



Research Report

Observation of the point-light animation of a grasping hand activates sensorimotor cortex in nine-month-old infants



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ABSTRACT

Measuring changes in sensorimotor alpha band activity in nine-month-old infants we sought to understand the involvement of the sensorimotor cortex during observation of the Point-Light (PL) animation of a grasping hand. Attenuation of alpha activity was found both when the PL display moved towards the to-be-grasped object and when the object was deleted from the video. Before the beginning of the movement of the PL stimuli, only in the presence of the object evoked attenuation of sensorimotor alpha activity was documented, possibly interpreted either as movement prediction or as graspable object perception. Our main findings demonstrate that, during observation of stimuli moving with biological kinematics, the infants' sensorimotor system is activated when the pictorial information is absent or highly reduced, and independently of the presence of the goal-directed object. The possible compensatory function of the sensorimotor system during observation of highly degraded moving stimuli is discussed.

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1. Introduction

After almost thirty years of experimental confirmations, it is now possible to state that in humans (seminal study: [Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995](#)) and at least some other

primates (seminal study: [di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992](#)), the sensorimotor system is involved in the perception of others' actions. In humans this evidence is based on an impressive body of functional magnetic resonance imaging (for a meta-analysis see [Caspers, Zilles, Laird, & Eickhoff, 2010](#)), magnetoencephalography (for

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a review see Hari, 2006) electroencephalography (for a review see Vanderwert, Fox, & Ferrari, 2013) and transcranial magnetic stimulation (for a review see Naish, Houston-Price, Bremner, & Holmes, 2014) studies, that has demonstrated the presence of overlapping neural networks associated with action perception and execution. These studies suggest the presence of a functional identity between motor command and sensory consequences of motor execution based not on the way the action is executed but on its goal. The origin of this link goes back to prenatal life during which the start of motor experience (Sparling & Wilhelm, 1993; Sparling, Van Tol, & Chescheir, 1999) contributes to the development of a process in which the sensory consequences of a movement are anticipated and used to plan an action related to the nature of the target (Zoia et al., 2007). Already at birth, this process manifests itself with the presence of primitive sensorimotor associations revealed by the ability of 2-day-old newborns to discriminate between visual cues indicating goal directed or non-goal-directed actions (Craighero, Leo, Umiltà, & Simion, 2011). In adults the activation of sensorimotor representations during action observation is considered to be fundamental for inferring others' motor intentions, for predicting the consequences of their actions to the purpose of collaborating or contrasting them, or understanding what others are doing (Iacoboni, 2009; Rizzolatti & Craighero, 2004; Rizzolatti & Fogassi, 2014; Rizzolatti & Sinigaglia, 2007). The crucial role that this mechanism plays in effectively integrating individuals within their social milieu justifies the evidence that even more abstract forms of actions, those that have lost almost all the hallmarks of action, may activate the sensorimotor system. Some examples are given by transcranial magnetic stimulation (TMS) experiments showing that the observation of static snapshots representing a mimicked grasping action induces a corticospinal activation (Urgesi et al., 2010; Urgesi, Moro, Candidi, & Aglioti, 2006), as well as the observation of a handled object out of reach for participants provided that it was ready to an avatar's hand (Cardellicchio, Sinigaglia, & Costantini, 2013). Therefore, the sensorimotor system seems to be involved when the observed movement is taking place, when it is known that it will be carried out, and when it is probable to occur. The necessity to understand and predict what others are doing can even become vital in situations where visibility is reduced due to obscurity or to the presence of obstacles. The possibility to recognize gender, actions, intentions, and emotions of an agent in the absence of pictorial information is well known (Blake & Shiffrar, 2007), as you can check at the following link www.biomotionlab.ca/Demos/BMLwalker.html (Troje, 2002). The trick to experimentally study this issue was invented by Gunnar Johansson (Johansson, 1976, 1973) who devised the technique known as point-light (PL) animation of biological motion: he attached small point lights to the main joints of a person's body and filmed the scene so that only the lights were visible on a dark background. Static frames of the resulting animation typically appear as meaningless assemblages of dots, but the rapid succession of consecutive PL frames is immediately experienced as an apparent motion of a human form engaged in a specific activity. Johansson's work was an outgrowth of his applied research on traffic safety: putting lights or reflective tape on pedestrians can allow drivers to

instantaneously recognize them as human beings at night (Wood, Tyrrell, & Carberry, 2005). Indeed, Johansson used the term biological motion in the title of his seminal article (Johansson, 1973) to separate the perception of human movement from other motion, and ten years later Viviani (Viviani & Terzuolo, 1982) proposed the two-thirds power law that characterises the velocity of a point on a moving animal projected onto a plane with respect to the curvature of the projected arc at that point, and demonstrated that our perceptual system is very well attuned to this relation between velocity and curvature (Viviani, Baud-Bovy, & Redolfi, 1997; Viviani & Stucchi, 1992).

This specific sensitivity is supported by the evidence that a network of areas in the cortex responds to biological motion. Neuroimaging, neurophysiology, and neurostimulation studies, by generally contrasting an intact PL walker with one that is spatially scrambled, have shown that relevant areas include ventral extrastriate regions but also portions of the frontal and parietal cortex (Bonda, Petrides, Ostry, & Evans, 1996; Grèzes et al., 2001; Grosbras, Beaton, & Eickhoff, 2012; Grossman & Blake, 2002; Peelen, Wiggett, & Downing, 2006; Saygin, 2007; Saygin, Wilson, Hagler, Bates, & Sereno, 2004; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001; van Kemenade, Muggleton, Walsh, & Saygin, 2012). The involvement of the sensorimotor cortex during observation of PL animation of biological motion is particularly evident in the suppression of the alpha sensorimotor rhythm (SMR) (8–13 Hz, also called the mu rhythm) recorded with scalp electrodes from central electrode sites in human adults (Ulloa & Pineda, 2007). Suppression of this rhythm, due to a decrease in neuronal synchrony reflecting cortical involvement, is typically observed while participants execute movements or observe movements executed by others (Cochin, Barthelemy, Lejeune, Roux, & Martineau, 1998; Muthukumaraswamy & Johnson, 2004; Pineda, Allison, & Vankov, 2000), and it is assumed to reflect the downstream modulation of motor neurons by cells in the premotor cortex involved in the processing of movement-related information (Pineda, 2005). In line with this interpretation are the results of a single pulse TMS study that showed that the activation induced by the observation of PL stimuli extends to primary motor area resulting in a modulation of corticospinal excitability (Craighero, Jacono, & Mele, 2016).

Several behavioral studies investigated the perception and discrimination of PL animations in infancy, showing that newborns prefer a PL walking hen, walking human, or legs of a walking animal, than a scrambled version of them (Bardi, Regolin, & Simion, 2011, 2014; Bidet-Ildei, Kitromilides, Orliaguet, Pavlova, & Gentaz, 2014; Simion, Regolin, & Bulf, 2008), and that they are sensible to the velocity of single dots or dots configurations (Craighero, Lunghi, Leo, Ghirardi, & Simion, 2016; Méary, Kitromilides, Mazens, Graff, & Gentaz, 2007). Three-month-old infants differentiate walking and running PL motions (Booth, Bertenthal, & Pinto, 2002), and by 5 or 6 months infants recognize PL walk direction (Kuhlmeier, Troje, & Lee, 2010), and discriminate canonical PL walkers from those modified (Bertenthal, Proffitt, & Kramer, 1987). By 7–9 months, infants discriminate PL versions of their own leg motions (Schmuckler & Fairhall, 2001), emotional expression in PL faces (Soken & Pick, 1992), and timing of self-occlusion of

limbs in PL walkers (Bertenthal, Proffitt, Spetner, & Thomas, 1985).

