



Mirror Neuron Function within the Action Observation Network: A Review

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Abstract

Typically, when an observer witnesses an action being performed by an agent, their Mirror Neuron System initiates a motor simulation of that action. It has been argued that mirror neurons and the cortical areas of the action observation network (AON) enable our capacity to comprehend activities at these levels. The empirical evidence for this suggested role is scant but according to existing theories, the visual brain of primates is split into two functionally separate networks. The dorsal route calculates an object's position and any activities associated with it, while the ventral pathway computes an object's identity. In this two-route paradigm, mirror neurons encode this concrete representation of the event, which serves as a precedent to forecast the sensory effects of this activity via the AON pathway of dorsal route. Although still popular, the two visual pathways concept needs to be updated. This review gives an idea about mirror neurons and discusses their role in AON.

Keywords: Action observation network (AON), Mirror Neurons, Visual pathways, social cognition, Neurorehabilitation, Dorsal Pathway, Ventral Pathway.

1. Introduction

Mirror neurons (MN) in the brain are triggered immediately after a person performs a certain motor activity or watches another person doing a comparable motion. These neurons fire in response to both personal performance and observation of others doing identical action. MN were discovered in the premotor cortex of macaque monkeys, notably in the F5 area, by Giacomo Rizzolatti's research group [1]. Specific neurons that were active while a monkey was doing specific motor actions directed towards a particular goal, for instance grasping an article using its hand, were

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also active while the animal just watched the scientist execute the similar movement, the researchers discovered. As a result, MN function as both motor and sensory neurons. Their dual purpose implies a direct resonance, or shared coding, between participant and observer throughout performance and observation. These neurons automatically fire, regardless of who is performing or witnessing the action, resulting in direct and immediate experience. Similar research employing less invasive techniques has shown that human brain activity mirrors that of animals [2] [3]. The findings about MN are revolutionary because they expand our understanding of the basic principles behind imitation as well as the neurophysiological bases of social cognition more generally. In addition to providing evidence in favor of the theories of imitation put out by developmental psychologists, MN raise our knowledge of mimetic reciprocity to a completely advanced level of investigation and underlying mechanisms, that of brain structure and neural integration. MN will respond to a variety of alterations in the form and pattern of activity. When compared to the other half, more than half of people react to just one action. MN also show selectivity for the action (e.g., gripping vs manipulating) and the way the activity is carried out (whole hand grasping vs. a precision grip with two fingers). Additional types for MN include broadly congruent or fully congruent neurons. The neurons that are "strictly congruent" are those in which the seen and performed actions match (precision grip only by both participant and observer). "Broadly consistent" neurons have similar but different activity.

Thus, the wide-ranging cerebral restructuring that enabled the coevolution of more sophisticated social and representational capacities may have been significantly influenced by the emergence of MN, a more evolved "mirror system," and the imitative brain [4]. In addition to being relevant to evolution, their dual coding capability (1994, 1997). Developmental theories of imitation, like Meltzoff and Moore's AIM theory, get convergent validation from neurons (1994, 1997).

Many people think that MNs and regions of brain forming a grid called the action-observation network (AON) are what enable us to comprehend other people's activities. There is scant proof that MN along with AON allow for the inference of the purpose of observed actions, despite over two decades of study into them. According to hypotheses, action selection during execution entails imprinting conceptual features through observation. This is accomplished by a ventral channel that connects the middle temporal gyrus to the anterior inferior frontal gyrus [5]. In a description of the primate cortex published over 4 decades ago, Ungerleider and Mishkin hypothesized two visual circuits [6]. Based on investigations on lesion in primates other than humans, every route was described in terms of anatomical and functional characteristics. The ventral route extends down the surface of brain which

is ventral and determines the identification of objects in the visual field (e.g., faces, animals, cars, or tools). The vision for action route, also known as the dorsal pathway[7], extends over the dorsal surface of the brain and calculates the locations of visual items and the activities associated with those things (e.g., reaching, grasping, throwing, or utilizing). By creating a comprehensive cognitive framework, researchers successfully integrated data from various species (including humans and macaques) and diverse experimental approaches. This was achieved by mapping behavioral functions to visual pathways, resulting in a shared framework of cognition that bridged across different species and methodologies[8], [9]. However, promising evidence has been presented regarding one more visual pathway situated on the brain surface on lateral side.

