

THE INFLUENCE OF BODY POSTURE ON THE MIRROR NEURON SYSTEM

A.A. RAGIMOVA^{a,b}, C.M. NIETO-DOVAL^a, M.I. SALAMATIN^a,
A.N. VOROBIOVA^{a,c}, O.I. SHEVTSOV^a, A.O. VIAZMIN^a, M. FEURRA^a

^a HSE University, 20 Myasnitskaya Str., Moscow, 101000, Russian Federation

^b Scientific Center of Neurology, 80 Volokolamskoe highway, Moscow, 125367, Russian Federation

^c Center for Neurocognitive Research (MEG-center) MSUPE, 2A build. 2 Shelepikhinskaya embankment, Moscow, 123290, Russian Federation

Влияние положения тела на систему зеркальных нейронов

А.А. Рагимова^{a,b}, К.М. Нието-Доваль^a, М.И. Саламатин^a, А.Н. Воробьева^{a,c},
О.И. Шевцов^a, А.О. Вязьмин^a, М. Феурра^a

^a Национальный исследовательский университет «Высшая школа экономики», 101000, Россия, Москва, ул. Мясницкая, д. 20

^b Научный центр неврологии, 125367, Россия, Москва, Волоколамское шоссе, д. 80

^c Центр нейрокогнитивных исследований (МЭГ-центр) ФГБОУ ВО МГППУ, 123290, Россия, Москва, Шелепихинская набережная, д. 2а, стр. 2

Abstract

Though the mirror neuron system (MNS) is studied in the scientific community, the influence of the body posture on the functioning of the MNS, as well as on the excitatory and inhibitory system of the brain,

Резюме

Система зеркальных нейронов (СЗН) широко изучается в научном сообществе, однако до сих пор не выявлено влияние положения тела на функционирование СЗН, а также на возбуждающую и ингибиторную системы мозга.

This work/article is an output of a research project implemented as part of the Basic Research Program at the HSE University and Strategic Project “Human Brain Resilience: Neurocognitive Technologies for Adaptation, Learning, Development and Rehabilitation in a Changing Environment”, which is part of Higher School of Economics’ development program under the “Priority 2030” academic leadership initiative. The “Priority 2030” initiative is run by Russia’s Ministry of Science and Higher Education as part of National Project “Science and Universities”.

Исследование осуществлено в рамках Программы фундаментальных исследований НИУ ВШЭ и стратегического проекта «Устойчивый мозг: нейрокогнитивные технологии адаптации, обучения, развития и реабилитации человека в изменяющейся среде» по программе развития НИУ ВШЭ в рамках участия в программе Минобрнауки России «Приоритет-2030». Программа «Приоритет-2030» реализуется в рамках национального проекта «Наука и университеты».

has not been revealed yet. In our study, we investigated the functioning of the MNS in case of head rotation. Participants underwent a session of the mirror task, while they were observing movements of the little finger and the index finger of a static hand in three head positions (left, straight and right), combined with transcranial magnetic stimulation (TMS) that was applied at various time intervals. Results showed significant interactions between the movement type and the targeted muscle ($F[1,113-16,688] = 9.47$, $MSE = 56296.14$, $p = .006$, $\text{partial } \eta^2 = .39$). This indicates a robust increase in the activation of the First Dorsal Interosseous (FDI) muscle during the index finger movement ($p = .01$) and the neutral movement ($p \leq .001$) observation compared to the little finger movement. Conversely, a significant inhibition of the Abductor Digiti Minimi (ADM) muscle activity was observed during the index finger movement compared to neutral ($p = .026$). A reversed effect emerged during the little finger movement observation, with higher activation for the ADM muscle and inhibition of the FDI muscle ($p = .037$). These findings suggest an intricate interplay between MNS activation and muscle activation, indicating an increase in muscle activity corresponding to the observed finger movement and simultaneous inhibition of the muscle not involved in the observed movement.

Keywords: mirror neurons; action observation; transcranial magnetic stimulation; head positioning; motor cortex excitability; primary motor cortex; rehabilitation.

Aynur A. Ragimova – Research Fellow, HSE University; Scientific Center of Neurology, PhD in Medical Sciences. Research Area: neuroscience, noninvasive brain stimulation, brain stimulation, psychiatry, psychoneurology. E-mail: ragimovaasia@gmail.com

В нашем исследовании мы изучали работу СЗН при повороте головы. Участники наблюдали за движением руки на видео: за движениями мизинца, указательного пальца неподвижной руки в трех положениях головы (с поворотом головы налево, направо и в прямом положении), в сочетании с транскраниальной магнитной стимуляцией (ТМС) в различные промежутки времени. Результаты выявили значительное взаимодействие между типом движения и целевой мышцей ($F[1,113-16,688] = 9.47$, $MSE = 56296.14$, $p = 0.006$, $\text{частичное } \eta^2 = 0.39$), что указывает на значительное увеличение активации первой дорсальной межкостной мышцы (FDI) во время наблюдения за движением указательного пальца ($p = 0.01$) и нейтральным движением ($p < 0.001$) по сравнению с движением мизинца. И наоборот, значительное торможение активности мышцы ADM наблюдалось во время движения указательного пальца по сравнению с нейтральным ($p = 0.026$). Обратный эффект возник при наблюдении за движениями мизинца: более высокая активация мышцы ADM и торможение мышцы FDI ($p = 0.037$). Эти результаты предполагают сложное взаимодействие между активацией СЗН и активацией соответствующих мышц, что указывает на увеличение мышечной активности, соответствующее наблюдаемому движению пальца, и одновременное торможение мышц, не участвующих в наблюдаемом движении.

Ключевые слова: зеркальные нейроны; наблюдение за действиями; транскраниальная магнитная стимуляция; положение головы; возбудимость моторной коры; первичная моторная кора; реабилитация.

Рagимova Айнуp Алигейдаровна – научный сотрудник, НИУ ВШЭ; Научный центр неврологии, кандидат медицинских наук. Сфера научных интересов: нейронауки, неинвазивная стимуляция мозга, стимуляция мозга, психиатрия, нейробиология поведения, психоневрология. E-mail: ragimovaasia@gmail.com

Carlos M. Nieto-Doval — Junior Research Fellow, HSE University, Master's Degree in Psychology.

Research Area: neuroscience, noninvasive brain stimulation, transcranial magnetic stimulation.

E-mail: carlosnietodoval@hotmail.com

Mikhail I. Salamatin — Research Assistant, HSE University, Bachelor's Degree in Psychology.