Results from research using electroencephalogram (EEG) in infancy support evidence obtained from behavioral studies by highlighting the presence of neural sensitivity to biological motion as early as 5 months of age. Specifically, in five-month-old infants significant differences were observed between event-related potential (ERP) waveforms to the canonical and scrambled PL displays depicting the human actions of walking, kicking, throwing, and running at mid-parietal, lateral parietal, temporal, and occipital electrode sites (Marshall & Shipley, 2009). Other studies indicate that infants within the first year of life detect differences between upright and inverted or scrambled PL animation of human actions, with differences mainly localized to right parietal regions. In detail, in healthy 8-month-old infants, the averaged negative amplitude of the ERPs in the right hemisphere is greater in response to canonical than to scrambled PL of a walking person (Hirai & Hiraki, 2005), and, while viewing upright as compared with inverted PL of a walking and kicking person, infants of this age exhibit larger positive ERP amplitude over the right parietal cortex at a latency of 200–300 msec (Reid, Hoehl, & Striano, 2006).

Despite the rich behavioral literature and the few electrophysiological studies, to date there is a sizable lack of studies specifically examining whether during infancy and childhood biological motion observation determines the involvement of the sensorimotor cortex as occurs in adults, evident in the suppression of the alpha SMR (Ulloa & Pineda, 2007). Like in adults, infants and children demonstrate alpha SMR desynchronization during action observation and action execution, which indirectly reflects the early emergence of action-perception coupling (Marshall, Bar-Haim, & Fox, 2002; Marshall & Meltzoff, 2011). SMR desynchronization occurs in the frequency range of 6–9 Hz in the first two years of life, compared with the 8–13 Hz range that characterizes it in adults, and increases from infancy to adulthood (Thorpe, Cannon, & Fox, 2016), being in nine-month-olds around 10% when executing an action, and around 5% when observing an action (Southgate, Johnson, Osborne, & Csibra, 2010).

In the present study, for the first time, we used EEG to measure changes in SMR alpha band activity in nine-month-old infants during observation of PL animation moving with biological kinematics. Furthermore, stimuli were not PL displays depicting human total body movements such as walking or running, but consisted in a PL display in which the velocity and motion profile of the PL markers followed the typical velocity profile of human goal-directed hand actions, which is characterized by a fast-velocity initial phase and a low-velocity final phase (Jeannerod, 1984). According to the biological motion hypothesis of action anticipation (Elsner, Falck-Ytter, & Gredebäck, 2012), the observation of this biological kinematics is sufficient to automatically implement in the observer the motor programs equivalent to those used in action (Iacoboni et al., 1999; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001), such as proactive-gaze (Flanagan & Johansson, 2003; Rotman, Troje, Johansson, & Flanagan, 2006). Unlike PL displays of walkers which are immediately and easily recognized as such, those of a grasping hand are recognized as hands only by few adult

participants, both when markers are attached on the major joints of the hand (Elsner et al., 2012), and when they are placed along the contour of the hand (Craighero, Jacono, et al., 2016; Craighero, Lunghi, et al., 2016). Nevertheless, Elsner et al. (2012) reported that no gaze behavior differences were observed between participants who recognized the hand and those who did not, indicating that participants' performance was not affected by the familiarity of the observed movement. The difference in the ability to recognize PL animations of walkers in comparison with PL animations of a grasping hand may depend from the different type of information the two kinematics provide to the observer. The first kinematics is formalized by the two-third-power law of motion generation and perception (Viviani & Terzuolo, 1982), which defines the dynamic regularities that reflect the structure and the control schemes of the musculo-skeletal system, and it is explained by the rules of biomechanics (Gribble & Ostry, 1996). The second one concerns the typical biological kinematics of a hand reaching for an object, which depends from the central programming of the relationship between velocity of the hand and position of the to-be-reached object (Jeannerod, 1984). Therefore, walking is a cycling movement whose regularities are strictly linked to the shape of the body that limits the biomechanical possibilities, and, probably for this reason, the shape of the body results immediately evident when the rapid succession of consecutive PL frames are presented, but static frames appear as meaningless assemblages of dots. Instead, reaching-grasping is a goal-directed action specifically programmed according to the distance and the intrinsic properties of the to-be-grasped object, and the typical accelerated-decelerated kinematics of the reaching phase is not necessarily restricted to the hand effector but it is common to every biological effector or tool used to reach the same goal (Quinlan & Culham, 2015; Zheng & MacKenzie, 2007), and it is also common to monkeys' actions (Roy, Paulignan, Farnè, Jouffrais, & Boussaoud, 2000). The absence of a direct inference from the kinematics to the identity of the effector may be the reason for the lack of precise recognition of the original hand effector when observing the relative PL animation.

The decision to use hand PL displays instead of walkers PL displays lies in the possibility to specifically investigate transitive goal-directed actions and verify whether the presence of a graspable object at the end of the movement influences SMR alpha band activity in three phases of the observed movement: an anticipatory phase, in which the PL animation is still in its initial position, a reaching phase, corresponding to the accelerating period of the reaching movement, and a grasping phase, corresponding to the decelerating period of the reaching phase in which the movement ends.

2. Methods

No part of the study procedures or analyses was pre-registered prior to the research being conducted.

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria established prior to data analysis, all manipulations, and all measures in the study.

Study data and digital study materials have been archived in the following publicly accessible repository: <https://osf.io/cjmr7/>.

2.1. Participants

Thirty-eight 9-month-old infants and their families were recruited from a diverse urban environment including the metropolitan and suburban areas of Milan by using mailing lists. In order to participate, infants had to be born at term (37–42 weeks gestation), had a normal birth weight (>2500 g), did not suffer of any neurological or other medical conditions, and were observed to have normal vision and hearing. The EEG analyses were carried out for nineteen 9-month-old infants (10 females, mean age = 281.47 days; SD = 8.55; range 269–292 days). The remaining infants were excluded due to fussiness ($n = 10$), excessive artifacts ($n = 7$), or technical problems with data collection ($n = 2$). The proportion of excluded infants is similar to other EEG studies investigating SMR alpha activity with infants this age (e.g., Southgate, Johnson, El Karoui, & Csibra, 2010). Our sample size is in line with that of previous research measuring alpha activity across several scalp locations in infants (e.g., Cannon et al., 2016). Moreover, an a priori power analysis indicated that 19 participants would be needed in order to have 80% probability of detecting a significant three-way interaction ($\alpha = .05$) with a medium effect size ($r = .25$) (Cohen, 1992) in the repeated measures ANOVA. The procedure has been carried out in accordance with The Code of Ethics of the World Medical Association (the Declaration of Helsinki, BMJ 1991; 302:1194) for experiments involving humans, and was approved by the University ethical committee. Parents filled out an informed consent form for their infants' participation and a questionnaire on their infants' motor development prior to the study.

2.2. Stimuli and procedure

EEG activity was recorded while infants observed stimuli presented using E-Prime software v2.0 (Psychology Software Tools Inc., Pittsburgh, PA). Stimuli were the same PL animations previously used both in a TMS experiment in adults (Craighero, Jacono, et al., 2016), and in an infant-control preferential looking technique study on 2-day-old newborns (Craighero, Lunghi, et al., 2016), with the only exception that they were shortened to 2000 msec by cutting the initial static part of the video in order to adapt them to the EEG procedure. PL animations were obtained by the graphic manipulation of the video of a real hand reaching to grasp a blue ball. The video was segmented into frames and each frame was inserted as a single slide in Microsoft Powerpoint (Microsoft Corp., Redmond, WA). The outline of the hand was drawn by hand using 44 white dots in each slide. The initial position of the dots was established in slide 1, when the hand was still in the starting pinch position, to cover the outline of the wrist, the thumb, and the forefinger. Each dot maintained its original position on the hand during all the slides. Afterwards, the original video was removed, leaving the dots and the ball (Ball stimulus), or leaving only the dots (NoBall

stimulus), and the final slides were used as frames to obtain the videos used in the current experiment. Both studies that used the same stimuli of the present experiment verified the possibility of recognizing the action behind PL animation. In the TMS study (Craighero, Jacono, et al., 2016), at the end of the experimental sessions, participants were asked to estimate what the PL animation depicted, and none of them reported that the stimuli included a human hand. In the infant-control preferential looking technique study (Craighero, Lunghi, et al., 2016), the efficacy of PL transformation of cancelling every pictorial information about the hand was pretested on 12 adult naïve individuals. Only six out of 12 participants reported that the PL stimuli might include a human hand. To verify whether the presence of a ball increased the ability to recognize the acting hand behind PL animation, here, two groups of 15 naïve adults each were presented with the Ball stimulus or the NoBall one, showed in a loop, and they were asked to report what they depicted. Only nine out of 15 participants in the Ball condition and seven out of 15 participants in the NoBall condition reported that the PL animation represented a human hand. The remaining participants did not recognize the PL in the videos as a hand. Moreover, a Mann–Whitney test showed that there was no significant difference ($U = 97.5$, $p = .53$, $d = .23$) between the recognition of the PL in the Ball and NoBall conditions. Thus, the presence of the ball did not increase the possibility to recognize the grasping hand.

