Mirror neurons and their clinical relevance

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SUMMARY

One of the most exciting events in neurosciences over the past few years has been the discovery of a mechanism that unifies action perception and action execution. The essence of this 'mirror' mechanism is as follows: whenever individuals observe an action being done by someone else, a set of neurons that code for that action is activated in the observers' motor system. Since the observers are aware of the outcome of their motor acts, they also understand what the other individual is doing without the need for intermediate cognitive mediation. In this Review, after discussing the most pertinent data concerning the mirror mechanism, we examine the clinical relevance of this mechanism. We first discuss the relationship between mirror mechanism impairment and some core symptoms of autism. We then outline the theoretical principles of neurorehabilitation strategies based on the mirror mechanism. We conclude by examining the relationship between the mirror mechanism and some features of the environmental dependency syndromes.

REVIEW CRITERIA
PubMed was searched using Entrez for articles published up to September 2008. The search term was "mirror neuron" OR "mirror neurons" OR "mirror neuron system" OR "mirror system". Owing to limitations on the number of references, we cited only articles that we judged to be most important from a theoretical or clinical point of view.

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INTRODUCTION

Traditionally, it has been assumed that the understanding of actions performed by others depends on inferential reasoning.[1–3] Theoretically, when we witness the actions of others, the information could initially be subjected to sensory processing and then be sent to higher order 'association' areas where it is elaborated on by sophisticated cognitive mechanisms and compared with previously stored data. At the end of this process, we would know what others are doing.[4]

It is possible that this cognitive operation might indeed occur in some situations when the behavior of the observed person is difficult to interpret.[5–7] However, the ease with which we usually understand what others are doing suggests that an alternative mechanism might be involved in action perception. The essence of this alternative system is that actions performed by others, after being processed in the visual system, are directly mapped onto observers' motor representations of the same actions. The observers are aware of the outcomes of their own actions, so the occurrence of a neural pattern similar to that present during their own voluntary motor acts will enable them to understand the actions of others.

Evidence in favor of the existence of this direct sensory–motor mapping mechanism came from the discovery of a set of motor neurons, known as mirror neurons, that fire both when a monkey performs a given motor act and when it observes another individual performing an identical or similar motor act.[8,9] In this article, we will first review the basic properties of this mechanism, which is known as the mirror mechanism. We then examine the relevance of the mirror mechanism for the interpretation of clinical syndromes such as autism, and for the development of motor rehabilitations strategies.

MIRROR NEURONS IN THE MONKEY

Mirror neurons were originally discovered in the ventral premotor cortex (area F5) of the macaque monkey.[8,9] The defining characteristic

of these neurons is that they discharge both when the monkey performs a motor act and when the monkey, at rest, observes another individual (a human being or another monkey) performing a similar motor act (Figure 1). The degree of similarity that is required between executed and observed motor acts in order to trigger a given mirror neuron varies from one neuron to another. For most mirror neurons, however, the relationship between the effective observed and executed motor acts is based on their common goal (e.g. grasping), regardless of how this goal is achieved (e.g. using a two-finger or a whole-hand prehension). Importantly, mirror neurons do not discharge in response to the presentation of food or other interesting objects.

Mirror neurons have also been described in the PFG and anterior intraparietal areas of the inferior parietal lobule (IPL; Figure 1). The general properties of parietal mirror neurons seem to be similar to those of mirror neurons in the premotor cortex. Like the latter neurons, the parietal mirror neurons code for the goals of motor acts rather than the movements from which they are constructed.[8,9]

The PFG and anterior intraparietal areas are both connected with the F5 area and the cortex of the superior temporal sulcus. Neurons in the superior temporal sulcus have complex visual properties, and some respond to the observation of motor acts done by others.[10,11] However, they lack the motor properties that are defining features of mirror neurons, and cannot, therefore, be considered to be part of the mirror system.

The organization of the cortical motor system

To understand the functional role of mirror neurons in the premotor cortex and IPL, it is necessary to frame them within the modern conceptualization of the organization of the cortical motor system. Clear evidence exists that most of the parietal and frontal motor areas code for motor acts (i.e. movements with a specific goal) rather than mere active displacement of body parts.[12–18] Even in the primary motor cortex, approximately 40% of neurons code for motor acts.[15,18]

Studies in which the properties of single neurons were studied in a naturalistic context have been particularly important for establishing this new view on cortical motor organization.[12] These studies showed that many neurons discharge when a motor act (e.g. grasping) is performed

with effectors as different as the right hand, the left hand, or the mouth. Furthermore, for the vast majority of neurons, the same type of movement (e.g. an index finger flexion) that is effective at triggering a neuron during one particular motor act (e.g. grasping) is not effective during another motor act (e.g. scratching). By using motor acts as classification criteria, premotor neurons have been subdivided into various categories such as 'grasping', 'reaching', 'holding', and 'tearing' neurons.