Research Area: neuroscience, noninvasive brain stimulation, TMS, tDCS, psychology.

E-mail: mihail.salamatin@gmail.com

Alicia N. Vorobiova — Lecturer, HSE University; Research Fellow, Center for Neurocognitive Research (MEG-center) MSUPE, PhD in Cognitive Sciences.

Research Area: neuroscience, neuroplasticity, non-invasive brain stimulation.

E-mail: anvorobiova@hse.ru

Oleg I. Shevtsov — Lead Engineer, HSE University, Master's Degree in Psychology.

Research Area: neuroscience, bioelectronics, IT.

E-mail: olegshevts@gmail.com

Aleksander O. Viazmin — PhD Student, HSE University, Specialist Degree in Systems Engineering.

Research Area: neuroscience, noninvasive brain stimulation, TMS, EEG, tDCS, kinematic study, neurorehabilitation.

E-mail: aovyazmin@hse.ru

Matteo Feurra — Lead Research Fellow, HSE University, PhD in Psychological Sciences, Associate Professor.

Research Area: memory encoding, motor control, sensorimotor cortex, neuroscience, noninvasive brain stimulation, TMS, EEG, tDCS, kinematic study, neurorehabilitation.

E-mail: matfeu@gmail.com

Нieto-Доваль Карлос Муриель — младший научный сотрудник, НИУ ВШЭ, магистр психологии.

Сфера научных интересов: нейронауки, неинвазивная стимуляция мозга, транскраниальная магнитная стимуляция.

E-mail: carlosnietodoval@hotmail.com

Саламатин Михаил Игоревич — стажер-исследователь, НИУ ВШЭ, бакалавр по специальности «Психология».

Сфера научных интересов: нейронауки, неинвазивная стимуляция мозга, ТМС, ТЭС, психология.

E-mail: mihail.salamatin@gmail.com

Воробьева Алисия Нуньес — доцент, НИУ ВШЭ; научный сотрудник, Центр нейрочувствительных исследований (МЭГ-центр), ФГБОУ ВО МГППУ, кандидат когнитивных наук.

Сфера научных интересов: нейронауки, нейропластичность, неинвазивная стимуляция мозга.

E-mail: anvorobiova@hse.ru

Шевцов Олег Игоревич — ведущий инженер, НИУ ВШЭ, магистр психологии.

Сфера научных интересов: нейронауки, биоэлектроника, информационные технологии.

E-mail: olegshevts@gmail.com

Вязьмин Александр Олегович — аспирант, НИУ ВШЭ, специалист по специальности «Инженер-системотехник».

Сфера научных интересов: нейронауки, неинвазивная стимуляция мозга, ТМС, ЭЭГ, ТЭС, кинематические исследования, нейрореабилитация.

E-mail: aovyazmin@hse.ru

Феурра Маттео — ведущий научный сотрудник, НИУ ВШЭ, PhD, доцент.

Сфера научных интересов: нейробиологические механизмы памяти, моторный контроль, сенсомоторная кора, неинвазивная стимуляция мозга, ТМС, ЭЭГ, ТЭС, кинематические исследования, нейрореабилитация.

E-mail: matfeu@gmail.com

The mirror neuron system (MNS), a crucial element in understanding social interaction and empathy (Häusser, 2012), serves various functions, including action imitation and involvement in language development, and it is also believed to play a role in comprehending written descriptions of actions (Iacoboni, 2009; Zarr et al., 2013; Gallese, 2008, Hickok, 2010). The MNS was initially discovered in the area F5 in the premotor cortex, which is connected to the inferior parietal lobule (Rizzolatti et al., 1996; Bonini et al., 2022; Fogassi et al., 2005), with studies confirming similar neural networks in humans, such as inferior frontal gyrus (IFG), the lower part of the precentral gyrus, the rostral part of the inferior parietal lobule and also the temporal, occipital and parietal visual areas and their involvement in cognitive processes (Gallese, 2008; Fox et al., 2016; Rajmohan & Mohandas, 2007; Rizzolatti & Craighero, 2004).

According to Rajmohan and Mohandas (2007), both common and distinct characteristics of the MNS in monkeys and humans are observed. These traits include:

1. The MNS responds when performing or observing actions that involve interaction between a biological effector and an object.
2. Specific brain regions, such as the premotor cortex in monkeys and the inferior frontal gyrus (IFG) in humans, show activation.
3. The system exhibits somatotopic organization, where different regions correspond to specific body parts or actions.
4. The MNS is activated by both strictly congruent actions (exact effector-object interactions) and broadly congruent actions (similar but not exact).
5. In humans, the MNS is activated during the observation of both meaningful (transitive) actions and meaningless (intransitive) movements, which contrasts with monkeys where this activation pattern is not observed.

The role of the MNS in language development and comprehension is a notable distinction between human and monkey MNS. Embodied accounts of language comprehension suggest that understanding action-related sentences activates neural mechanisms involved in action control, including the MNS. This results in bidirectional adaptation effects between the MNS, a component of the motor system, and language processing. Specifically, repeatedly performing an action in one direction can slow down the comprehension of sentences describing similar actions. Conversely, as shown in recent studies, comprehending sentences that describe an action in one direction can interfere with the perception of actual actions in the same direction (Zarr et al., 2013; Hickok, 2010).

The developmental framework for computational MNS presented in the study conducted by Dawood (2016) offers a novel approach to imitation learning through self-exploration. This model is studying the proposed MNS in robots and is predicated on the assumption that humanoid robots initially lack a priori knowledge about themselves, necessitating the construction of a self-model. The model suggests that action imitation can arise from the intrinsic properties of a neural associative network, driven by spontaneous actions and their visual feedback. This approach aligns with current trends in developmental robotics and cognitive neuroscience, emphasizing the importance of embodied learning and self-exploration in the development of imitation capabilities. It provides a computational framework

that could potentially bridge the gap between biological MNS and artificial implementations, offering insights into the emergence of imitative behaviors in both natural and artificial systems (Dawood & Loo, 2016).

Transcranial magnetic stimulation (TMS) is a pivotal tool in studying the influence of human mirror neurons on the excitability of brain areas. Research using TMS has shed light on the role of mirror neurons in various conditions, encompassing motor disorders and aspects of social interaction disorders (Feurra et al., 2019; Basavaraju et al., 2018; Cao et al., 2021; Tarhan et al., 2015). For instance, Fadiga et al. (1995) demonstrated that TMS-induced motor cortex excitability changes during action observation, indicating the presence of mirror neuron activity in humans. This ability to non-invasively measure cortical excitability makes TMS an invaluable tool for understanding how the brain processes and mirrors observed actions (Cracco et al., 2016).