In the present experiment, each video lasted 2000 msec, and it was mirrored to obtain PL animations coming both from the left (Video 1; Video 2) or the right side (Video 3; Video 4) of the monitor, so that the movement direction was counter-balanced between trials. Videos were presented pseudo-randomly, with the only constraint that stimuli from the same condition could not occur more than two times consecutively, and the inter-stimulus interval, consisting in a white fixation cross displayed in the center of the display, varied randomly between 1000 and 1200 msec. There was no restriction in the number of trials displayed and the experiment was interrupted when infants became too bored or fussed out. The mean number of presented trials was 52.45 (Ball: 52.47, standard deviation = 12.17; NoBall: 52.42, standard deviation = 11.93). Infants sat on their parents' lap at a distance of approximately 60 cm from a 24-inch monitor in a dimly lit, soundproofed and electrically shielded cabin. The size of the presented videos was 17×19 cm (subtending a visual angle of 17° in width). Parents were instructed to remain as still as possible and to keep silence during the experimental session. The experiment proceeded automatically and, whenever needed, the experimenter presented a looming fixation point between trials for the duration necessary to redirect the infant's attention to the monitor. When an infant's attention could no longer be redirected to the monitor, the session was terminated. The whole experiment was recorded through an infrared camera, hidden over the monitor, which was synchronized with stimulus presentation for offline coding of eye and body movements occurring during stimulus presentation.

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.cortex.2019.07.006>.

2.3. Electroencephalogram collection and processing

EEG was recorded using a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic Inc., Eugene, OR) and sampled at 500 Hz by means of an EGI NetAmps 300 amplifier. The signal was recorded with respect to the vertex electrode and re-referenced to the average reference. A bandpass filter of .1–100 Hz was applied online and impedances were checked prior to the beginning of each session and considered acceptable if lower than 50 K Ω . EEG data were further high-pass filtered offline (.3 Hz) and segmented into 3400 msec epochs beginning 1000 msec before and ending 2400 msec after stimulus onset. Trials were excluded if more than eighteen bad channels were detected (e.g., Halit, De Haan, & Johnson, 2003). Of the remaining trials, individual bad channels were replaced using spherical spline interpolation. To ensure that we measured sensorimotor activation in response to observation of movement rather than as a consequence of infant own concurrent movements, a careful double-step procedure for eliminating movement artifacts was adopted. Firstly, all trials containing more than 15% of channels with signal exceeding ± 200 μ V were detected and excluded via an automated algorithm. The mean number of artifact-free trials per infant after the automated procedure was 28.32 (Ball: 28.8, standard deviation = 13.62; NoBall: 27.76, standard deviation = 12.84). Secondly, video recordings of the infants, obtained through the infrared camera hidden over the monitor, were coded offline independently from the automated artifact detection procedure, and served to exclude from analysis all trials presenting any gross or fine movements not automatically detected, or trials in which the infant did not attend to the screen. Infants who did not provide at least 8 artifact-free trials for each condition were excluded from the analyses ($n = 7$). After manual rejection procedure the mean number of artifact-free trials per infant contributing to analyses dropped to 17.29 (Ball: 17.47, standard deviation = 8.39; NoBall: 17.12, standard deviation = 8.08). There were no significant differences between the two conditions in the number of artifact-free trials, $t(18) = .578$; $p = .57$.

Time-frequency analyses were performed on each artifact-free trial using continuous wavelet transform with Morlet wavelets at 1 Hz intervals in the 3–20 Hz range. After similar studies investigating SMR alpha band modulation (e.g., de Klerk, Johnson, Heyes, & Southgate, 2015; Pomiechowska & Csibra, 2017; Quadrelli, Geangu, & Turati, 2019) or performing time-frequency analysis to uncover other stimulus-induced oscillatory responses in infancy (e.g., Csibra, Davis, Spratling, & Johnson, 2000; Parise & Csibra, 2013), we calculated the absolute value (i.e., the amplitude) of the resulting complex coefficients. In order to eliminate distortion created by the wavelet transform, the first and the last 400 msec of each epoch were removed and a 200 msec baseline period starting 300 msec before stimulus onset was selected. Based on previous work showing that in infants of this age the frequency band most reactive to movement observation is the 6–9 Hz band (Marshall et al., 2002; Marshall & Meltzoff, 2011), we averaged activity over this range. Averaged activity in the 6–9 Hz range during the 200 msec baseline period was then subtracted from that recorded during stimulus presentation.

Average wavelet coefficients within infants were calculated by taking the mean across the trials. As in previous studies investigating SMR alpha band modulation in infancy (de Klerk, Johnson, & Southgate, 2015; Saby, Marshall, & Meltzoff, 2012), activity over a cluster of electrodes disposed over the left- (30, 36, 37, and 42), and right-hemispheres (87, 93, 104, and 105) was analyzed. The scalp locations of these left and right electrode clusters correspond to the locations of C3 and C4 in the international 10–20 system of electrode placement and are located over the bilateral arm/hand representation areas. Additionally, we wanted to know whether alpha band activity elicited by PL animations was specific to the central region or extended to the frontal and occipital regions (Cuevas, Cannon, Yoo, & Fox, 2014). Thus, we also analyzed the channels over the occipital cortex (70, 71, 76, 83) and over the frontal cortex (24, 23, 19, 3, 4, 124), respectively corresponding to O1/O2 and F3/F4 according to the international 10–20 system of electrode placement. The average activity in the alpha range was extracted for statistical analyses from these regions in three time windows defined by the phases of the PL animation: an Anticipatory Phase (AP: 0–500 msec) in which the dots are still in their initial position, a Reaching Phase (RP: 500–1200 msec) in which the PL animation is in the accelerating period of the reaching movement, and a Grasping Phase (GP: 1200–2000 msec) in which the PL animation is in the decelerating period of the reaching and concludes its movement (Fig. 1).

EEG data were recorded, pre-processed using Netstation v4.6.4, and analyzed using WTools (see Parise & Csibra, 2013). All statistical tests were conducted on a .05 level of significance (two-tailed), and pairwise comparisons were performed by applying t -tests and the Fisher's least significant difference procedure (Howell, 1987), and Holm-Bonferroni correction

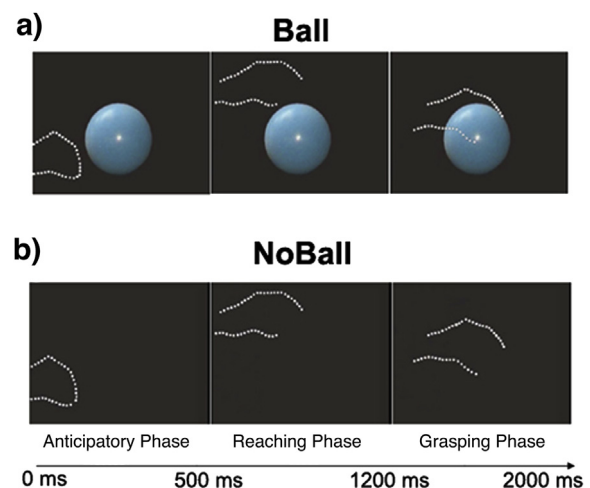


Fig. 1 – Schematic representation of the trials displayed, with the crucial frames of the movement phases of the (a) Ball and (b) NoBall conditions. Anticipatory Phase (0–500 msec): the dots are still in their initial position. Reaching Phase (500–1200 msec): the PL animation is in the accelerating period of the reaching movement. Grasping Phase (1200–2000 msec): the PL decelerates and concludes its movement.

was used where appropriate (Abdi, 2010). The Greenhouse-Geisser correction for non-sphericity has been used to adjust degrees of freedom as appropriate. Effect sizes were estimated using the partial eta square measure (η_p^2), and the data are reported as the mean and the standard deviation (SD). Analyses focused on SMR alpha activity at electrode sites overlying the hand areas (C3 and C4) of the sensorimotor cortex. Preliminary analyses deriving from an ANOVA with Condition (Ball, NoBall), Animation Phase (AP, RP, GP), and Hemisphere (C3, C4), did not reveal significant differences in sensorimotor activation between C3 and C4, $F(1,18) = 3.76$; $p = .07$, or interactions with Hemisphere (all $ps > .13$). Thus, similarly to Saby and colleagues (Saby, Meltzoff, & Marshall, 2013), SMR alpha activity from C3 and C4 was averaged to index sensorimotor activation over the bilateral hand areas.