The paper highlights the importance of MN and briefly explains various pathways of an AON. We mainly aim to understand various cortical components involved in the AON and their role in mirror network systems.

2. Discovery and Nature of MN

2.1. Discovery

In the 1980s and 1990s, neurophysiologists at the University of Parma implanted electrodes into the ventral premotor cortex of macaque monkeys. Their goal was to examine neurons that specialize in actions involving the hand and mouth, such as grasping and manipulating an object. The monkey was permitted to reach for food throughout each trial, and the researchers observed specific neurons in the animal's brain to determine how each neuron responded to different actions. It was reported that certain groups of neurons fired both when the monkey was only observing someone take up food and when the monkey itself took up the food as shown in **Figure1**.

After some years, the same group of researchers published a pragmatic paper discussing action recognition and association of mirror system with it and arguing that the human Broca's area was the human equivalent ventral premotor cortex of monkey [10]. Even though these studies characterized MN only reacting to hand movements, later it was reported that MN were also responding to movements of lip and facial expressions [11] .

Additional research verified that 10% of the neurons present in the inferior frontal and inferior parietal cortex of monkey exhibit "mirror" qualities and react similarly to viewed and executed hand movements. According to a 2002 study, many actions related to objects can be recognized with sound in both monkeys and humans[12].

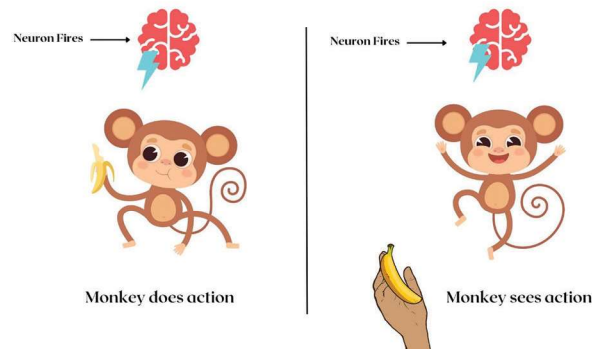


Figure 1: Illustration of mirror mechanism

2.2. Location

MN have been reported in both established and new areas of the brains of monkeys specifically the *Macaca nemestrina* and *Macaca mulatta* species. These regions include the ventral premotor cortex and the inferior parietal lobule, as well as the primary motor cortex. The primary motor cortex was not previously considered a classic area for mirror neurons, nor was the dorsal premotor cortex [13]

Research has shown that in typical regions of brain in humans, such as the parts of inferior frontal gyrus (IFG) which are posterior in position are known to be homologous with monkey F5, and the inferior parietal cortex [14], there are reports of single neurons or small ensembles of neurons with sensorimotor matching capabilities [15]. Additionally, atypical regions of brain in humans, including the cerebellum, superior parietal lobule, and dorsal premotor cortex [16], along with the medial temporal lobe and accessory motor region have also exhibited similar neural characteristics [17]

2.3. Evidence of MN in Humans

Only one research claims to provide direct proof of MNs in the brain of humans, which comes from single cell recording [17]. Despite some uncertainty, there are several reports indicating that humans possess MNs or similar "mirror mechanisms" in specific areas of cortical region involved in both action execution and observation. This evidence is derived from various research techniques, which include neuroimaging, transcranial magnetic stimulation (TMS), functional magnetic resonance imaging (fMRI), positron emission tomography, magnetoencephalography, electroencephalography, as well as studies of human behavior [18].