Recently, evidence was provided that both inferior parietal and premotor (area F5) neurons are organized in motor chains.[19,20] Grasping neurons recorded from these areas were tested in two main conditions (Figure 2). In one condition, a monkey reached and grasped a piece of food located in front of it and brought it to its mouth. In the other condition, the monkey reached and grasped an object and placed it into a container. The results showed that the majority of the recorded neurons discharged with a different intensity according to the final goal of the action (e.g. eating or placing) in which the grasping motor act was embedded ('action-constrained' neurons). This 'chained' organization seems to be particularly well adapted for providing fluidity to action execution. Individual neurons not only code for specific motor acts, but, by virtue of being wired to neurons that code for the subsequent motor acts, they facilitate the activity of these downstream neurons, thereby ensuring smooth execution of the intended action.

The functional role of the mirror neurons

The existence of a class of motor neurons that discharge during the observation of actions done by others is not as bizarre as it might initially seem. While it is true that an action done by others could be recognized by inference on the basis of previous visual experience without involving the motor system, visual perception *per se* does not provide the observer with the experiential aspects of the action. Furthermore, the mirror system provides a particularly efficient way to establish links between the observed action and other actions with which it is functionally related.[21]

Evidence in favor of the notion that mirror neurons mediate action understanding came from experiments in which monkeys were not allowed to see the actions performed by others, but were given clues for understanding them. In one series of experiments, monkeys were presented with noisy motor acts (e.g. peanuts
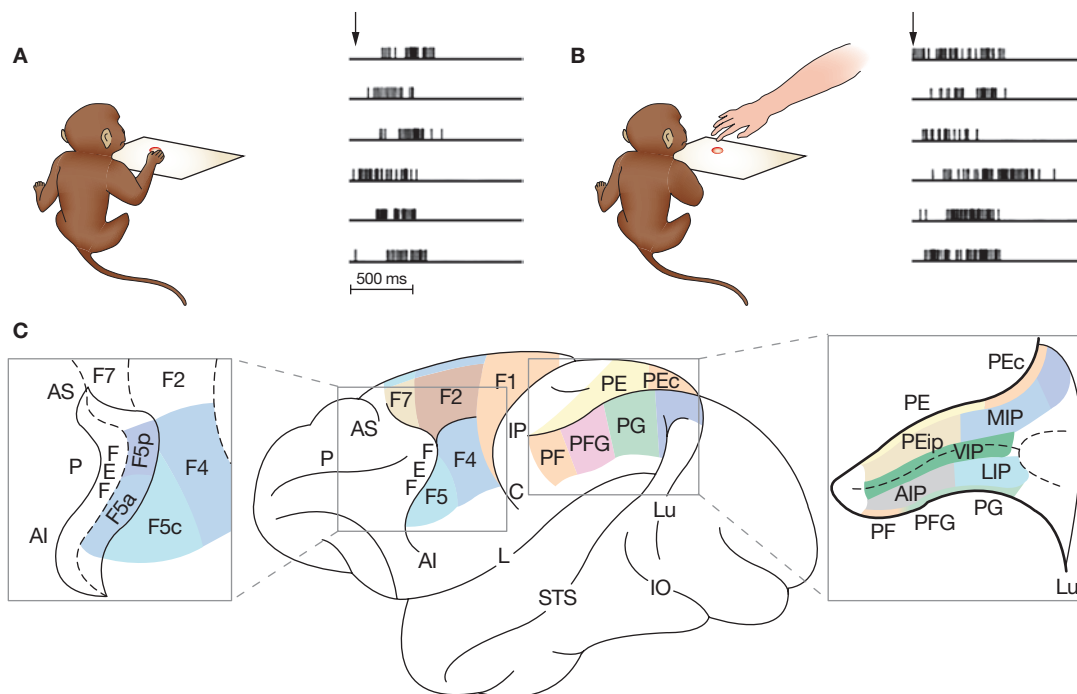
Figure 1 A cytoarchitectonic map of the monkey cortex and an example of a mirror neuron. The upper part of the figure shows the activity of a mirror neuron recorded from area F5. The neuron discharges both when the monkey grasps an object (**A**) and when it observes the experimenter grasping the object (**B**). (**C**) The cytoarchitectonic parcellation of the agranular frontal cortex and the parietal lobe. PE, PEc, PEip, PF, PFG and PG are parietal areas. An enlargement of the frontal region (inset on the left) shows the parcellation of area F5 into three parts: F5c, F5p and F5a. The mirror neurons are typically found in F5c. The inset on the right shows the areas buried within the intraparietal sulcus. Abbreviations: AI, inferior arcuate sulcus; AIP, anterior intraparietal area; AS, superior arcuate sulcus; C, central sulcus; FEF, frontal eye field; IO, inferior occipital sulcus; IP, inferior precentral sulcus; L, lateral sulcus; LIP, lateral intraparietal area; Lu, lunate sulcus; MIP, medial intraparietal area; P, principal sulcus; STS, superior temporal sulcus; VIP, ventral intraparietal area. Permission obtained from Elsevier Ltd © Rizzolatti G and Fabbri-Destro M (2008) *Curr Opin Neurobiol* **18:** 179–184.

breaking, tearing a piece of paper), which they could either both see and hear or only hear.[22] The researchers found that many mirror neurons in area F5 responded to the sound of the motor act, even when it was not visible.