3. Results

A repeated-measures Analysis Of Variance (ANOVA) on alpha activity with Phase (AP, RP, GP), Condition (Ball, NoBall), and Region (Central, Occipital, Frontal) as within-subject factors was performed. The ANOVA yielded a significant main effect of Phase, $F(2,36) = 26.00$; $p < .001$, $\eta_p^2 = .59$, and a main effect of Region $F(2,36) = 16.82$; $p < .001$, $\eta_p^2 = .48$. These results were qualified by the significant interactions Phase \times Condition, $F(2,36) = 12.54$, $p < .001$, $\eta_p^2 = .41$, and Phase \times Region, $F(1.82, 32.67) = 12.25$, $p < .001$, $\eta_p^2 = .44$. A significant three-way Phase \times Condition \times Region interaction, $F(2.42, 43.53) = 3.99$, $p = .02$, $\eta_p^2 = .18$, was also revealed, which was inspected by means of paired samples comparisons within each region (Fig. 2).

Follow-up paired samples t-tests conducted over the Central Region (i.e., C3, C4) demonstrated that:

- In the Ball condition, attenuation was significantly greater during the AP (mean = $-.22 \mu\text{V}$, SD = $.27 \mu\text{V}$) than during the GP (mean = $-.07 \mu\text{V}$, SD = $.19 \mu\text{V}$), $t(18) = -24.99$; $p = .02$, $d = .57$, and attenuation was greater during the RP (mean = $-.31 \mu\text{V}$, SD = $.32 \mu\text{V}$) than during the GP, $t(18) = -38.71$; $p = .001$, $d = .89$.
- In the NoBall condition, attenuation was greater during the RP (mean = $-.33 \mu\text{V}$, SD = $.32 \mu\text{V}$) compared to the AP (mean = $-.06 \mu\text{V}$, SD = $.19 \mu\text{V}$), $t(18) = 41.16$; $p < .001$, $d = .94$, and to the GP (mean = $-.07 \mu\text{V}$, SD = $.14 \mu\text{V}$), $t(18) = -36.44$; $p = .002$, $d = .84$.

Furthermore, only in the AP a statistically significant difference, $t(18) = -2.312$; $p = .033$, was present between the Ball condition (mean = $-.22 \mu\text{V}$, SD = $.27 \mu\text{V}$) and the NoBall condition (mean = $-.06 \mu\text{V}$, SD = $.19 \mu\text{V}$). All other differences over the Central Region were not significant (all $ps > .09$).

Follow-up paired samples t-tests conducted over the Occipital Region (i.e., O1, O2) demonstrated that:

- In the Ball condition, attenuation was significantly greater during the RP (mean = $-.39 \mu\text{V}$, SD = $.31 \mu\text{V}$), $t(18) = 3.42$; $p = .003$, $d = .79$, and the GP (mean = $-.36 \mu\text{V}$, SD = $.32 \mu\text{V}$), $t(18) = 2.75$; $p = .01$, $d = .63$, compared to the AP (mean = $-.18 \mu\text{V}$, SD = $.31 \mu\text{V}$).

- Similarly, in the NoBall condition attenuation was significantly greater during the RP (mean = $-.39 \mu\text{V}$, SD = $.31 \mu\text{V}$), $t(18) = 6.67$; $p < .001$, $d = 1.53$, and the GP (mean = $-.36 \mu\text{V}$, SD = $.32 \mu\text{V}$), $t(18) = 6.55$; $p < .001$, $d = 1.50$, compared to the AP (mean = $-.18 \mu\text{V}$, SD = $.31 \mu\text{V}$). No other comparisons over the Occipital Region attained significance (all $ps > .11$).

Follow-up paired samples t-tests were conducted also over the Frontal Region (i.e., F3, F4) but did not produce any significant results (all $ps > .10$).

Lastly, one sample t-tests were performed to investigate the magnitude of alpha suppression as compared to baseline in the three animation phases and in both conditions.

- In the Central Region, the decrease in activity in the Ball condition was significantly different from zero during the AP, $t(18) = -3.44$; $p = .003$, $d = .79$ and during the RP, $t(18) = -4.12$; $p < .001$, $d = .95$. In the NoBall condition, alpha suppression was significantly different from zero only during the RP, $t(18) = -4.45$; $p < .001$, $d = 1.03$.
- In the Occipital Region, the alpha activity attenuation in the Ball condition was significantly different from zero during the AP (mean = $-.24 \mu\text{V}$, SD = $.31 \mu\text{V}$), $t(18) = -3.44$; $p = .003$, $d = .79$, during the RP (mean = $-.39 \mu\text{V}$, SD = $.31 \mu\text{V}$), $t(18) = -5.39$; $p < .001$, $d = 1.24$, and during the GP (mean = $-.36 \mu\text{V}$, SD = $.32 \mu\text{V}$), $t(18) = -4.85$; $p < .001$, $d = 1.11$. In the NoBall condition attenuation was significantly different from zero during the RP (mean = $-.49 \mu\text{V}$, SD = $.29 \mu\text{V}$), $t(18) = -4.39$; $p < .001$, $d = 1.01$ and during the GP (mean = $-.52 \mu\text{V}$, SD = $.51 \mu\text{V}$), $t(18) = -4.85$; $p < .001$, $d = 1.11$.
- In the Frontal Region no attenuation attained statistical significance (all $ps > .14$).

4. Discussion

We measured changes in SMR alpha band activity in nine-month-old infants, in order to survey the involvement of the sensorimotor cortex during observation of a PL animation of a hand grasping an object and during observation of the same PL animation after deletion of the object. Sensorimotor activity was recorded both prior to the onset of the PL display movement and during it.

We found a stronger attenuation of alpha activity during the observation of the accelerating period of the PL stimuli movement compared to the observation of the PL stimuli still in their initial position. However, during this anticipatory phase, a significant decrease in activity was evident in trials in which the to-be-grasped object was present. No alpha activity attenuation was present during the decelerating period of the movement, a result in agreement with EEG studies in adults reporting that SMR rebounds at the end of the observed reaching-grasping movement (Avanzini et al., 2012; Lapenta, Ferrari, Boggio, Fadiga, & D'Ausilio, 2018).