In summary, mirror neurons in both humans and monkeys play a role in action understanding, imitation, speech, and emotion processing. However, the roles of mirror neurons may vary between species. For instance, human mirror neurons are implicated in understanding both the goal and the intention behind an action, whereas monkey mirror neurons primarily respond to the observation of specific motor acts (Fabbri-Destro & Rizzolatti, 2008).

The MNS is an extraordinary automated system devoted to understanding and learning motor actions. Although mirror neurons generally operate relatively independently, their functioning can be subtly influenced by external or internal conditions including addiction, neurological, and psychiatric disorders (Basavaraju et al., 2018; Cao et al., 2021).

Perception of meaningful (transitive) movements is associated with activation of various sectors of Broca's area and the premotor cortex, contingent on the effector involved in the observed action. This activation follows a somatotopic pattern resembling the classical motor cortex homunculus (Buccino et al., 2004). A widely accepted theory suggests that the mu rhythm reflects resting activity in the sensorimotor cortex, and suppression of this rhythm indicates activation of these brain areas (Gastaut & Bert, 1954). Studies utilizing electroencephalography (EEG) have shown that predictable movements significantly affect cortical activity by suppression of the mu rhythm (Takahashi et al., 2008). This underscores the importance of action predictability in regulating mirror neuron responses. In a meta-analysis conducted by Van Overwalle & Baetens (2009), it is proposed that not only does a perceptual component of the MNS exist, responsive to logical and sequential movements, but also is a mentalizing component, including the temporo-parietal junction, medial prefrontal cortex, and precuneus, activated when making inferences about terms or situations expressed in abstract concepts or contextually incompatible situations (Van Overwalle & Baetens, 2009).

Key aspects of the MNS include its ability to function autonomously, its modulation in response to prior learning, and a significant influence of logical context in action perception. Another crucial factor in mirror neuron activation, which we will explore in this article, is the impact of task presentation methods on MNS activation under experimental conditions.

One of the controversial aspects of the functioning of the mirror neuron system (MNS) is its involvement in understanding actions from a first-person perspective. This point remains debatable due to limitations in experimental design. Some studies, such as those by Burgess et al. (2013), demonstrate a lack of distinction between egocentric (i.e., self) and allocentric (i.e., other) viewpoints.

The way tasks are presented plays a crucial role in mirror neuron research (Bianco et al., 2012; Rossini et al., 1999). The activation of the mirror system is related to the number of observed agents, for example, MNS activation during the observation of two hands was higher than during the observation of a single hand (Cracco et al., 2016). Studies that use live demonstrations of movements by an assistant have shown promising results (Feurra et al., 2019), but they also come with limitations. For instance, synchronizing movement demonstrations with TMS stimulation can be challenging, and exactly replicating movements with consistent spatial and temporal characteristics can be difficult. Recent studies on stimulus presentation for mirror neuron research suggest that using photographic or video formats (Catmur et al., 2011; Barchiesi & Cattaneo, 2012; Errante & Fogassi, 2020; Nietto-Doval et al., 2023) can provide a more precise replication of movements, offering a potential solution to these challenges.

In this study, we are focusing on the relationship between the mirror neuron function and body posture, using neck turning as an example. Our investigation is inspired by the findings of Popa et al. (2018), which demonstrated that neck turning can alter responses to paired associative stimulation (PAS), bringing them closer to the state observed in cervical dystonia (CD) patients. Popa et al. (Ibid.) provided evidence that abnormal cerebellar processing of proprioceptive information drives dysfunctions in CD, suggesting that proprioception plays a crucial role in the pathogenesis of CD.

The cerebellum is integral to the MNS, influencing both action observation and execution. However, our study did not modulate or test cerebellar activity, focusing instead on the specificity of MNS function in relation to body position changes. This distinction is crucial as it highlights that our research bypasses cerebellar contributions, which are important for body posture changes and action execution, potentially involved in mirror neuron effects (Fabbri-Destro & Rizzolatti, 2008; Rajmohan & Mohandas, 2007; Morton & Bastian, 2004).

This study explores the connection between mirror neuron (MNS) function, neck muscle activity, and body posture. It aims to determine, among other things, whether mirror neurons respond to changes in posture, how neck muscles influence MNS activity, and whether neck muscles are activated in non-specific mirror tasks involving unrelated muscle groups, including the hand muscles. Sommerich et al. (2000) pointed out that methodological issues with prior research on neck muscles included differences in electrode positioning, data normalization procedures, and the effect of heart rate on electromyography (EMG) measurements. It is challenging to reach firm conclusions regarding the function of the neck muscles because of these contradictions. However, recent developments have illuminated this field. Virtual reality (VR) and online EMG were used by Figas et al. (2023) to show that there is an asymmetry in the tension in the neck muscles, specifically in the left

sternocleidomastoid (SCM) and trapezius muscles. According to an individual's awareness of a potential threat, Pashaei et al. (2023) also found distinct EMG patterns in the SCM, upper trapezius, and cervical erector spinae muscles, suggesting specific muscular activation methods for limiting neck extension and flexion. These results provide opportunities to investigate the relationship between brain excitability and neck muscle activation, as investigated by Popa et al. (2018) in regard to the Cajal nuclei. The extent of this association, however, might be constrained by Popa et al.'s methodology lacking neck muscle recordings.

Aim of the Study

This research investigates the influence of head position on the activity of MNS. The study will examine how different head orientations, specifically left, right, and straight, affect the neural processes involved in mirroring. By exploring this relationship, the researchers aim to gain a deeper understanding of how head position variations impact the way we perceive and understand the actions of others.

Materials & Methods

Subjects

Only healthy right-handed individuals (total number $N = 16$, 8 females, mean age 22, range [19; 29]) participated in the study. To minimize potential confounding factors, as well as for safety reasons (Rossi et al., 2009), only participants who had reported of absence of personal or family history of neurological or mental disorders were recruited. Additionally, they were asked to refrain from any psychoactive substances prior to each experimental session. All participants signed an informed consent form. The study received approval from the local ethical committee (the Ethical Committee of the National Research University Higher School of Economics in Moscow) and complied with the international ethical standards outlined in the Declaration of Helsinki. During the experiment, participants were seated comfortably in a chair with their heads tilted back, hands still and right arm in a relaxed state, perpendicular position relative to the presentation screen.