In another series, F5 'grasping' and 'holding' mirror neurons were tested both when the monkey observed the experimenter grasping a piece of food and when the monkey was prevented from seeing the experimenter's hand movements by use of a black screen.[23] Despite the fact that the monkey could not see the hand–object interaction (the visual triggering feature of the recorded neurons) in the latter condition, many mirror neurons in F5 were active in this situation. The neurons typically began to discharge at the beginning of the hand-reaching movement, indicating that the monkey had a representation of the action performed behind the screen, even when it could not see the performed motor act.

The activity of mirror neurons *per se* describes only what is happening in the precise moment of occurrence of the observed actions. There is, however, a broader function of mirror neurons. This function is related to the recent discovery that most action-constrained neurons (see above) have mirror properties and selectively discharge when the monkey observes motor acts embedded in a specific action (e.g. grasping for eating but not grasping for placing; see Figure 2).[19] The activation of action-constrained mirror neurons, therefore, codes not only 'grasping', but 'grasping for eating' or 'grasping for placing'. This coding implies that when the monkey observes grasping done by another, it is able to predict, on the basis of contextual cues (e.g. repetition, presence of specific objects), what will be the individual's next motor act. In other words, the monkey is able to understand the intentions behind the observed motor act.

THE MIRROR SYSTEM IN HUMANS
Understanding of goals and intentions

A large number of studies based on noninvasive electrophysiological (e.g. EEG, magnetoencephalography [MEG]) or brain imaging (e.g. PET, functional MRI [fMRI]) techniques have demonstrated the existence of the mirror mechanism in humans.[8,9] Brain imaging studies have enabled the mirror areas to be located. These studies showed that the observation of transitive actions done by others results in an increase in blood oxygen level-dependent (BOLD) signal not only in visual areas, but also in the IPL and the ventral premotor cortex, as well as the caudal part of the inferior frontal gyrus (IFG). These latter three areas have motor properties and closely correspond to the areas that contain mirror neurons in the monkey (Figure 3).

Both the premotor and the parietal areas of the human mirror system show a somatotopic organization.[24] Observation of motor acts done with the leg, hand or mouth activates the precentral gyrus and the *pars opercularis* of the IFG in a medial-to-lateral direction, as in the classical homunculus model of Penfield[25] and Woolsey.[26] In the IPL, mouth motor acts are represented rostrally, hand and arm motor acts are represented caudally, and leg motor acts are represented even more caudally and dorsally, extending into the superior parietal lobule.

Most studies on the mirror mechanism in humans have investigated transitive movements such as grasping. In a recent fMRI study in which volunteers were asked to observe video clips showing a hand transport movement without an effector–object interaction, activations were found in the dorsal premotor cortex and also in the superior parietal lobule, with the activation extending into the intraparietal sulcus.[27] This finding indicates that the human brain is endowed with a reaching mirror mechanism that is anatomically separated from the mirror mechanism that codes for the distal motor act.

As in the monkey, the parietal and frontal mirror areas in humans code mostly for the goals of motor acts. Gazzola *et al.*[28] instructed volunteers to observe either a human or a robot arm grasping objects. In spite of differences in shape and kinematics between the human and robot arms, the parietofrontal mirror network was activated in both conditions. Further evidence in favor of goal coding was obtained in an fMRI study based on repetition suppression[29]—a technique that exploits the trial-by-trial reduction

of a physiological response to repeated stimuli. The results showed that repeated presentation of the same goal caused suppression of the hemodynamic response in the left intraparietal sulcus, but this region was not sensitive to the trajectory of the agent's hand.
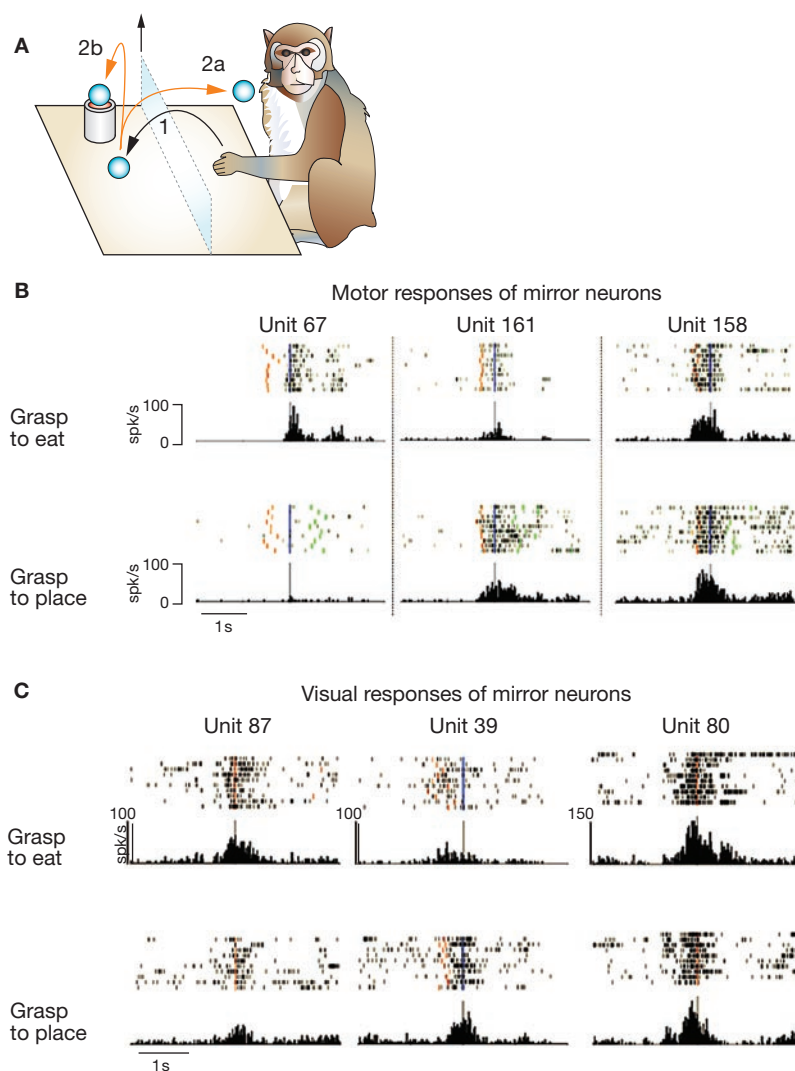