Present results for the first time indicated that in infants, as in adults (Ulloa & Pineda, 2007), the observation of point-light biological motion displays produced SMR alpha activity suppression relative to baseline. Our findings demonstrate that

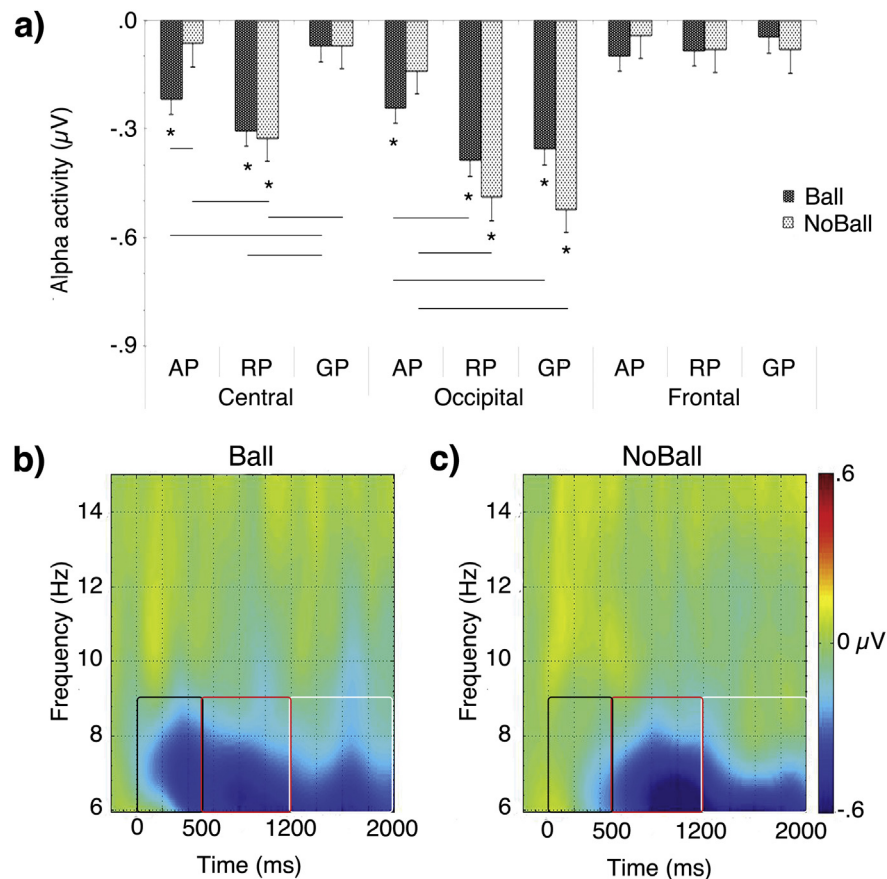


Fig. 2 – The upper panel (a) displays alpha activity (μV) over the selected electrode clusters (Central, Occipital, Frontal) averaged over the Anticipatory Phase (0–500 msec), the Reaching Phase (500–1200 msec), and the Grasping Phase (1200–2000 msec) for the Ball (black bars) and NoBall (grey bars) conditions. Error bars represent the standard errors of the means. Significant suppression from baseline and significant comparisons between conditions are illustrated, $*p < .05$. In the bottom panels (b, c), time–frequency plots display baseline corrected activity respectively for the Ball and NoBall conditions averaged over the Central electrode cluster, and over all participants. The time and frequency region of analysis is highlighted for the Anticipatory (black rectangles), Reaching (red rectangles), and Grasping (white rectangles) Phases.

observation of biological kinematics in the absence of pictorial information related to the real hand is able to determine SMR alpha activity suppression in nine-month-old infants, as it happens in children of the same age during grasping execution and during the mere observation of a real hand grasping an object (Southgate, Johnson, Osborne, & Csibra, 2009), and as it happens in adults when subjects move, imagine movement, observe movements (Babiloni et al., 1999; Cochin et al., 1998; Gastaut & Bert, 1954; Pineda et al., 2000), or when they observe point-light biological motion animation videos of jumping jacks and kick (Ulloa & Pineda, 2007).

Importantly, the stimuli used here were not the transformation in PL animation of walkers, but of a hand that grasps an object. This type of stimuli was used only in three previous studies, investigating gaze performance in adults (Elsner et al., 2012) and infants (Craigheero, Lunghi, et al., 2016), and corticospinal excitability in adults (Craigheero, Jacono, et al., 2016). It is interesting to note that all three studies reported that the PL views of a moving hand, even after substantial repetition, are recognized precisely and immediately

only by some observers, unlike the detection of whole body movement that is constantly rapid and precise (Troje, 2002). Despite the lack of recognition of the action behind PL animation, all three studies were able to replicate findings obtained during observation of a real moving hand: the presence of anticipatory gaze shifts towards the goal in adults (Elsner et al., 2012), of orienting of attention towards the final part of the observed movement in newborns (Craigheero, Lunghi, et al., 2016), and of motor resonance in adults (Craigheero, Jacono, et al., 2016), excluding that these effects merely depend on the recognition of an acting hand. In line with these studies, here, in a preliminary experiment, we found that adults were not capable to reliably recognize a grasping hand from the PL stimuli we used. Also, the presence of a ball at the end of the PL movement did not increase adults' ability to recognize the grasping hand as source stimulus of the animation. Nonetheless, our study shows that, during the reaching phase, 9-months-old infants' sensorimotor system was recruited during the observation of the moving PL displays, suggesting that, regardless of the presence of a

graspable object, kinematic information is sufficient to engage the activation of the sensorimotor cortex. The only study partially investigating this same issue in infants, investigated real hand observation and reported different results (Southgate, Johnson, Karoui, & Csibra, 2010). In the study, to verify whether infants can generate online predictions about action outcomes, nine-month-old infants were presented either with a real hand in a grasping posture disappearing behind an occluder, or the same mimed action without any occluder. Results showed a significant attenuation of SMR alpha activity from baseline only for movements disappearing behind the occluder. This was interpreted as evidence that sensorimotor activity is present only if the observed action permits infants to infer a likely outcome (i.e., that the hand is likely grasping for an occluded object), an interpretation supported by the presence of higher desynchronization of the SMR alpha in eight-month-old infants during observation of a goal-directed action than of a spatially similar non-goal-directed movement (Nyström, Ljunghammar, Rosander, & Von Hofsten, 2011). However, it has been shown that greater suppression of alpha activity is also present in response to unusual actions compared with ordinary ones (Stapel, Hunnius, van Elk, & Bekkering, 2010) and explained by the authors as evidence that, since the motor system is used to generate predictions about actions, when we observe actions that deviate from what expected, additional predictions have to be generated, resulting in a stronger motor activation. Indeed, while the totally visible hand shown by Southgate and colleagues (Southgate et al., 2010) requires no prediction, the disappearing hand, more attractive and interesting, probably involves some predictive activity. This may represent a possible alternative explanation for the difference in alpha attenuation between the two conditions, without strictly attributing it to the inference of the presence of a hidden object. In addition, in adults the motor system is assigned a compensatory role when it is necessary to compensate for the noisy or missing sensory input (D'Ausilio, Bufalari, Salmas, Busan, & Fadiga, 2011; D'Ausilio, Bufalari, Salmas, & Fadiga, 2012; D'Ausilio, Jarmolowska, Busan, Bufalari, & Craighero, 2011), when we lack related sensorimotor experience (Schmitz et al., 2018), and when we need to refine a sensorimotor skill-set (Aglioti, Cesari, Romani, & Urgesi, 2008; Bangert & Altenmüller, 2003; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006). The results of the present experiment support the hypothesis of a compensatory role of the sensorimotor system by showing a strong involvement of the sensorimotor cortex during observation of highly degraded moving stimuli, not modulated by the presence of a graspable object.

Therefore, object presence did not affect our results during observation of PL moving stimuli (Reaching Phase). Nonetheless, the presence of the ball induced attenuation of alpha activity during the observation of the PL stimuli still in their initial position (Anticipatory Phase), not evident when the object was absent. So, it seems that when a graspable object is present, the sensorimotor system is activated even before the action actually begins, possibly in an independent fashion from its actual execution. This finding is similar to what Southgate and colleagues (Southgate et al., 2009) found in nine-month-old infants during the observation of actions

presented in a live setting: the infants were seated in front of a puppet stage with the curtains closed, and when infants were still and attentive, curtains opened to reveal a graspable object that after a while a hand grasped and removed from the scene. Their findings showed an attenuation of the alpha rhythm prior to the onset of the observed action. This sensorimotor activity was interpreted as a predictive motor activation evoked by the learning that a hand would appear after the curtains were opened. A similar interpretation can be adopted for current results, arguing that the presence of the object stronger suggests that a movement will occur and therefore the attenuation of alpha activity during the observation of the PL stimuli still in their initial position in the presence of the ball could reflect a prediction process.

