram of the cycle can be seen in Figure 4.9.

4.4.3 Underlying reasoning

The traditional view that human cognition and behaviour is governed by two types of processes, the conscious and flexible *voluntary*, and fast and rigid *automatic*, underpinned by two different mechanisms (Schneider and Shiffrin, 1977; Shiffrin and Schneider, 1977), has recently been the topic of several reviews (Eimer and Schlaghecken, 2003; McBride et al., 2012; Sumner and Husain, 2008). These suggest that evidence against this distinction is starting to accumulate and that the voluntary and automatic might be linked more intricately than previously thought.

One example are studies on the “visual grasp reflex”, where a suddenly appearing irrelevant visual stimulus causes a saccade towards it, even when it is not intended (Theeuwes et al., 1998). McBride et al. (2012) reviewed several studies showing that distractors can cause curving or slowing of saccades during their flight towards a target, suggesting an occulomotor command interfering with the ongoing saccade.

Another fascinating evidence comes from rare neurological cases. Patients suffering from *alien hand syndrome* spontaneously and involuntarily grasp objects or people in their surroundings, aware of their hand making these movements, but unable to control them (Scepkowski and Cronin-Golomb, 2003). Instead, they report feelings of being controlled by an external agent. A related disorder, aptly named *utilization behaviour*, causes patients to automatically grasp and use objects placed within their reach, even when the objects are not wanted, needed or do not belong to them (Boccardi et al., 2002). Both disorders are associated with several localised brain lesions, but the area mentioned the most and of particular interest is the medial frontal lobe, i.e. supplementary motor cortex (Boccardi et al., 2002; Lhermitte, 1983). The interest stems from what was reviewed on the SMA in Chapter 1, their role in organization of complex motor sequences and temporal planing, sharing strong inputs with prefrontal cortex Rizzolatti et al. (1998). Furthermore, two fMRI case studies with alien hand syndrome patients revealed abnormal activity in inferior frontal gyrus and precuneus (Assal et al., 2007; Schaefer et al., 2010), areas amongst other functions associated with inhibitory control and self-awareness respectively, along with activation of areas normally associated with movement. This not only suggests an unsuccessful attempt in inhibition of the alien hand, and thus a critical role of executive motor control, but also shows an incredible overlap of brain areas causing seemingly automatic behaviour with brain areas employed during voluntary movement.

These, and a number of other studies exploring this voluntary-automatic relation (see McBride et al., 2012; Sumner and Husain, 2008, for review), reignited interest in a long-established view that mere visual processing of an object automatically evokes motor plans suitable for interaction with it, thus priming the observer to act in regard to *affordances* (Gibson, 1979). Imaging studies by Grèzes and Decety (2002) and Grèzes et al. (2003) explored the neural correlates of object perception and found several areas of the parieto-frontal motor circuit indeed active during mere observation of the object. They also drew a parallel directly to the mirror and canonical neurons, and promoted the F5-AIP circuit as a crucial part in visuomotor encoding of affordances as suggested by Jeannerod et al. (1995).

The canonical neurons no doubt seem as a fitting substrate to account for object affordances in the motor cortex, but they share the same inexplicable atomic definition as was given to the mirror neurons. However, if agreed that both canonical and mirror activity is simply the observed cause of sensory projections into the motor cortex (as elaborated in the previous section) it would be possible to assume that they are essentially the same, i.e. sensory-motor coupling neurons if you will, that differ only in their parietal origins where one facilitates object affordances, the other movement affordances. I propose that our brains do not represent movements simply in a simulative fashion, nor do they employ direct matching to understand what is seen. Instead, multiple parallel representations of possible – affordable – motor acts are dynamically generated during both observation and execution, allowing for a flexible representation capable of simulative and interactive motor acts.

The choice of the according motor act then rests on two mechanisms: neural competition utilising lateral inhibition, enabled by disynaptic connections through inhibitory interneurons, and the drive from cortical and subcortical go/no-go areas, mainly the prefrontal cortex and basal ganglia, which are well established to partake in motor control (Hoshi et al., 2000; Redgrave et al., 1999), and were also implied in "mirror" activity by multiple studies (Braadbaart et al., 2013; Kessler et al., 2006).

The lateral inhibition is a well known phenomenon prevalent especially in sensory and motor areas (Guyton and Hall, 2006; Sherrington, 1916; Swadlow and Gusev, 2002), which I already indirectly suspected to be the cause of the suppression MNs reported by Kraskov et al. (2009), and which was also fairly recently examined in M1 and suggested to reflect a competition process aiding in dynamic modulation of corticospinal excitability (Michelet et al., 2010).