Figure 2 Action-constrained neurons in the monkey IPL. (**A**) Apparatus and paradigm used for a task designed to demonstrate action-constrained neurons. The monkey starts from the same position in all trials, reaches for an object (1) and brings it to the mouth (2a) or places it into a container (2b). (**B**) Activity of three IPL neurons during the motor task in conditions 2a (grasp to place) and 2b (grasp to eat). Raster histograms are synchronized with the moment when the monkey touched the object to be grasped. Unit 67 fires during grasping to eat and not during grasping to place. Unit 161 is selective for grasping to place. Unit 158 does not show any task preference. (**C**) Visual responses of IPL mirror neurons during the observation of grasping to eat and grasping to place performed by an experimenter. Unit 87 is selective for grasping to eat, unit 39 is selective for grasping to place and unit 80 does not display any task preference. Abbreviation: IPL, inferior parietal lobule. Permission obtained from American Association for the Advancement of Science © Fogassi L *et al.* (2005) *Science* **308:** 662–667.
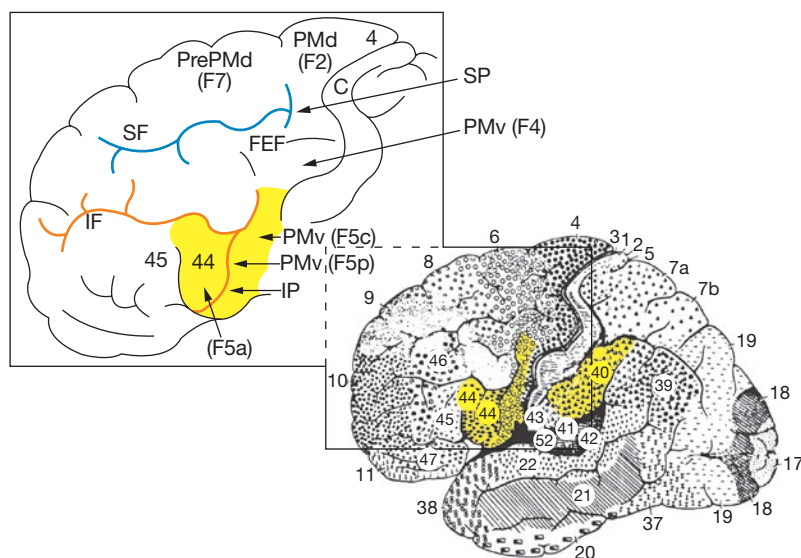
Figure 3 The parietofrontal mirror system in humans. Lateral view of the human cerebral cortex showing Brodmann cytoarchitectonic subdivision. The areas in yellow correspond to areas that respond to the observation and execution of hand motor acts. The left-hand panel shows an enlarged view of the frontal lobe. The possible homology between monkey and human premotor cortex is indicated by arrows. Note that in monkeys area F5 consists of three subareas: F5c, F5p and F5a. Area 44 is considered to be the most likely human homolog of area F5. Abbreviations: C, central sulcus; FEF, frontal eye field; IF, inferior frontal sulcus; IP, inferior precentral sulcus; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; PrePMd, pre-dorsal premotor cortex; SF, superior frontal sulcus; SP, upper part of the superior precentral sulcus. Permission obtained from Elsevier Ltd © Rizzolatti G and Fabbri-Destro M (2008) *Curr Opin Neurobiol* **18:** 179–184.

The study of aplasic individuals born without arms and hands provided further evidence in favor of a goal-coding mirror mechanism.[30] During MRI scanning, two aplasic individuals and a group of nonaplasic volunteers were instructed to watch videos showing hand actions. All participants also made actions with their feet, mouths, and, in the case of the nonaplasic volunteers, hands. The results showed that in aplasic individuals, the observation of hand motor acts, which they had never themselves performed, activated the mirror areas. The communality of goals between the never-executed hand motor acts and those performed with the mouth and feet was the most probable explanation for this activation.