However, in the current study Ball and NoBall stimuli have been mixed up, and following the repeated observation of the stimuli, either the presence or the absence of the object had the possibility to suggest the incoming movement. Moreover, the PL animation was a degraded stimulus not easily recognized as a grasping hand, and it was already present at the beginning of the video. Furthermore, during the reaching phase the presence of the object did not modulate results. Therefore, a possible alternative interpretation is that the attenuation of SMR alpha activity prior to PL movement can be attributed to the presence of the object that could be the target of an action rather than to a learning process occurring during the testing session. This interpretation requires that our nine-month-old participants were able to use pictorial depth cues to infer three-dimensional structure in the presented two-dimensional depiction of the ball, and the results of a series of habituation-dishabituation and preferential-looking studies are in favor of this possibility, showing that the ability to extract pictorial 3D information emerges at about 6 months (see, Kavšek, Yonas, & Granrud, 2012).

Indeed, it is known that the mere observation of objects that have the potential for being manipulated is effective in modulating the activity of the motor system in both monkeys and humans. In monkeys, a set of premotor neurons known as “canonical neurons” discharges during the presentation of graspable objects (Murata et al., 1997; Raos, Umiltà, Murata, Fogassi, & Gallese, 2006; Rizzolatti et al., 1988; Umiltà, Brochier, Spinks, & Lemon, 2007), and in humans, both brain imaging studies (Chao & Martin, 2000; Grèzes, Armony, Rowe, & Passingham, 2003; Grèzes, Tucker, Armony, Ellis, & Passingham, 2003; Mruczek, von Loga, & Kastner, 2013), and electrophysiological and psychophysical investigations (Craighero, Fadiga, Rizzolatti, & Umiltà, 1998, 1999; Craighero, Fadiga, Umiltà, & Rizzolatti, 1996; Craighero, Zorzi, Canto, & Franca, 2014; Ellis & Tucker, 2000; Makris, Hadar, & Yarrow, 2011; Symes, Ellis, & Tucker, 2007; Tucker & Ellis, 1998) showed that the observation of graspable objects recruits the same sensorimotor representations involved in their actual manipulation.

Several studies have evidenced that SMR alpha activity in adults is sensitive to mere object observation (Proverbio, 2012; Wamain, Gabrielli, & Coello, 2016; Wamain, Sahai, Decroix, Coello, & Kalénine, 2018). In Proverbio (2012), the level of manipulability of the object affected the amplitude of alpha suppression. In Wamain et al. (2016), manipulable objects induced a stronger suppression when they were presented in

peripersonal space in comparison to extrapersonal space, and in Wamain et al. (2018), SMR alpha activity was extinguished when the observed object afforded simultaneously different structural and functional gesture representations, suggesting that it may have a role in action selection processes during object perception. Present findings showing that the presence of an object induced attenuation of alpha activity during the observation of not moving PL stimuli suggest that even in infants object sight may recruit the sensorimotor cortex. However, further investigation is necessary to discriminate between the two alternative interpretations of these results, specifically testing in infancy the presence of sensorimotor involvement during the mere observation of graspable objects.

Importantly, modulation of alpha attenuation differed in the central, occipital and frontal regions. In particular, alpha attenuation was completely absent in the frontal region. It was present in the occipital region, but significantly greater in both the reaching and grasping phase as compared to the anticipatory phase. Conversely, in the central region, SMR desynchronization was modulated differently both as a function of the three selected phases of the action and the presence of the ball. Specifically, SMR desynchronization was absent in the grasping phase, it was not affected by the presence of the ball in the reaching phase, and it was significantly different in the ball and no ball condition in the anticipatory phase. Our findings are consistent with previous reports showing that in infants (Filippi et al., 2016) and in adults (Marshall, Bouquet, Shipley, & Young, 2009) SMR desynchronization over central regions is accompanied by alpha desynchronization at occipital regions during action observation. Occipital alpha is known to be linked to visual attention (Debnath, Salo, Buzzell, Yoo, & Fox, 2019; Warreyn et al., 2013). In this vein, the occipital alpha attenuation we have found regardless of the presence of the object (i.e., ball) might reflect the involvement of an attentional component during observation of a moving stimulus as compared to observation of a static one. A further interpretation, not necessarily alternative to the previous one, is that the observed occipital alpha desynchronization in response to PL animations moving with the accelerated-decelerated kinematics of goal-directed hand actions might be due to an ongoing canalization process responsible for the development of a specialized sensorimotor mechanism involved in the processing of others' actions (Quadrelli & Turati, 2016). Indeed, as demonstrated in a previous study (Yoo, Cannon, Thorpe, & Fox, 2016), observation of goal-directed actions elicited the recruitment of occipital regions to a greater extent in 9-month-olds as compared to 12-month-olds. Thus, from a developmental perspective, it is possible that action observation requires the recruitment of broader cortical areas within the first months of life and that acquired active and observational experiences with actions are responsible for shaping the gradual specialization of sensorimotor representations (Cannon & Woodward, 2012; Sommerville, Woodward, & Needham, 2005). Future infant research should further explore the relation between occipital and central alpha attenuation, possibly investigating the role of kinematics specificity by comparing accelerated-decelerated biological

kinematics with constant velocity non-biological kinematics across development.

5. Conclusions

Here for the first time we showed attenuation of SMR alpha band activity in nine-month-old infants during observation of a PL animation of a hand grasping an object and during observation of the same PL animation after deletion of the object. These results demonstrate that early in life the sensorimotor cortex responds to moving stimuli in which the physical appearance of the grasping hand is so highly diminished that adults are not always able to recognize it as such. Thus, current data supports the hypothesis of a compensatory role of the sensorimotor system during observation of highly degraded moving stimuli, not necessarily based on the inference of a goal-related outcome. Furthermore, the suppression of alpha activity during observation of a graspable object prior to the onset of the PL movement could indicate either a role of the object as cue of the incoming movement inducing a predictive motor activation or, alternatively, a role of the sensorimotor cortex in object perception even in infancy.

Competing financial interests

The authors declare no competing financial interests.

Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the study are available at https://osf.io/cjmr7/?view_only=61020c728b0845f7ac94c9d65ae9b6e3.

CRedit authorship contribution statement

Ermanno Quadrelli: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - review & editing, Visualization. **Elisa Roberti:** Formal analysis, Investigation, Data curation, Writing - review & editing. **Chiara Turati:** Conceptualization, Methodology, Funding acquisition, Resources, Supervision, Writing - review & editing. **Laila Craighero:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing.