This approach to movement representation enables prompt dynamic behaviour adaptive to the changes in perceptual representations, as it projects perceived changes directly to motor areas, where the lateral inhibition simply extinguishes previous activity and establishes a new prime. I chose the term *prime* and *priming* because the motor representation is prepared automatically and before we decide to act, enabling a fast movement initiation, but in a way congruent to the situation – it is quite improbable that while observing a cup of coffee, picking up a pen "comes to mind". Such anticipatory bias has been shown in several studies (Kilner et al., 2004; Urgesi et al., 2006, 2010). Furthermore, priming occurs in any modality, which might also be the case with motor representations, given the reports of mirror activations elicited by auditory stimuli (Kohler et al., 2002).

4.4.4 Comparison to motor resonance

In a relation to the explanatory power of mirror neuron centric views, not only is there the possibility to encompass much of their role (at least that part which is reasonable), but also several problematic instances such as “How do I understand a dog barking?” or “What does resonate in me when someone is handing me a cup?” are easily solved through parallel primes.

First, I assume that observed actions are not simply mapped into observer’s brain. Instead, there are two types of priming that might take place – *simulative* and *reactive*. Due to the generative nature of the model it is not needed for an action to be represented in one’s motor repertoire.

Second, a simulative representation roughly corresponds to the notion of motor resonance, i.e. it simply mirrors what is being observed and may be a facilitator of emulative/imitative learning and to some minor extent add to recognition or understanding. The reactive prime is what is usually employed in any social or interactive context. To explain using the dog and cup sentences: a barking dog might elicit a petting, scratching, stroking, or even some defensive motor acts. The one that might get selected depends on additional semantic context, such as “Is it my dog?”. The handing of the cup, too, requires non-simulative action, more precisely a complementary one, therefore, the default two motor acts that become primed might be both handing of the cup and receiving the cup, with the receiving being ultimately picked due to one being the receiver of the cup. An experiment by Sartori et al. (2013) examined exactly this situation, and found out that there is a flexible shift from imitative to complementary action that takes place precociously in time, if the observer sees an initiation of an interactive movement. This finding aptly seconds the competitive aspect of the representation – the initial representation gets inhibited due to the more correct one being more excited.

The last point is the action and intention understanding (in whatever sense). As I do not agree that mirror neurons facilitate either, I do not propose that this model does. Understanding alters the result of the representation in a profound way – if I know or recognise my dog, I certainly do not need to defend or run – therefore I believe it has to come prior to reaching the motor cortex. However, I also believe that the representations become more closely associated with repeated co-occurrence, which in return might lead to a relatively unambiguous resonance with only one, or a small set of actions.

As a concluding remark, I would like to say that while I was contemplating everything there is to about mirror neurons, how they fit in the grand scheme of things, whether they are really such a wonder, or if we can effectively replace them with another concept, as a mental image of an alternative approach was forming my mind, I did not for a second think that I am creating something all that novel. Knowing I was considerably influenced by Greg Hickok, I at least aimed for something a little more distinct. Alas, after finally conceiving a capable concept, I discovered the work of Paul Cisek while searching for an image of a brain to outline how I view the interactions between pertaining areas. I was astonished to not only find basically an exact diagram of what I had in mind, but also that he had beaten me to the idea by more then ten years. In his papers Cisek (2001, 2007); Cisek and Kalaska (2010) he wonderfully elaborates his *affordance competition hypothesis*, a refined vision of the rough concept that was presented in here.

So in the end it seems that Gallese and Goldman (1998) were right. The mirror neurons *do* indeed make *mind reading* possible.

Summary

The objective of this thesis was to investigate the functions attributed to the mirror neurons by their proponents in the light of the existing evidence, while eluding the influence of popular beliefs. During the course of this investigation I strived to delineate an unbiased view of the mirror neuron system from its biological foundations to the putative functions. In doing so, I intended to allow the reader to gradually develop an informed opinion on the matter before stepping into the concluding parts of the thesis.

The mirror neurons are without a doubt an interesting piece of neural machinery. However, two decades of research have focused more on pushing the mere notion of these cells further beyond the meaning of interesting than making a genuine attempt to understand their nature. As a consequence, I consider the theories embracing the mirror neurons as the basis of well-nigh all cognition lacking scientific ground, consistency, and being reliant on speculative assumptions put forward only to support their cause.

The future of the mirror neurons therefore rests on the willingness of its proponents to establish a definition that would unambiguously identify their role. An attempt to fulfil this proposition was provided with the outline for the DCP model, which although seemingly weakens the position of the mirror neurons in the workings of the brain also specifies their function accordingly. Endeavours to further develop the DCP model will be actively considered due to its potential for improvement of the physiological aspect of the simulation theory, or possible implications for applied branches of cognitive science.

I predict that the current view of the mirror neurons and the motor resonance will gradually fall out of favour to more complex theories, which will incorporate them into their mechanism albeit not in a central role. Despite the apparent failure of the mirror neurons to become the simple explanation for complex behaviour as they promised to, the sheer amount of research sparked and knowledge gathered on their account still allows them to retain the title of one of the most acclaimed discoveries from the turn of the century.

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