- *Neuroimaging*: fMRI has pointed out regions in the premotor cortex, including both classic Brodmann area 6 and Brodmann area 44, as well as areas of inferior parietal regions, that exhibit activity during both action

observation and execution [19]. In single-subject analysis of unsmoothed data, matching reactions to action observation and completion have been discovered [20], demonstrating that the findings are not the result of group mean artefacts. Repetition suppression techniques have most frequently been applied to show that mirror populations encode both visual and motor perceptions of the same activity. These patterns make use of the idea that a reduction in brain responses results from repeated stimulus presentation or action execution [21]. There have been reports on effect of cross-modal suppression of repetition, in which repeat suppression in the inferior parietal areas and PMC is induced by action observation succeeded by completion of the identical action, or vice versa (Rance et al., 2008b); [23] [24] [23]

- *Motor evoked potentials (MEPs) of Mirror pattern:* Knowledge about mirror systems in humans during action scrutiny is enhanced by MEPs [25]. When TMS is used on the primary motor cortex (M1) while passively observing an action, the electrical activity in the muscles needed to perform that action (measured by MEPs) is stronger than when watching an unassociated action. When individuals observe the isolated movement of their index and little fingers, there is a discernible increase in electrical activity in the corresponding muscles responsible for those movements, such as the first dorsal interosseus and abductor digiti minimi. This is confirmed by the greater amplitude of recorded MEPs, indicating a direct neural response to the examined action [26]. This selective enhancement of corticospinal excitability in muscles relevant to the observed action supports the existence of "mirror" sensorimotor connections.

3. Mirror Neurons (MN) and Action observation network (AON)

The AON refers to a group of regions in brain that are bilateral in nature and include the inferior parietal lobule, ventral premotor cortex, and superior temporal sulcus (STS). These regions are known to contain MN's, which are involved in the neural processes related to action observation and execution [27]. As a result, the AON is also called the MN's system [28].

Actions can be understood at various levels, including [29], [30]:

- (i) The kinematic level involves the velocity and trajectory of the movement, encompassing the reaching and grasping phases of the action together.
- (ii) The motor level focuses on the muscular activity necessary to generate the observed kinematics.
- (iii) The goal level pertains to the specific goal of the activity, such as the act of grasping an object.
- (iv) The intention level relates to the broader intention or reason behind performing the action.

These levels—kinematics, motor execution, goal, and intention—are all connected and arranged hierarchically. Kinematics depends on motor execution, which in turn relies on the goal level, and the goal level is influenced by the intention [31].

3.1 Model of Action Understanding including two pathways

According to current theories, the ventral inferior frontal gyrus (IFG) is known to be organized along its rostral-caudal axis in a way that reflects different extents of abstraction associated with an activity. The regions situated most anteriorly, specifically Brodmann area 47 (BA47), are thought to hold the most abstract semantic representations, while the regions situated most posteriorly, such as Brodmann areas 44 and 6 (BA44/BA6)[29], [32].

When examining the actions associated with drinking from a glass of water, the overall goal is to drink from the glass. To accomplish this, one must reach out and hold the glass. However, there are multiple ways to reach and hold the glass, and not all of them are appropriate for the primary goal of drinking from the glass. To successfully drink from a glass, it is important to choose the most suitable reach and grasp action from among all the available options, to achieve the intended goal.

The final goal in this scenario is to drink from a glass of water. The initial phase includes the processing of visuals and recognition of the article as a cup. The next phase involves retrieving actions related to that object. The third stage is selecting the most likely actions based on the goal. The fourth phase is encoding the motor characteristics of the chosen action, which leads to a prognosis of the sensory outcome of the observed activity. It amounts to noting that more than one action can be ciphered at this stage. The final stage is predicting the sensory implications of the most likely action. In this model, initial steps would be ciphered in a pathway which is ventral and includes connected regions like the middle temporal gyrus, Brodmann areas 47, 45, and 44/6, with the depiction of the action shifting to concrete form rather than abstract through these steps. The last stages would entail the production of anticipated sensory outcomes of the action, which are encoded within the pathway of the AON in dorsal region [33].