Growing evidence exists that, in addition to goal coding, the human mirror mechanism has a role in the ability to understand the intentions behind the actions of others. In an fMRI study, volunteers observed motor acts (e.g. grasping a cup) embedded in specific contexts (a condition in which the agent's intention could be easily understood) or devoid of context (a condition in which the agent's intention was ambiguous).[31] The results showed that the mirror network was active in both conditions. However, the understanding of intention produced a stronger signal increase in the caudal IFG of the right hemisphere.

The importance of the mirror system in understanding the intentions of others was confirmed by a repetition-suppression fMRI experiment.[32] Participants were asked to observe repeated movies showing either the same movement or the same action outcome regardless of the executed movement. The result showed activity suppression in the right IPL and the right IFG when the outcome was the same.

Movement, emotions and language

As we have discussed, the mirror mechanism located in the parietal and frontal areas codes mostly for the goals of observed motor acts. However, studies that involved transcranial magnetic stimulation (TMS) have shown that the human motor system also responds to the observation of movements devoid of a goal.[33,34] This 'movement mirror mechanism' seems to be extremely sensitive to movement kinematics. Dayan *et al.*[35] studied brain responses to the observation of curved hand movements that either obeyed or disobeyed the law—known as the 2/3-power law—that describes the coupling between movement curvature and velocity. Mirror hand areas were more active during the observation of movements that obeyed this law than during other types of motion.

The mirror mechanism is located not only in centers that mediate voluntary movement, but also in cortical areas that mediate visceromotor emotion-related behaviors.[36,37] Brain imaging studies showed that when an individual feels or observes emotions in others caused by disgusting stimuli or stimuli representing pain, there is activation in two structures: the cingulate cortex and the insula. Interestingly, the same voxels are activated in these two structures in both 'feeling' and 'observing' conditions. This finding strongly suggests that feeling emotions and recognizing them in others are mediated by the same neural substrate.

It should be made clear that the anterior insula, where the aforementioned activations were found, has a dysgranular–agranular structure,[38] and is, therefore, cytoarchitectonically similar to motor areas. Electrical stimulation of the insula in the monkey produces movements of various body

parts, accompanied by a variety of visceromotor responses.[39–40] Similar effects have also been described in humans.[41,42] It is, therefore, appropriate to define these structures as 'mirror areas' in which the motor response includes a visceral component.

In humans, the mirror mechanism is also located in Broca's area, which is involved in language processing and speech production. Evidence for a mechanism that translates heard phonemes into the motor programs necessary to produce them has been provided by TMS experiments.[43] The mouth motor field was stimulated in volunteers while they heard words containing phonemes requiring tongue movements (e.g. "birra") or not requiring tongue movements (e.g. "baffo"). Motor evoked potentials recorded from the tongue muscles increased with the presentation of verbal material containing a double 'r' relative to those containing a double 'f'.

THE MIRROR SYSTEM IN NEUROLOGY
The mirror system and autism

Autism spectrum disorder (ASD) is a heterogeneous developmental syndrome characterized by a marked impairment in social interaction and communication.[44] Communication deficits include disturbances in most domains of language and are not limited to its pragmatic aspects.[45] Impairment in the domains of affective links and emotion recognition is another important component of ASD.[46] A restricted repertoire of activity and interests, repetitive motion, and hypersensitivity to certain sounds are other symptoms that are often present in ASD.

Autism affects a variety of nervous structures, from the cerebral cortex to the cerebellum and brainstem.[47] However, in a context of a broader neurodevelopmental deficit, a set of ASD symptoms (impairment in communication, language and emotion, as well as in the capacity to understand others) seems to match the functions mediated by the mirror mechanism. A hypothesis has, therefore, been advanced that this set of deficits might depend on an impairment of the mirror mechanism,[48,49] and there is growing evidence to support this view.[50–53]

One classical EEG observation is that mu rhythm (an EEG rhythm recorded from the motor cortical areas) is blocked when a person makes a voluntary movement. This rhythm is also suppressed when a person observes another person performing a movement. Oberman et al.[50] used this phenomenon to test the mirror mechanism in children with ASD. The results showed that although individuals with ASD exhibited a suppression of mu rhythm during voluntary movements, this suppression was absent when they watched some one else performing the movement (Figure 4). Martineau et al.[54] have reported similar observations.

Oberman et al.[55] recently reported an interesting observation concerning the mirror system of children with ASD. The authors investigated how familiarity between an observing individual and a person performing a movement modulates the entity of mu rhythm suppression. Typically developing children and children with ASD viewed video clips showing the hand of a stranger performing a grasping action, the hand of a child's guardian or sibling performing the same action, and the participant's own hand performing the action. The study revealed that mu suppression depended on the familiarity of the observer with the agent, and that children with ASD showed mu suppression when a familiar person performed the action but not when it was performed by an unfamiliar person.

An fMRI study has provided strong evidence in favor of a deficit of the mirror mechanism in ASD. High-functioning children with ASD and matched controls were scanned while they imitated and observed emotional expressions. The results showed a markedly weaker activation in the IFG in children with ASD than in typically developing children. Most interestingly, the degree of activation was inversely related to symptom severity.[53]

Impaired motor facilitation during action observation has been reported in individuals with ASD by use of TMS.[52] Furthermore, unlike typically developing individuals, children with ASD tend not to imitate other individuals in a mirror fashion when viewing them face-to-face.[56] This imitation peculiarity is probably attributable to a deficit in the ability of the mirror mechanism to superimpose another person's movements on one's own.