Transcranial Magnetic Stimulation

The left primary motor cortex (M1) was subjected to transcranial magnetic stimulation (TMS) using C-B60 and C-B85 coils connected to the MagPro X100 stimulator (MagVenture, Denmark). Accurate targeting was ensured by a frameless neuronavigation device (Localite TMS Navigator, Germany) that guided the coil placement based on individual MRI images. The first dorsal interosseus (FDI) and abductor digiti minimi (ADM) muscles were used to elicit Motor Evoked Potentials (MEPs), which allowed for the identification of the hotspot, or an ideal stimulation point. These muscles had an average MEP amplitude ratio of 3:1. The C-B60 coil was used to manually locate the hotspot; it was then swapped out for a

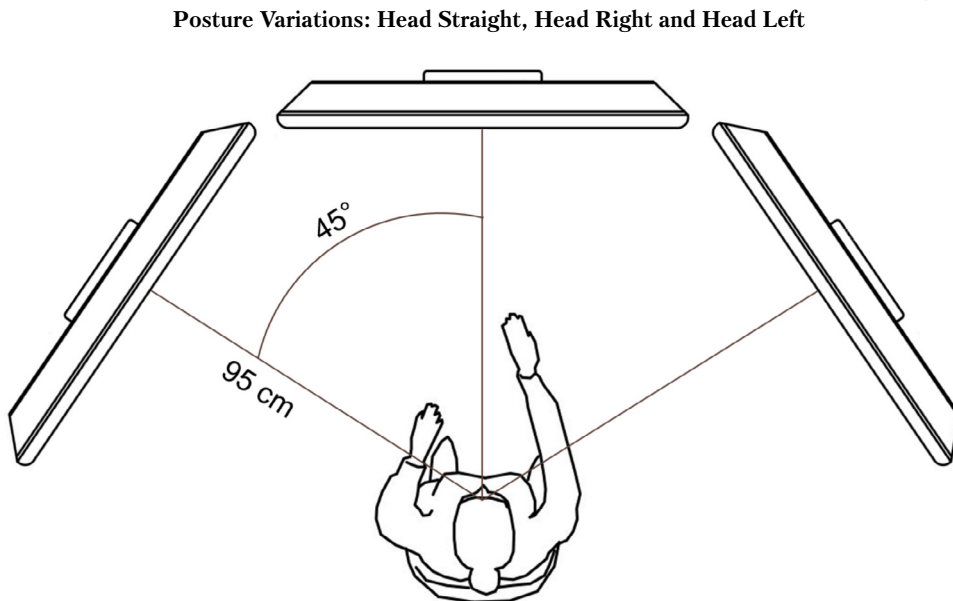
C-B85 induction coil installed on an Axilum TMS Cobot System (Brainbox Ltd., UK). The magnetic field strength, the diameter (75 mm), and the butterfly shape of both coils were identical. Throughout the experiment, the robotic arm system compensated for head motions and ensured exact stimulation at the predefined hotspot, maintaining the accuracy of neuronavigation. To define the rMT we gradually increased and decreased an output stimulator intensity, according to the standard procedure described in Rossini et al. (1994). The resting motor threshold (rMT) was set as a minimal intensity eliciting MEPs with a peak-to-peak amplitude of at least 50 μV in 50% of trials. TMS intensity was set at 110% of the rMT in the dominant (left) hemisphere for the experimental tasks. We used pre-gelled adhesive Ag/AgCl electrodes (EB Neuro S.p.A., Italy) connected to a DC amplifier (BrainAmp, Brain Products GmbH, Germany) to register EMG from the target muscles of the right hand at a sampling rate of 5 kHz.

Task and Stimulation Protocol

Participants sat facing a screen and completed a protocol that comprised baseline assessments before and after the primary task. For 27 MEP recordings, the baseline consisted of observing a black screen with a white fixation cross. Then the MEPs were recorded in three different postures in randomized order: head straight, head right, and head left (Figure 1).

Participants' heads were rotated to the 45 degrees from the midline for the head right and head left conditions, so that the middles of their chins and collarbones lined up. The distance of ninety-five centimetres to the screen was maintained. The

Figure 1



head rotation conditions were arranged in a randomized order, with three sets of 54 stimulus presentations on each side and three-minute rest intervals for the participants in between.

Each trial followed a specific sequence of visual stimulation:

a) A fixation cross for 2.5 s; b) A resting hand for a duration of 8, 1.6 or 2,4 s; c) A video of a hand movement (sideways index finger, sideways little finger, or no movement) for 1 s. Each movement type occurred in 54 instances in a randomized sequence; d) A resting hand image for 1 s; e) single TMS pulses were triggered with a randomly chosen jitter of 0, 0.32, or 0.64 s from the onset of the second resting hand presentation (post-movement phase); f) a black screen for 1 m (Figure 2).

All stimuli were presented using E-Prime 3.0 software, and TMS pulses were synchronized with the visual presentation using TTL marks.

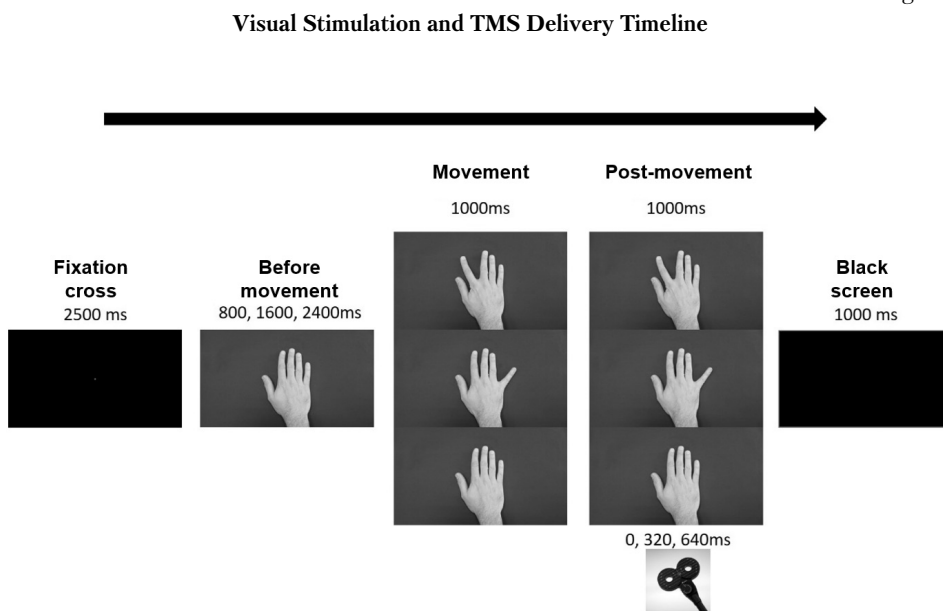
Similar to the pre-task baseline, a second baseline measurement was conducted following the main task. Over the course of the experiment, 216 TMS pulses were given, and the accompanying MEPs from the FDI and ADM muscles were recorded.