The implication of this two-pathway design is that MN oversee encoding the specific details of activities instead of abstract concepts and intentions associated with the action. It has been suggested that the characteristics of MN in the macaque monkey's area F5 match this function, as these neurons are believed to encode the "goal" of an observed action since their discovery [34], [35], [36]. Scientists found out that a subgroup MN in area F5, known as broadly congruent MN, activate when a specific action is performed with the hand and when observing a similar activity executed with either the mouth or hand. This led to the hypothesis that MN encode more abstract features of

the action which are observed. These MN were observed to be active when the end-goal of the action was the same, regardless of the body part used to perform the action[37], regardless of how it was reached. This is explained by the two-pathway framework's parallel action selection [38]. In simpler terms, during the observation of action, various possible actions are picked and assessed, but only one of them is depicted more prominently or in a stronger way than the others.

3.2. Significance of the Third Visual Pathway in Social Perception

Studies on both humans and nonhuman primates have indicated the presence of an extra visual pathway on the brain's outer surface. This route connects the primary visual cortex to the STS via motion-sensitive areas. According to research, STS specializes in dealing with the ever-changing components of social perception. These components include the interpretation of dynamic facial and physical movements such as expressions, eye contact, aural and visual cue integration, intents, and emotional states [39].

Tracer study in macaques provides compelling evidence for the presence of a separate cortical route from the primary visual cortex (V1) to the middle temporal area (MT), a region specialized in motion perception. The ventral route is bypassed by this cortical channel. These findings clearly imply that V1 and the area of STS which has motion selectivity in nonhuman primates have a direct corticocortical relationship [40], [41]. Studies indicate that the FST exhibits connectivity with the dorsal region and fundus of the STS, primarily in anterior sections. Notably, this connectivity differs from the corticocortical connections observed between the V1, secondary visual cortex (V2), and the fourth visual area (V4), which directly project inside the inferior temporal cortex of the pathway of ventral region [39], [42].

While direct evidence of neuroanatomical nature is lacking in human studies, tractography studies have recognized a distinct pathway of white matter that extends into the STS, separate from the white matter pathways on the ventral surface [43], [44]. The findings of studies on humans and animal models suggest the existence of direct recent research has revealed the existence of a distinct pathway that originates from the early visual cortex and projects into the dorsal bank and fundus of the STS in macaques. Notably, this pathway bypasses the traditional ventral pathway, which includes the inferior temporal cortex [45]. The involvement of the middle temporal area in this alternate pathway underscores the significance of motion processing. As a result, employing dynamic visual stimuli is crucial in comprehending the functional properties of this unique circuitry.

Neuropsychological investigations of individuals with lesions in cortical regions offer a valuable opportunity to interpret the functional and anatomical connectivity which is independent of the third pathway. As early

as 1984, the chances of an uninterrupted pathway into the STS was initially proposed hinged on behavioral evidence from a patient with prosopagnosia. Such studies provide crucial insights into the distinct role and contribution of this pathway in cortical processing. However, the absence of structural brain imaging technology at the time made this hypothesis speculative [46]. Even though they have lesions in the area of the brain where the fusiform face area and occipital face area are typically located, research has found that several patients with prosopagnosia still exhibit responses which are face-selective in the STS through functional brain imaging studies [47], [48], [49], [50].