Deficits in the mirror mechanism in ASD have also been addressed from another perspective.[57] Typically developing children and children with ASD were tested while they observed an experimenter either grasping a piece of food for eating or grasping a piece of paper to place it into a container (Figure 5). The EMG activity of the mylohyoid muscle, which is involved in opening of the mouth, was recorded. The results showed that observation of food grasping produced activation
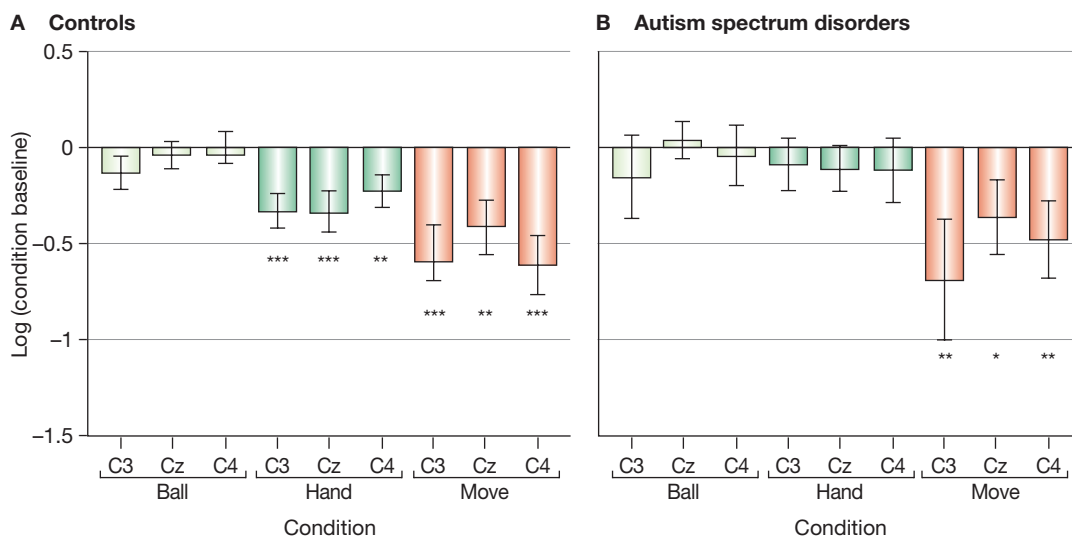
Figure 4 Absence of mirror EEG responses in autism. The charts show suppression of the mu rhythm in controls (**A**) and patients with autism spectrum disorder (**B**) during observation of movement of an inanimate object (ball, pale green) or movements made with a hand (hand, green), and during active hand movements made by the individual from whom recordings were being taken (move, red). The bars represent the amount of mu activity in central scalp locations; C3, Cz and C4 refer to scalp coordinates of the 10/20 EEG system. Significant suppression of this activity, indicated by asterisks, is present for the hand observation condition only in controls, showing that patients with autism spectrum disorder fail to respond in a standard way to the observation of other people's actions. Permission obtained from Elsevier Ltd © Oberman LM *et al.* (2005) *Brain Res Cogn Brain Res* **24:** 190–198.

of the mylohyoid muscle in typically developing children, but not in children with ASD. In other words, whereas the observation of an action done by another individual intruded into the motor system of a typically developing observer, this intrusion was lacking in children with ASD. This finding indicates that, in this disorder, the mirror system is silent during action observation, and that the immediate, experiential understanding of the intentions of others is absent.

Both children with ASD and typically developing children were also asked to perform the two actions described above (grasp to eat and grasp to place) while the EMG activity of the mylohyoid muscle was recorded.[57] In typically developing children, the muscle became active as soon they moved the arm to reach the food. By contrast, no mylohyoid muscle activation was observed during food reaching and grasping in children with ASD; activation of the muscle was evident only when these children brought the food to their mouths. These data indicate that children with ASD are not only unable to organize their own motor acts into a unitary action characterized by a specific intention, but that they also show a deficit in the mirror mechanism, as

reflected in the absence of motor activation of the muscles involved in an observed action.