Data Processing

Power-line noise was eliminated from the data by using a 50-Hz notch filter. Furthermore, the data was high-passed at 15-Hz before the Motor Evoked Potentials (MEPs) analysis. The exclusion criteria for MEPs were: insufficient peak-to-peak amplitude ($<50 \mu\text{V}$), artifacts, or high latency variability.

Next, for each condition, the raw amplitude data from the FDI and ADM muscles were averaged and sorted based on the type of stimulus and timing of stimulation.

Figure 2



This data was adjusted using the mean baseline MEP amplitude for each muscle (FDI and ADM) and head position (Straight, Right, Left) for both pre- and post-black screen stimuli. Since there were no discernible changes between the pre- and post-baseline measurements, the baselines were pooled for normalization (repeated measures ANOVA indicated non-significant findings for both FDI and ADM muscles).

Normalization was implemented to account for inter-subject variability in raw MEP amplitudes during stimulus presentation. The effects of the experimental manipulations on MEP size were assessed as percentage changes from the mean baseline amplitude (set at 100%) for both target muscles (Feurra et al., 2019; Rossini et al., 1999).

This approach ensured that the analysis focused on the relative changes in MEP amplitude induced by the experimental conditions, rather than absolute amplitude differences between individuals.

Statistical Analysis

We ran a four-factor analysis of variance (ANOVA) with repeated measures for the following independent variables: Target Muscle (FDI, ADM), observed Type of Movement (Index finger, Little finger, Neutral), Head Posture (Straight, Right, Left), and Stimulation Jitter (0, 3.2, 6.4 s). We employed the Bonferroni correction in post-hoc pairwise comparisons due to significant interactions between these factors. Due to the exploratory character of the investigation, this strategy was selected to increase the power to identify differences between particular pairings of conditions while controlling the overall error rate (Type I error) at the standard significance threshold ($\alpha = .05$). Furthermore, we used the Greenhouse-Geisser correction to modify the degrees of freedom and preserve the validity of the ANOVA results when Mauchly's test of sphericity revealed a breach of the sphericity assumption ($p > .05$).

Results

The four-factor repeated measures ANOVA yielded a significant interaction between Type of Movement and Target Muscle ($F[1,113-16,688] = 9.47$, $MSE = 56296.14$, $p = .006$, $\eta^2 = .39$). This suggests an interrelation between the muscle activity and visually presented movement.

Post-hoc comparisons showed that FDI muscle activity was significantly higher during the index finger movement and static hand observation compared to the little finger movement ($p = .01$ and $p < .001$, respectively). This suggests a strong inhibitory effect on FDI activation during little finger movement observation. Similarly, ADM muscle activity was higher during the static hand observation compared to the index finger movement ($p = .026$), indicating its suppression in response to the observation of the index finger movement (Figure 3).

The observed difference between the target muscles activity during the little finger movement ($p = .037$) further highlights this pattern of excitation for the

Figure 3

Averaged normalized MEP Amplitude for Target Muscle by Type of Movement

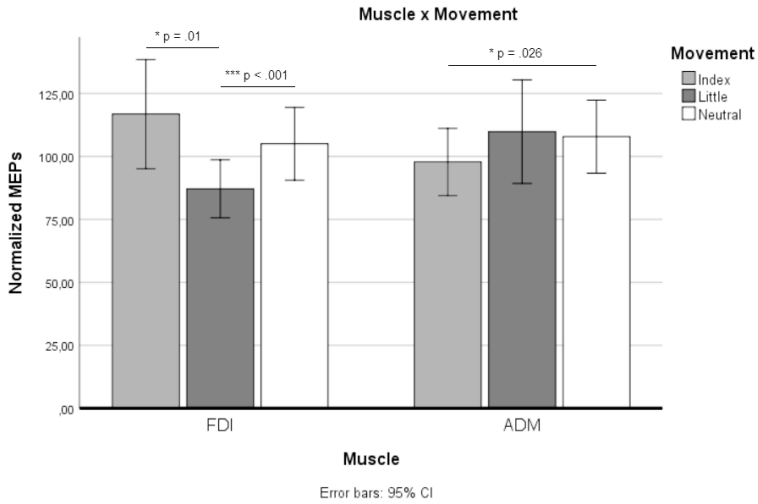
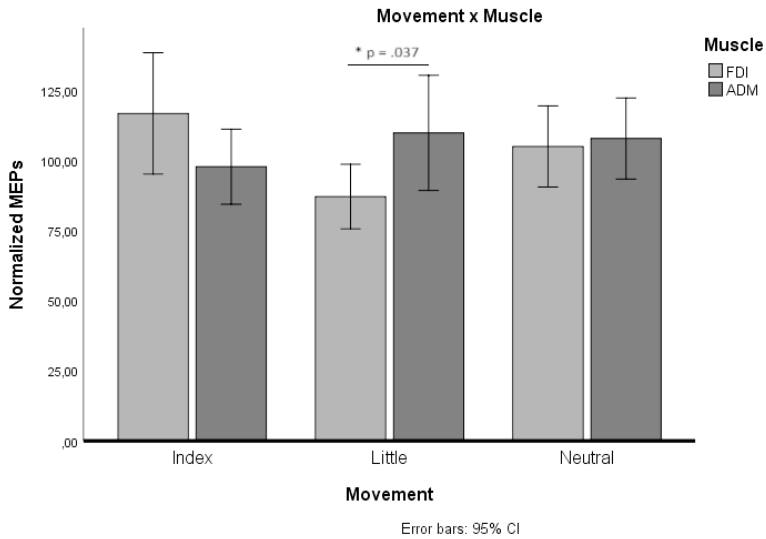


Figure 4

Averaged Normalized MEP Amplitude for Type of Movement by Target Muscle



* $p < 0.05$, *** $p < 0.001$.

muscle related to the observed movement and inhibition for the unrelated muscle, with a facilitation of ADM and suppression of FDI MEPs size (Figure 4).

Interestingly, while no significant differences in MNS activation related to the Head Posture variation were observed ($p = .138$), this could be considered a promising

trend. However, the present results only allow the conclusion that the MNS response to action observation does not vary upon the head posture changes.