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REFERENCES

- Abdi, H. (2010). Holm's sequential Bonferroni procedure. *Encyclopedia of Research Design*, 1(8), 1–8. <https://doi.org/10.4135/9781412961288>.
- Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, 11(9), 1109–1116. <https://doi.org/10.1038/nn.2182>.
- Avanzini, P., Fabbri-Destro, M., Dalla Volta, R., Daprati, E., Rizzolatti, G., & Cantalupo, G. (2012). The dynamics of sensorimotor cortical oscillations during the observation of hand movements: An EEG study. *PLoS One*, 7(5), e37534. <https://doi.org/10.1371/journal.pone.0037534>.
- Babiloni, C., Carducci, F., Cincotti, F., Rossini, P. M., Neuper, C., Pfurtscheller, G., et al. (1999). Human movement-related potentials vs desynchronization of EEG alpha rhythm: A high-resolution EEG study. *NeuroImage*, 10(6), 658–665. <https://doi.org/10.1006/nimg.1999.0504>.
- Bangert, M., & Altenmüller, E. O. (2003). Mapping perception to action in piano practice: A longitudinal DC-EEG study. *BMC Neuroscience*, 15(4), 26. <https://doi.org/10.1186/1471-2202-4-26>.
- Bardi, L., Regolin, L., & Simion, F. (2011). Biological motion preference in humans at birth: Role of dynamic and configural properties. *Developmental Science*, 14(2), 353–359. <https://doi.org/10.1111/j.1467-7687.2010.00985.x>.
- Bardi, L., Regolin, L., & Simion, F. (2014). The first time ever I saw your feet: Inversion effect in newborns' sensitivity to biological motion. *Developmental Psychology*, 50(4), 986–993. <https://doi.org/10.1037/a0034678>.
- Bertenthal, B. I., Proffitt, D. R., & Kramer, S. J. (1987). Perception of biomechanical motions by infants: Implementation of various processing constraints. *Journal of Experimental Psychology: Human Perception and Performance*, 13, 577–585. <https://doi.org/10.1037/0096-1523.13.4.577>.
- Bertenthal, B. I., Proffitt, D. R., Spetner, N. B., & Thomas, M. A. (1985). The development of infant sensitivity to biomechanical motions. *Child Development*, 56, 531–543. <https://doi.org/10.1111/j.1467-8624.1985.tb00126.x>.
- Bidet-Ildei, C., Kitromilides, E., Orliaguet, J.-P., Pavlova, M., & Gentaz, E. (2014). Preference for point-light human biological motion in newborns: Contribution of translational displacement. *Developmental Psychology*, 50(1), 113–120. <https://doi.org/10.1037/a0032956>.
- Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology*, 58, 47–73. <https://doi.org/10.1146/annurev.psych.57.102904.190152>.
- Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience*, 16, 3737–3744. <https://doi.org/10.1523/JNEUROSCI.16-11-03737.1996>.
- Booth, A. E., Bertenthal, B. I., & Pinto, J. (2002). Perception of the symmetrical patterning of human gait by infants. *Developmental Psychology*, 38, 554–563. <https://doi.org/10.1037/0012-1649.38.4.554>.
- Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, 15, 1243–1249. <https://doi.org/10.1093/cercor/bhi007>.
- Cannon, E. N., Simpson, E. A., Fox, N. A., Vanderwert, R. E., Woodward, A. L., & Ferrari, P. F. (2016). Relations between infants' emerging reach-grasp competence and event-related desynchronization in EEG. *Developmental Science*, 19(1), 50–62. <https://doi.org/10.1111/desc.12295>.
- Cannon, E. N., & Woodward, A. L. (2012). Infants generate goal-based action predictions. *Developmental Science*, 15(2), 292–298. <https://doi.org/10.1111/j.1467-7687.2011.01127.x>.
- Cardellicchio, P., Sinigaglia, C., & Costantini, M. (2013). Grasping affordances with the other's hand: A tms study. *Social Cognitive and Affective Neuroscience*, 8(4), 455–459. <https://doi.org/10.1093/scan/nss017>.
- Caspers, S., Zilles, K., Laird, A. R., & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, 8, 455–459. <https://doi.org/10.1016/j.neuroimage.2009.12.112>.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, 12, 478–484. <https://doi.org/10.1006/nimg.2000.0635>.
- Cochin, S., Barthelemy, C., Lejeune, B., Roux, S., & Martineau, J. (1998). Perception of motion and qEEG activity in human adults. *Electroencephalography and Clinical Neurophysiology*, 107(4), 287–295. [https://doi.org/10.1016/S0013-4694\(98\)00071-6](https://doi.org/10.1016/S0013-4694(98)00071-6).
- Cohen, J. (1992). Statistical power analysis. *Current Directions in Psychological Science*, 1(3), 98–101.
- Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1998). Visuomotor priming. *Visual Cognition*, 5(1–2), 109–125. <https://doi.org/10.1080/713756780>.
- Craighero, L., Fadiga, L., Rizzolatti, G., & Umiltà, C. (1999). Action for perception: A motor-visual attentional effect. *Journal of Experimental Psychology: Human Perception and Performance*, 25(6), 1673–1692. <https://doi.org/10.1037/0096-1523.25.6.1673>.
- Craighero, L., Fadiga, L., Umiltà, C. A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *NeuroReport*, 8(1), 347–349. <https://doi.org/10.1097/00001756-199612200-00068>.
- Craighero, L., Jacono, M., & Mele, S. (2016). Resonating with the ghost of a hand: A TMS experiment. *Neuropsychologia*, 84, 181–192. <https://doi.org/10.1016/j.neuropsychologia.2016.02.014>.
- Craighero, L., Leo, I., Umiltà, C., & Simion, F. (2011). Newborns' preference for goal-directed actions. *Cognition*, 120(1), 26–32. <https://doi.org/10.1016/j.cognition.2011.02.011>.
- Craighero, L., Lunghi, M., Leo, I., Ghirardi, V., & Simion, F. (2016). Newborns' attention is driven by the translational movement. *Visual Cognition*, 24(9–10), 487–498. <https://doi.org/10.1080/13506285.2017.1322651>.
- Craighero, L., Zorzi, V., Canto, R., & Franca, M. (2014). Same kinematics but different objects during action observation: Detection times and motor evoked potentials. *Visual Cognition*, 22(5), 653–671. <https://doi.org/10.1080/13506285.2014.904460>.
- Cross, E. S., Hamilton, A. F. d. C., & Grafton, S. T. (2006). Building a motor simulation de novo: Observation of dance by dancers. *NeuroImage*, 31, 1257–1267. <https://doi.org/10.1016/j.neuroimage.2006.01.033>.
- Csibra, G., Davis, G., Spratling, M. W., & Johnson, M. H. (2000). Gamma oscillations and object processing in the infant brain. *Science*, 290(5496), 1582–1585.
- Cuevas, K., Cannon, E. N., Yoo, K., & Fox, N. A. (2014). The infant EEG mu rhythm: Methodological considerations and best practices. *Developmental Review*, 34(1), 26–43.
- de Klerk, C. C., Johnson, M. H., Heyes, C. M., & Southgate, V. (2015). Baby steps: Investigating the development of perceptual-motor couplings in infancy. *Developmental Science*, 18(2), 270–280.
- de Klerk, C. C. J. M., Johnson, M. H., & Southgate, V. (2015). An EEG study on the somatotopic organisation of sensorimotor cortex activation during action execution and observation in infancy. *Developmental Cognitive Neuroscience*, 15, 1–10. <https://doi.org/10.1016/j.dcn.2015.08.004>.
- Debnath, R., Salo, V. C., Buzzell, G. A., Yoo, K. H., & Fox, N. A. (2019). Mu rhythm desynchronization is specific to action