These findings show an apparent contradiction between the cognitive capacities of children with ASD to report the purpose of an experimenter's action and their lack of motor resonance with the action. To clarify this incongruity, a further experiment was performed in which typically developing children and children with ASD observed an actor performing goal-directed motor acts and were asked to report what the actor was doing and why he was doing it (Rizzolatti G *et al.*, unpublished data). These tasks test two different abilities: the ability to recognize a motor act (e.g. grasping an object) and the ability to understand the intention behind it (e.g. grasping to eat). The results showed that both typically developing children and children with ASD were able to recognize what the actor was doing, but children with ASD failed to recognize why the act was being performed. Children with ASD systematically attributed to the actor the intention that could be derived by the semantics of the object— for example, an intention to cut when scissors were shown—regardless of how the object was grasped. This finding indicates that children
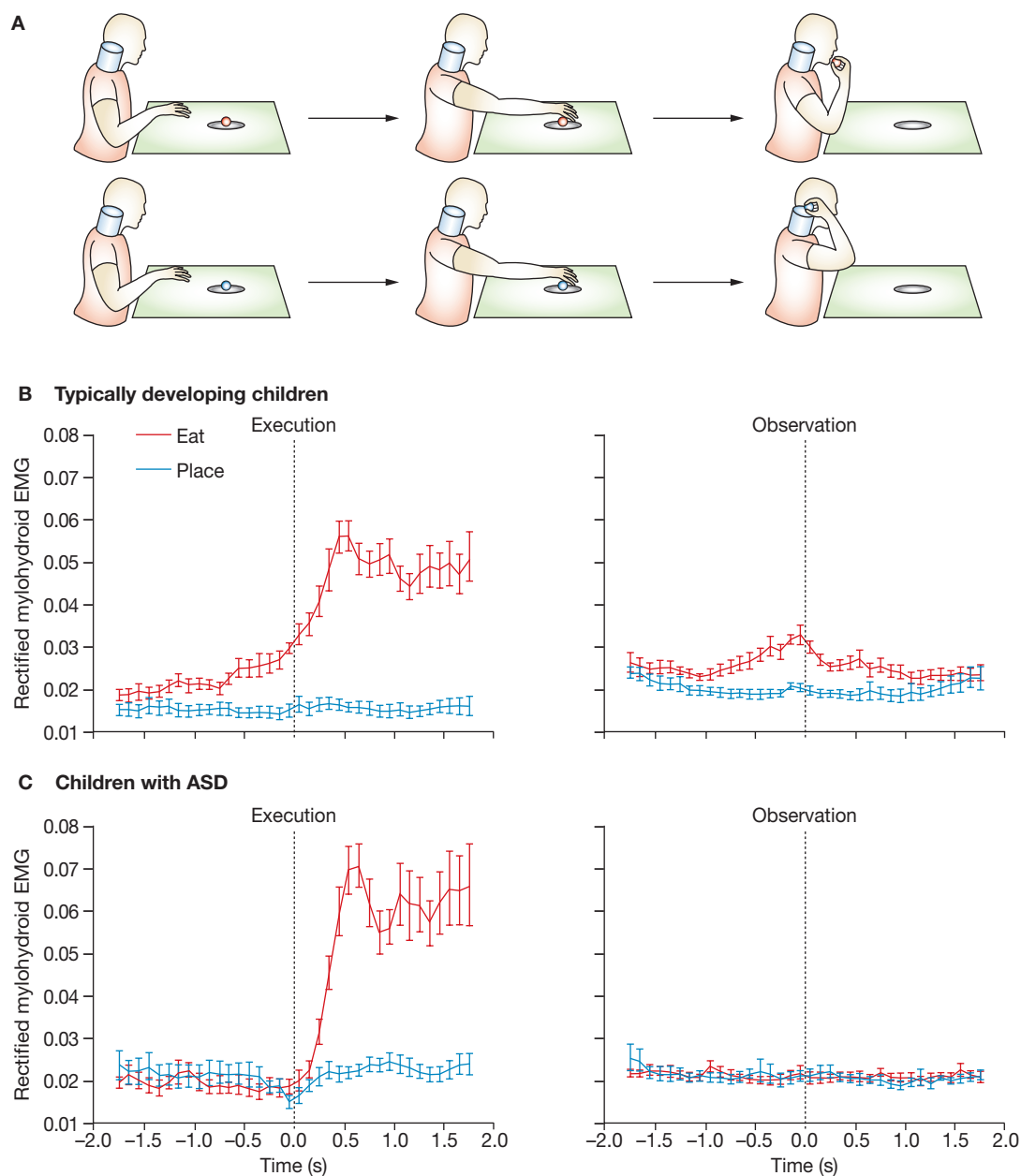
Figure 5 Motor behavior in typically developing children and children with ASD. This experiment was designed to assess whether an action-constrained motor organization is present in typically developing children and children with ASD.[57] (**A**) Schematic representation of the tasks. The individual reaches for an item on a plate and either brings it to their mouth or puts it into a container placed on their shoulder. Time course for typically developing children (**B**) and children with ASD (**C**) of the rectified electromyographic activity of mouth-opening muscles during the execution (left side) and observation (right side) of the 'bringing-to-the-mouth' action (red line) and of the 'placing' action (blue line). All curves are aligned with the moment of object lifting from the touch-sensitive plate (time = 0). The results demonstrate a lack of anticipatory motor activity during execution and a lack of mirror motor activation during observation of a given action in children with ASD. Abbreviations: ASD, autism spectrum disorder; EMG, electromyography.

with ASD interpret the behavior of others on the basis of the standard use of objects rather than the actual behavior of a person performing a task. Children with ASD, therefore, seem to lack the ability to read the intentions of others on the basis of behavior.