Another interesting trend was observed for the MEP amplitudes facilitation during head rotation ($p = 0.24$), suggesting a potential link between head posture and motor cortex excitability (Figure 5). Further investigation is required to disentangle the role of head posture in modulating motor activity.

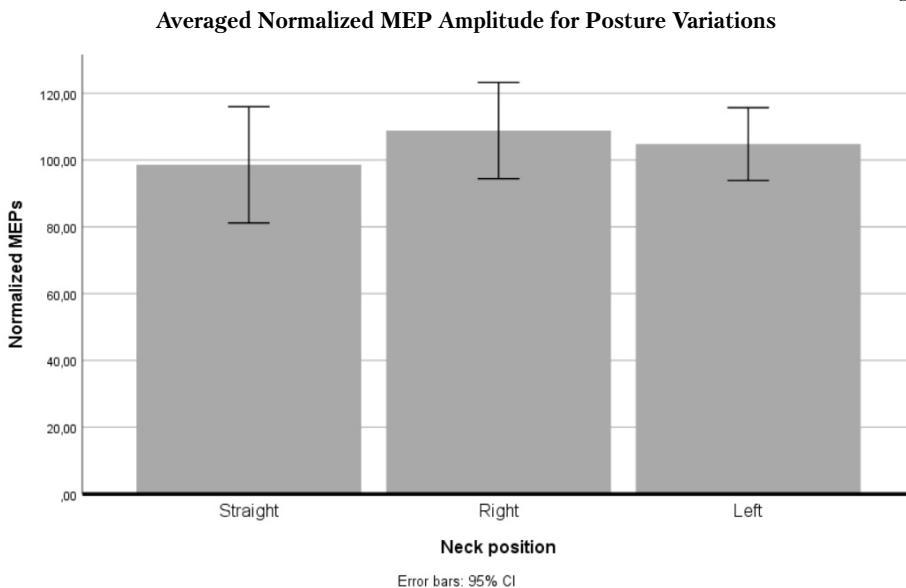
Discussion

This study explored the relationship between mirror neuron activation and motor excitability during the visual presentation of hand movements with varying time jitter. Participants viewed videos of finger movements (little finger and index finger) or a resting hand. TMS pulses were delivered after cessation of each movement with a jitter of 0 s, 3.2 s, and 6.4 s.

Single-pulse TMS (spTMS) was chosen for its unique advantages in studying mirror neuron activity. Its high temporal precision (within 1 millisecond) allows for precise measurement of muscle responses (MEPs) within 10-40 milliseconds after stimulation. This level of accuracy surpasses methods such as fMRI and EEG. By comparing MEP amplitudes during action observation to baseline levels, researchers can draw inferences about how observing actions modulates motor pathways (Naish et al., 2014).

Our findings shed light on the complex interplay between mirror neuron activation, muscle activity, and head position during action observation. Notably, head orientation did not significantly influence mirror neuron activity. This suggests that the mirror system operates similarly regardless of head position. This self-

Figure 5



aligning activation of one's own motor representations during observed actions emulates the processes involved in performing actions oneself. As Rizzolatti & Craighero (2004) propose, the mirror system automatically and unconsciously translates observed actions into knowledge (Gallese, 2001). This negative finding suggests that, under the experimental conditions tested, the MNS appears to be agnostic to the position of the head relative to the body. This could imply that the MNS operates effectively across various body postures, offering an evolutionary advantage by allowing flexible and robust action observation and learning irrespective of the observer's position. The lack of influence from neck position on MNS responses likely indicates that the MNS primarily relies on visual and cognitive cues related to observed actions, rather than proprioceptive inputs regarding the observer's own body position. This supports the notion that the MNS is specialized for understanding actions from a third-person perspective, which might not be affected by the first-person body schema adjustments due to neck positioning. In light of these findings, while neck position can modulate interactions between the cerebellum and cortex as shown by Popa et al. (2018), it does not appear to impact the MNS activity. This reinforces the idea that the MNS can function independently of the observer's proprioceptive state, thereby enhancing its capability to observe, understand, and learn from others' actions in a wide range of postural contexts.

Mirror neuron activity appears to be extremely particular to the seen motion, based on the substantial relationships between muscle activation and movement type that have been reported. According to earlier TMS research (Cengiz et al., 2017; Fitzgerald, 2010), this result is consistent with muscle-specific activation during mirror neuron tasks. The notion of a direct connection between visual input and motor output is supported by the significant activation of the FDI muscle during index finger observation ($p=0.006$), suggesting the involvement of the mirror neuron system.

It is interesting to note that when the index finger was moving, we saw a decrease of MEPs in the ADM muscle ($p=0.026$). In addition to the anticipated activation of the corresponding muscle, this inhibitory impact points to a more intricate relationship between motor responses and mirror neuron activation. This discovery emphasizes how inhibitory systems influence motor reactions when watching actions. This finding can be explained by motor surround inhibition, a crucial mechanism for a precise motor control that describes the activation of the correct muscles for a specific movement while inhibiting neighboring muscles that are not involved in the task. The primary M1 and other cortical motor areas, as well as subcortical-cortical loops potentially including the basal ganglia, play a key role in generating surround inhibition, which adapts in response to changes in the motor system (Beck & Hallet, 2010; Kaji, 2001; Mink, 2003; Sohn & Hallet, 2004).

The intricacy of the brain processes underlying action observation and motor mimicry is highlighted by the observed inhibition of non-corresponding muscles during action observation (Buccino et al., 2004). This implies that the mirror neuron system (MNS) actively suppresses unrelated muscles while simultaneously activating the muscles engaged in the observed activity. The precision and speci-

ficity of motor responses are probably enhanced by this inhibitory regulation, which makes sure that only the necessary muscles are triggered.

Our findings align with previous research demonstrating similar inhibitory patterns during action observation (Nietto-Doval et al., 2023). This supports the concept of muscle-specific inhibition within the MNS.

The existence of inhibition advances our knowledge of motor mimicking and mirror neuron activity. It draws attention to the complex processes that are involved in interpreting activities that are seen and producing the proper motor reactions. To completely comprehend the brain mechanisms behind this inhibition and its significance for motor learning and rehabilitation, more research is required.

Additional evidence for the function of inhibition in the MNS—particularly in the setting of imitation—comes from the research of Cross & Iacoboni (2014). The authors suggest that in order to avoid interfering with motor responses, the MNS may decrease undesired imitation, while other studies have looked at how context and attention affect MNS activity and imitation.