4. The Practical Impact of MN system

Learning of MN mechanisms have opened a world of exciting possibilities for a wide range of therapeutic and practical uses. Research into the mirror mechanism on one hand has allowed researchers to investigate neuropsychiatric problems including autism and developmental abnormalities, as well as psychiatric and neurological ailments. For example, research has looked into how MN contribute to the understanding deficiencies in social cognition reported in people with autism [51], [52], as well as the potential therapeutic applications of MN-based interventions in psychiatric disorders [53] and neurological diseases [54]. Although there is no definitive proof of the "broken mirror theory" [55] these findings have shed light on the previously overlooked role of the coordination deficits and motor system in the diseases [51], [56]. These insights have highlighted the importance of motor impairments in conditions such as autism and developmental disorders and have spurred the development of novel neurorehabilitation techniques. For instance, strong evidence linking certain regions of the mirror network with imitative abilities has led to the creation of innovative approaches, such as action observation treatment (AOT). AOT involves enhancing corticospinal output during action observation and has shown promising results in neurorehabilitation settings. These findings have thus paved the way for novel interventions that capitalize on the MN system to improve motor function and coordination in clinical populations.

The utility of AOT has been extensively investigated, particularly to check the potential to remarkably enhance and quicken functional recovery in individuals with motor deficits stemming from diverse neurological disorders. Research has shown promising results of AOT in improving motor function of people affected from stroke, cerebral palsy, Parkinson's disease, as well as post-orthopedic surgeries of the knee or hip [57]. Some translations applications of MN are mentioned in **Table 1**. When undergoing a quintessential AOT rehabilitation session, patients are told to watch a specific action, which is directed at

a certain object, commonly involving the upper limb. This is observed in a video or a live demonstration, and then patients must reproduce it. Patients typically focus on practicing one action per rehabilitation session. This approach is based on the reports that advocate that motor brain area have increased excitability due to AOT [58]. The idea is that observing actions can lead to plastic changes that make it easier to perform relevant everyday actions[54] or even prevent the deterioration of motor skills caused by dis-use of the limb [59]. Furthermore, fMRI studies have revealed that AOT elicits robust activations in the MN's network, as compared to passive observation of actions without an instruction to imitate the gestures. This suggests that observational learning techniques, such as AOT, may contribute to increased neural plasticity and facilitate neuroplastic changes in the brain [60]. From a technological standpoint, using virtual reality can enable the customization of the optimal stimuli for inducing the desired plastic changes after an intervention. It can also be used effectively in telerehabilitation protocols [61]. Emerging evidence from the limited literature suggests that using stimuli that present actions demonstrated by models with similar extent of motor skill as the observer may be a promising approach in AOT protocols. This approach, also known as "matched motor skill" or "self-similarity" training, involves presenting action stimuli that are more closely aligned with the motor abilities of the individual undergoing AOT. This contrasts with using stimuli performed by highly skilled models, which may be too challenging for individuals with motor deficits [62]. Research has shown that children suffering from unilateral cerebral palsy, observing grasping actions exhibited by a model with the same condition resulted in increased activation in brain regions responsible for movement (MN) compared to observing a healthy hand action [63].

Table 1: Translational applications of MN

S. No.	Application Area	Description
1.	Autism Spectrum Disorder (ASD)	Addresses social cognition deficits via therapies aimed at improving imitation, social interaction, and understanding through MN's network engagement[64].

S. No.	Application Area	Description
2.	Psychiatric Disorders	Supports treatment of schizophrenia and mood disorders by targeting social cognitive impairments, focusing on self-other distinction and interpersonal skills enhancement[65].
3.	Neurorehabilitation	Utilizes mirror neuron-based AOT to enhance motor recovery, balance, and other neurological conditions in stroke patients [66].
4.	Pain Management	Mirror therapy is used to modulate pain perception and alleviate conditions like phantom limb pain and complex regional pain syndrome through sensory-motor resonance[67].
5.	Motor Skill Learning & Sports	Enhances motor learning and athletic performance by combining action observation with motor imagery, often using matched difficulty models for optimal learning[68].
6.	Post-surgical Rehabilitation	Facilitates accelerated recovery of limb function post orthopedic surgeries, employing AOT protocols that leverage MN activation[69].
7.	Telerehabilitation and Digital Health	Enables remote delivery of rehabilitation and therapy by integrating virtual and augmented reality systems designed to activate the MN system[70].
8.	Speech and Language Therapy	Improves speech production and aids recovery in aphasia patients' post-stroke via MN system engagement through action observation techniques[71].
9.	Cognitive & Social Training	Promotes empathy, social understanding, and interpersonal skills using VR and other platforms inspired by MN principles in social cognition [72].
10.	Emotion Regulation & Therapy	Assists in recognition and regulation of emotions by engaging MNs through imitation and empathy training to benefit mood disorders [73].
11.	Education & Skill Acquisition	Enhances learning efficiency in domains such as music and language by utilizing observational learning and imitation rooted in MN activity[74].