The mirror mechanism and motor rehabilitation

As well as having a role in action understanding, the mirror mechanism also modulates the motor behavior of the observer. This function forms the basis for the imitation of simple motor acts[58] and for learning through imitation.[59] Particularly interesting from a clinical point of view was the demonstration that the mirror mechanism is involved in the building of motor memories. The most convincing evidence for such a role came from studies by Stefan et al.[60,61] that involved TMS. The authors showed that when participants simultaneously performed and observed congruent movements, the learning of these movements was potentiated with respect to learning through motor training alone. These findings indicate that the coupling of observation and execution strongly facilitates the formation of motor memories.

Could this mechanism be exploited for motor rehabilitation? Many current behavioral neurorehabilitation techniques use strategies that induce long-term plasticity in the motor cortex either by depressing activity on the unaffected side or by potentiating activity on the affected side.[62] The possibility that plasticity might be induced in the motor cortex by coupling action observation and execution represents the theoretical basis of a recent study that examined the effect of an 18-day cycle of active motor training with the paretic limb in two groups of patients with chronic stabilized stroke in the middle cerebral artery territory.[63] The test group was required to perform hand motor acts prompted by movies showing similar motor acts, whereas the control group performed the same motor training without any visual cues. Functional assessment of the upper limb showed a significant improvement in the test group relative to the control group.

The mirror mechanism probably also forms the neurophysiological basis for 'mirror therapy' (the word 'mirror' being used here in its literal sense), which has been shown to improve upper-limb function in patients with stroke.[64,65] In mirror-therapy protocols, the patients are required to perform movements with their nonparetic hand while watching the hand and its reflection in a parasagittal mirror. This procedure gives a visual illusion of movement of the paretic hand. The generation of cortical plasticity and the consequent rehabilitative results strongly suggest a role in patient improvement for a mechanism that matches seen and executed actions, thereby implicating the mirror mechanism in this process.[66]

Deficits in the control of mirror mechanisms

Clinical observations have shown that frontal lesions can cause a series of disturbances characterized by the appearance of forced motor behavior triggered by external stimuli.[67] Among these manifestations, imitation behavior is particularly interesting in relation to the mirror mechanism. The main feature of this syndrome is the spontaneous imitation of motor acts done by others, and it is considered to be part of the so-called 'environmental dependency syndrome'.[68] The condition arises from unilateral, or, more frequently, bilateral prefrontal lesions.[68,69] Imitation behavior is generally attributed to an imbalance between exogenously and endogenously determined behaviors. The observation of actions done by others leads to the coding of potential motor acts in the parietal and premotor mirror areas by means of the mirror mechanism. These potential motor acts typically do not determine overt movements in the healthy adult brain because the manifestation of these acts is suppressed by the frontal lobe. Damage to this lobe would destroy this control mechanism, thereby transforming the potential motor acts into actual motor behavior. In view of the temporal latency between observation and imitation that patients often show, an additional mechanism could be also involved, but the essence of the phenomenon seems to depend on a release of potential motor acts.

Echopraxia is a term that describes forced and uncritical imitation of behaviors. The exogenously triggered behavior is sustained through endogenous mechanisms, resulting in its perseveration. In view of the simplicity of the imitated behaviors, combined with the total lack of criticism of the patient to the imitated behavior, echopraxia is perceived as a distinct disorder from imitation behavior. Echopraxia can arise in the context of basal ganglia dysfunction, as well as after frontal lobe damage. It is probable, however, that in both cases the mechanism that underlies echopraxia is a disinhibition of the mirror areas through loss of suppression by the frontal lobe.[70]

CONCLUSIONS AND FUTURE PROSPECTS

The discovery of the mirror mechanism radically changed our views on how individuals understand actions, intentions and emotions. The identification of this mechanism has had

a profound impact on a variety of disciplines, ranging from cognitive neurosciences to sociology and philosophy. Until recently, this discovery had influenced clinical research to a much lesser degree. However, it has now provided deeper insights into the interpretation of certain neurological syndromes, such as the environmental dependency syndrome, and has provided a new theoretical basis for establishing rehabilitation techniques in patients with motor deficits following stroke.

Autism is one condition in which the discovery of the mirror neuron mechanism could have important practical implications in the future. Recent experimental data suggest that individuals with ASD have a deficit in representing goal-directed actions, both when the actions are performed and when they are observed. Children with ASD, therefore, show impairments in organizing their own motor acts according to an action goal, as well as in using this motor mechanism to understand the intentions of others. This new view on ASD could be used to establish new rehabilitation strategies based on a motor approach. The rationale of such an approach is that if the motor knowledge of individuals with ASD is improved, their social knowledge and behavior would also be enhanced.

KEY POINTS

- The mirror mechanism is a neural system that unifies action perception and action execution

- The mirror mechanism is organized into two main cortical networks, the first being formed by the parietal lobe and premotor cortices, and the second by the insula and anterior cingulate cortex

- The role of the mirror mechanism is to provide a direct understanding of the actions and emotions of others without higher order cognitive mediation

- Limited development of the mirror mechanism seems to determine some of the core aspects of autism spectrum disorders

- The recently demonstrated link between limited development of the mirror mechanism and that of some aspects of the motor system suggests that rehabilitation in children with austism spectrum disorder should take into account both motor and cognitive strategies

- The use of action-observation-based protocols could represent a new rehabilitation strategy to treat motor deficits after stroke

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Competing interests
The authors declared no competing interests.

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