The trend of higher MEPs during head rotation that has been observed ($p = .24$) points to a possible relationship between motor cortical excitability and neck position. This calls for additional research to determine how neck movements affect motor responses, possibly via sensorimotor integration processes. It is important to note the limitations of this study, including the relatively small sample size. Future research could benefit from larger sample sizes to provide a more comprehensive understanding of mirror neuron activation and its modulation by head positioning and other contextual factors.

This study elucidates the intricate relationship between MNS activity, muscle activation, and head position during the observation of actions. Our findings indicate that the MNS is influenced not only by excitation when observing a moving finger but also by inhibition in muscles not related with the movement. For instance, we observed inhibition of the ADM during index finger movement and an inhibitory effect on the FDI during little finger movement. Additionally, while trends in MEP amplitude facilitation were noted during head rotation, head rotation itself did not significantly influence MNS activity. This suggests that the MNS operates automatically and is not affected by body posture. These results have important implications for motor rehabilitation, neurophysiology, and cognitive neuroscience. Future research can build on these findings to further investigate the complexities of human motor cognition.

References

- Barchiesi, G., & Cattaneo, L. (2012). Early and late motor responses to action observation. *Social Cognitive and Affective Neuroscience*, 8(6), 711–719. <https://doi.org/10.1093/scan/nss049>
- Basavaraju, R., Mehta, U. M., Pascual-Leone, Á., & Thirthalli, J. (2018). Elevated mirror neuron system activity in bipolar mania: Evidence from a transcranial magnetic stimulation study. *Bipolar Disorders*, 21(3), 259–269. <https://doi.org/10.1111/bdi.12723>

- Bianco, G., Feurra, M., Fadiga, L., Rossi, A., & Rossi, S. (2012). Bi-hemispheric effects on corticospinal excitability induced by repeated sessions of imagery versus observation of actions. *Restorative Neurology and Neuroscience*, 30(6), 481–489. <https://doi.org/10.3233/rnn-2012-120241>
- Beck, S., & Hallett, M. (2010). Surround inhibition is modulated by task difficulty. *Clinical Neurophysiology*, 121(1), 98–103. <https://doi.org/10.1016/j.clinph.2009.09.010>
- Bonini, L., Rotunno, C., Arcuri, E., & Gallese, V. (2022). Mirror neurons 30 years later: Implications and applications. *Trends in Cognitive Sciences*, 26(9), 767–781. <https://doi.org/10.1016/j.tics.2022.06.003>
- Burgess, J. D., Arnold, S. L., Fitzgibbon, B. M., Fitzgerald, P. B., & Enticott, P. G. (2013). A transcranial magnetic stimulation study of the effect of visual orientation on the putative human mirror neuron system. *Frontiers in Human Neuroscience*, 7, Article 679. <https://doi.org/10.3389/fnhum.2013.00679>
- Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition. *Brain and Language*, 89(2), 370–376. [https://doi.org/10.1016/s0093-934x\(03\)00356-0](https://doi.org/10.1016/s0093-934x(03)00356-0)
- Cao, K., Ma, M., Wang, C., Iqbal, J., Si, J., Xue, Y., & Yang, J. (2021). TMS-EEG: An emerging tool to study the neurophysiologic biomarkers of psychiatric disorders. *Neuropharmacology*, 197, Article 108574. <https://doi.org/10.1016/j.neuropharm.2021.108574>
- Catmur, C., Mars, R. B., Rushworth, M. F. S., & Heyes, C. (2011). Making mirrors: Premotor cortex stimulation enhances mirror and counter-mirror motor facilitation. *Journal of Cognitive Neuroscience*, 23(9), 2352–2362. <https://doi.org/10.1162/jocn.2010.21590>
- Cengiz, B., Vurall, D., Zinnuroğlu, M., Bayer, G., Golmohammadzadeh, H., Günendi, Z., Turgut, A. E., İrfanoğlu, B., & Arkan, K. B. (2017). Analysis of mirror neuron system activation during action observation alone and action observation with motor imagery tasks. *Experimental Brain Research*, 236(2), 497–503. <https://doi.org/10.1007/s00221-017-5147-5>
- Cracco, E., De Coster, L., Andres, M., & Brass, M. (2016). Mirroring multiple agents: Motor resonance during action observation is modulated by the number of agents. *Social Cognitive and Affective Neuroscience*, 11(9), 1422–1427. <https://doi.org/10.1093/scan/nsw059>
- Cross, K. A., & Iacoboni, M. (2014). To imitate or not: Avoiding imitation involves preparatory inhibition of motor resonance. *NeuroImage*, 91, 228–236. <https://doi.org/10.1016/j.neuroimage.2014.01.027>
- Errante, A., & Fogassi, L. (2020). Activation of cerebellum and basal ganglia during the observation and execution of manipulative actions. *Scientific Reports*, 10, Article 12008. <https://doi.org/10.1038/s41598-020-68928-w>
- Fabbri-Destro, M., & Rizzolatti, G. (2008). Mirror neurons and mirror systems in monkeys and humans. *Physiology*, 23(3), 171–179. <https://doi.org/10.1152/physiol.00004.2008>
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology*, 73(6), 2608–2611. <https://doi.org/10.1152/jn.1995.73.6.2608>
- Feurra, M., Blagovechtchenski, E., Nikulin, V. V., Nazarova, M., Lebedeva, A., Pozdeeva, D., Yurevich, M., & Rossi, S. (2019). State-dependent effects of transcranial oscillatory currents on the motor system during action observation. *Scientific Reports*, 9(1), Article 12858. <https://doi.org/10.1038/s41598-019-49166-1>
- Figas, G., Hadamus, A., Błażkiewicz, M., & Kujawa, J. (2023). Symmetry of the neck muscles' activity in the electromyography signal during basic motion patterns. *Sensors*, 23(8), Article 4170. <https://doi.org/10.3390/s23084170>
- Fitzgerald, P. B. (2010). Understanding mirror neurons: Evidence for enhanced corticospinal excitability during the observation of transitive but not intransitive hand gestures. *Neuropsychologia*, 48(9), 2675–2680. <https://doi.org/10.1016/j.neuropsychologia.2010.05.014>

- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*(5722), 662–667. <https://doi.org/10.1126/science.1106138>
- Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., Ferrari, P. F., & Van IJzendoorn, M. H. (2016). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. *Psychological Bulletin*, *142*(3), 291–313. <https://doi.org/10.1037/bul0000031>
- Dawood, F., & Loo, C. K. (2016). View-invariant visuomotor processing in computational mirror neuron system for humanoid. *PLoS ONE*, *11*(3), Article e0152003. <https://doi.org/10.1371/journal.pone.0152003>
- Gallese, V. (2001). The ‘shared manifold’ hypothesis. From mirror neurons to empathy. *Journal of Consciousness Studies*, *8*(5-6), 33–50.
- Gallese, V. (2008). Mirror neurons and the social nature of language: The neural exploitation hypothesis. *Social Neuroscience*, *3*(3-4), 317–333. <https://doi.org/10.1080/17470910701563608>
- Gastaut, H., & Bert, J. (1954). EEG changes during cinematographic presentation (Moving picture activation of the EEG). *Electroencephalography and Clinical Neurophysiology*, *6*, 433–444. [https://doi.org/10.1016/0013-4694\(54\)90058-9](https://doi.org/10.1016/0013-4694(54)90058-9)
- Häusser, L. F. (2012). Empathie und Spiegelneurone: Ein Blick auf die gegenwärtige neuropsychologische Empathieforschung [Empathy and Mirror Neurons: A Look at Current Neuropsychological Research on Empathy]. *Praxis der Kinderpsychologie und Kinderpsychiatrie*, *61*(5), 322–335. <https://doi.org/10.13109/prkk.2012.61.5.322>
- Hickok, G. (2010). The role of mirror neurons in speech and language processing. *Brain and Language*, *112*(1), 1–2. <https://doi.org/10.1016/j.bandl.2009.10.006>
- Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology*, *60*(1), 653–670. <https://doi.org/10.1146/annurev.psych.60.110707.163604>
- Kaji, R. (2001). Basal ganglia as a sensory gating device for motor control. *Journal of Medical Investigation*, *48*(3/4), 142–146.
- Mink, J. W. (2003). The basal ganglia and involuntary movements. *Archives of Neurology*, *60*(10), 1365–1368. <https://doi.org/10.1001/archneur.60.10.1365>
- Morton, S. M., & Bastian, A. J. (2004). Cerebellar control of balance and locomotion. *Neuroscientist*, *10*(3), 247–259. <https://doi.org/10.1177/1073858404263517>
- Naish, K. R., Houston-Price, C., Bremner, A. J., & Holmes, N. P. (2014). Effects of action observation on corticospinal excitability: Muscle specificity, direction, and timing of the mirror response. *Neuropsychologia*, *64*, 331–348. <https://doi.org/10.1016/j.neuropsychologia.2014.09.034>
- Nietto-Doval, C., Ragimova, A. A., & Feurra, M. (2023). Time course and visual presentation effects on the motor mirror neuron system induced by transcranial magnetic stimulation. *Zhurnal Vysshei Nervoii Deyatel'nosti im. I.P. Pavlova*, *73*(3), 334–347. <https://doi.org/10.31857/S0044467723030115> (in Russian)
- Pashaei, M., Babakhani, F., & Banihashemi, K. (2023). Evaluation of surface electromyography of selected neck muscles during the whiplash mechanism in aware and unaware conditions due to safe punching in kickboxing. *BMC Musculoskeletal Disorders*, *24*, Article 429. <https://doi.org/10.1186/s12891-023-06563-y>
- Popa, T., Hubsch, C., James, P., Richard, A., Russo, M., Pradeep, S., Krishan, S., Roze, E., & Meunier, S. (2018). Abnormal cerebellar processing of the neck proprioceptive information drives dysfunctions in cervical dystonia. *Scientific Reports*, *8*(1), Article 2263. <https://doi.org/10.1038/s41598-018-20510-1>
- Rajmohan, V., & Mohandas, E. (2007). Mirror neuron system. *Indian Journal of Psychiatry*, *49*(1), 66–69. <https://doi.org/10.4103/0019-5545.31522>

- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192. <https://doi.org/10.1146/annurev.neuro.27.070203.144230>
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., & Fazio, F. (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research*, 111, 246–252. <https://doi.org/10.1007/bf00227301>
- Rossi, S., Hallett, M., Rossini, P.M., & Pascual-Leone, A. (2009). Safety of TMS Consensus Group. Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology*, 120(12), 2008–2039. <https://doi.org/10.1016/j.clinph.2009.08.016>
- Rossini, P. M., Barker, A. T., Berardelli, A., Caramia, M. D., Caruso, G., Cracco, R. Q., Dimitrijevi, M. R., Hallett, M., Katayama, Y., & Lücking, C. H. (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: Basic principles and procedures for routine clinical application. Report of an IFCN committee. *Electroencephalography and Clinical Neurophysiology*, 91(2), 79–92. [https://doi.org/10.1016/0013-4694\(94\)90029-9](https://doi.org/10.1016/0013-4694(94)90029-9)
- Rossini, P. M., Rossi, S., Pasqualetti, P., & Tecchio, F. (1999). Corticospinal excitability modulation to hand muscles during movement imagery. *Cerebral Cortex*, 9(2), 161–167. <https://doi.org/10.1093/cercor/9.2.161>
- Sohn, Y., & Hallett, M. (2004). Surround inhibition in human motor system. *Experimental Brain Research*, 158, 397–404. <https://doi.org/10.1007/s00221-004-1909-y>
- Sommerich, C. M., Joines, S. M., Hermans, V., & Moon, S. D. (2000). Use of surface electromyography to estimate neck muscle activity. *Journal of Electromyography and Kinesiology*, 10(6), 377–398. [https://doi.org/10.1016/s1050-6411\(00\)00033-x](https://doi.org/10.1016/s1050-6411(00)00033-x)
- Takahashi, H., Shibuya, T., Kato, M., Sassa, T., Koeda, M., Yahata, N., Suhara, T., & Okubo, Y. (2008). Enhanced activation in the extrastriate body area by goal directed actions. *Psychiatry and Clinical Neurosciences*, 62(2), 214–219. <https://doi.org/10.1111/j.1440-1819.2008.01757.x>
- Tarhan, L., Watson, C. E., & Buxbaum, L. J. (2015). Shared and distinct neuroanatomic regions critical for tool-related action production and recognition: Evidence from 131 left-hemisphere stroke patients. *Journal of Cognitive Neuroscience*, 27(12), 2491–2511. https://doi.org/10.1162/jocn_a_00876
- Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: A meta-analysis. *NeuroImage*, 48(3), 564–584. <https://doi.org/10.1016/j.neuroimage.2009.06.009>
- Zarr, N., Ferguson, R., & Glenberg, A. M. (2013). Language comprehension warps the mirror neuron system. *Frontiers in Human Neuroscience*, 7, Article 870. <https://doi.org/10.3389/fnhum.2013.00870>