Future research should make greater use of the many findings from basic neurophysiological studies on the mechanism of MNs and the substantial information about the factors that affect its working [75]. For instance, a study using TMS found that intracortical inhibition caused by action observation was a significant predictor of a subject's improvement in a motor task after observing actions [76]. This suggests that the presumed inhibitory interneurons with properties similar to mirror system, that have been recently discovered [77] may be a factor in enhancing administrative control over actions imitated from others. In summary, these reports emphasize the need for close collaboration among basic and applied research

and the recognition of neurophysiological markers that can postulate and give clarity on the effectiveness of AOT at an individual level, which will help to develop more precise and tailored clinical methods.

5. Future Scope

The future scope of MN research points towards unprecedented integration with cutting-edge technology and a deepening focus on social cognition and clinical interventions. Ongoing advancements in single-cell transcriptomics and implantable neural devices are set to unveil the molecular features of MN, clarifying their role in self-awareness, empathy, and diverse social behaviors [69]. The emerging application of mirror-based therapies is expected to further enhance neurorehabilitation outcomes in stroke, Parkinson's disease, and autism spectrum disorders by exploiting neuroplasticity and fine-tuning personalized interventions. Multimodal neuroimaging and brain-computer interface technologies will likely refine diagnostics, fostering earlier detection and targeted treatments of neuropsychiatric and neurodegenerative diseases. Interdisciplinary research models, connecting neuroscience, artificial intelligence, and computational modeling, are predicted to revolutionize the understanding and practical application of the MN system in social and clinical contexts [69], [78].

5. Conclusion

Indeed, the terms "what," "where," and "how" are commonly used to describe different aspects of visual object recognition, but they may not be sufficient to capture the complexities of social interactions. The applications of the third visual pathway, which includes the STS, are not easily summarized by a single word. Visual data entering the STS is combined with other sensory information, allowing primates, including humans, to interpret and comprehend the actions of others. The STS is a key region for this function because it receives input from multiple senses, enabling it to process complex social cues

The findings of MNs and the embodied simulation model have facilitated a productive dialogue among the fields of neuroscience and humanities. The understanding of MN's, which are neurons that activate when an individual engages in an action and when they witness another individual performing a similar action, has provided insights into the neural foundations of social cognition and empathy. The embodied simulation model proposes that the motor system plays a crucial role in understanding the actions of others by simulating those actions internally, leading to a better understanding of their intentions, emotions, and experiences [79], [80]. Several stream of

investigations in the domain of visual arts [81], film [82], and narrative fiction [83] have started to demonstrate that even aesthetic experiences involve vicarious physiological mechanisms like those that mediate cognition during social events in real life, identifying the bodily dimension of our interaction with cultural antiquities that can now be examined experimentally. The discovery of MNs has opened new avenues for investigating various aspects of social cognition, including empathy, imitation, and understanding the actions and intentions of others. These neurons have produced insights into the neural mechanisms underlying human social interactions and have shed light on how the brain processes and represents social information. As advanced methodologies and neurotechnology's converge, MN research stands poised to deliver innovative interventions and diagnostic strategies for neurological and psychiatric disorders, shaping both fundamental neuroscience and practical clinical care for years to come.

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Author Contribution

Dr. Girima Nagda: Concept of Manuscript and Editing. Chhavi Bhalothia: Manuscript writing, Figure Drawing, and Editing.

Conflict of Interest

The authors declare that there are no conflicts of interest related to this study.

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