- execution and observation: Evidence from time-frequency and connectivity analysis. *NeuroImage*, 184, 496–507.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91, 176–180. <https://doi.org/10.1007/BF00230027>.
- D'Ausilio, A., Bufalari, I., Salmas, P., Busan, P., & Fadiga, L. (2011). Vocal pitch discrimination in the motor system. *Brain and Language*, 118, 9–14. <https://doi.org/10.1016/j.bandl.2011.02.007>.
- D'Ausilio, A., Bufalari, I., Salmas, P., & Fadiga, L. (2012). The role of the motor system in discriminating normal and degraded speech sounds. *Cortex*, 48(7), 882–887. <https://doi.org/10.1016/j.cortex.2011.05.017>.
- D'Ausilio, A., Jarmolowska, J., Busan, P., Bufalari, I., & Craighero, L. (2011). Tongue corticospinal modulation during attended verbal stimuli: Priming and coarticulation effects. *Neuropsychologia*, 49(13), 3670–3676. <https://doi.org/10.1016/j.neuropsychologia.2011.09.022>.
- Ellis, R., & Tucker, M. (2000). Micro-affordance: The potentiation of components of action by seen objects. *British Journal of Psychology*, 91, 451–471. <https://doi.org/10.1348/000712600161934>.
- Elsner, C., Falck-Ytter, T., & Gredebäck, G. (2012). Humans anticipate the goal of other people's point-light actions. *Frontiers in Psychology*, 3, 120. <https://doi.org/10.3389/fpsyg.2012.00120>.
- 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>.
- Filippi, C. A., Cannon, E. N., Fox, N. A., Thorpe, S. G., Ferrari, P. F., & Woodward, A. L. (2016). Motor system activation predicts goal imitation in 7-month-old infants. *Psychological Science*, 27(5), 675–684.
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, 424, 769–771. <https://doi.org/10.1038/nature01861>.
- Gastaut, H. J., & Bert, J. (1954). EEG changes during cinematographic presentation. *EEG 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).
- Grèzes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to “mirror” and “canonical” neurones in the human brain: An fMRI study. *NeuroImage*. [https://doi.org/10.1016/S1053-8119\(03\)00042-9](https://doi.org/10.1016/S1053-8119(03)00042-9).
- Grèzes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions? *NeuroImage*, 18, 928–937. <https://doi.org/10.1006/nimg.2000.0740>.
- Grèzes, J., Tucker, M., Armony, J., Ellis, R., & Passingham, R. E. (2003). Objects automatically potentiate action: An fMRI study of implicit processing. *European Journal of Neuroscience*, 13, 775–785. <https://doi.org/10.1046/j.1460-9568.2003.02695.x>.
- Gribble, P. L., & Ostry, D. J. (1996). Origins of the power law relation between movement velocity and curvature: Modeling the effects of muscle mechanics and limb dynamics. *Journal of Neurophysiology*, 76(5), 2853–2860. <https://doi.org/10.1016/j.pathophys.2007.07.002>.
- Grosbras, M. H., Beaton, S., & Eickhoff, S. B. (2012). Brain regions involved in human movement perception: A quantitative voxel-based meta-analysis. *Human Brain Mapping*, 33, 431–454. <https://doi.org/10.1002/hbm.21222>.
- Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, 35(6), 1167–1175.
- Halit, H., De Haan, M., & Johnson, M. H. (2003). Cortical specialisation for face processing: Face-sensitive event-related potential components in 3- and 12-month-old infants. *NeuroImage*, 19(3), 1180–1193.
- Hari, R. (2006). Action-perception connection and the cortical mu rhythm. *Progress in Brain Research*, 159, 253–260. [https://doi.org/10.1016/S0079-6123\(06\)59017-X](https://doi.org/10.1016/S0079-6123(06)59017-X).
- Hirai, M., & Hiraki, K. (2005). An event-related potentials study of biological motion perception in human infants. *Cognitive Brain Research*, 22(2), 301–304. <https://doi.org/10.1016/j.cogbrainres.2004.08.008>.
- Howell, S. J. (1987). Long-term EEG monitoring in epilepsy. *Lancet*, 1(8547), 1437.
- Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology*, 60, 653–670. <https://doi.org/10.1146/annurev.psych.60.110707.163604>.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 86, 2526–2528. <https://doi.org/10.1126/science.286.5449.2526>.
- Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, 16, 235–254. <https://doi.org/10.1080/00222895.1984.10735319>.
- Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, 14(2), 201–211. <https://doi.org/10.3758/BF03212378>.
- Johansson, G. (1976). Spatio-temporal differentiation and integration in visual motion perception. *Psychological Research*, 4, 379–393. <https://doi.org/10.1007/BF00309043>.
- Kavšek, M., Yonas, A., & Granrud, C. E. (2012). Infants' sensitivity to pictorial depth cues: A review and meta-analysis of looking studies. *Infant Behavior & Development*, 35(1), 109–128. <https://doi.org/10.1016/j.infbeh.2011.08.003>.
- Kuhlmeier, V. A., Troje, N. F., & Lee, V. (2010). Young infants detect the direction of biological motion in point-light displays. *Infancy*, 15, 83–93. <https://doi.org/10.1111/j.1532-7078.2009.00003.x>.
- Lapenta, O. M., Ferrari, E., Boggio, P. S., Fadiga, L., & D'Ausilio, A. (2018). Motor system recruitment during action observation: No correlation between mu-rhythm desynchronization and corticospinal excitability. *PLoS One*, 13(11), e0207476. <https://doi.org/10.1371/journal.pone.0207476>.
- Makris, S., Hadar, A. A., & Yarrow, K. (2011). Viewing objects and planning actions: On the potentiation of grasping behaviours by visual objects. *Brain and Cognition*, 77, 257–264. <https://doi.org/10.1016/j.bandc.2011.08.002>.
- Marshall, P. J., Bar-Haim, Y., & Fox, N. A. (2002). Development of the EEG from 5 months to 4 years of age. *Clinical Neurophysiology*, 113, 1199–1208. [https://doi.org/10.1016/S1388-2457\(02\)00163-3](https://doi.org/10.1016/S1388-2457(02)00163-3).
- Marshall, P. J., Bouquet, C. A., Shipley, T. F., & Young, T. (2009). Effects of brief imitative experience on EEG desynchronization during action observation. *Neuropsychologia*, 47, 2100–2106. <https://doi.org/10.1016/j.neuropsychologia.2009.03.022>.
- Marshall, P. J., & Meltzoff, A. N. (2011). Neural mirroring systems: Exploring the EEG mu rhythm in human infancy. *Developmental Cognitive Neuroscience*. <https://doi.org/10.1016/j.dcn.2010.09.001>.
- Marshall, P. J., & Shipley, T. F. (2009). Event-related potentials to point-light displays of human actions in 5-month-old infants. *Developmental Neuropsychology*, 1, 110–123. <https://doi.org/10.1080/87565640902801866>.
- Méary, D., Kitromilides, E., Mazens, K., Graff, C., & Gentaz, E. (2007). Four-day-old human neonates look longer at non-biological motions of a single point-of-light. *PLoS One*, 2(1), e186. <https://doi.org/10.1371/journal.pone.0000186>.
- Mruczek, R. E. B., von Loga, I. S., & Kastner, S. (2013). The representation of tool and non-tool object information in the human intraparietal sulcus. *Journal of Neurophysiology*, 109, 2883–2896. <https://doi.org/10.1152/jn.00658.2012>.
- Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., & Rizzolatti, G. (1997). Object representation in the ventral

- premotor cortex (area F5) of the monkey. *Journal of Neurophysiology*, 78(4), 2226–2230. <https://doi.org/10.1152/jn.1997.78.4.2226>.
- Muthukumaraswamy, S. D., & Johnson, B. W. (2004). Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology*, 41, 152–156. <https://doi.org/10.1046/j.1469-8986.2003.00129.x>.
- 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>.
- Nyström, P., Ljunghammar, T., Rosander, K., & Von Hofsten, C. (2011). Using mu rhythm desynchronization to measure mirror neuron activity in infants. *Developmental Science*, 14, 327–335. <https://doi.org/10.1111/j.1467-7687.2010.00979.x>.
- Parise, E., & Csibra, G. (2013). Neural responses to multimodal ostensive signals in 5-month-old infants. *PLoS One*, 8(8), e72360.
- Peelen, M. V., Wiggett, A. J., & Downing, P. E. (2006). Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron*, 49, 815–822. <https://doi.org/10.1016/j.neuron.2006.02.004>.
- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing”. *Brain Research. Brain Research Reviews*, 50(1), 57–68. <https://doi.org/10.1016/j.brainresrev.2005.04.005>.
- Pineda, J. A., Allison, B. Z., & Vankov, a. (2000). The effects of self-movement, observation, and imagination on?? Rhythms and readiness potentials (RPS): Toward a brain-computer interface (BCI). *IEEE Transactions on Rehabilitation Engineering*, 8(2), 219–222. <https://doi.org/10.1109/86.847822>.
- Pomiechowska, B., & Csibra, G. (2017). Motor activation during action perception depends on action interpretation. *Neuropsychologia*, 105, 84–91.
- Proverbio, A. M. (2012). Tool perception suppresses 10–12Hz μ rhythm of EEG over the somatosensory area. *Biological Psychology*, 91, 1–7. <https://doi.org/10.1016/j.biopsycho.2012.04.003>.
- Quadrelli, E., Geangu, E., & Turati, C. (2019). Human action sounds elicit sensorimotor activation early in life. *Cortex*, 117, 323–335. <https://doi.org/10.1016/j.cortex.2019.05.009>.
- Quadrelli, E., & Turati, C. (2016). Origins and development of mirroring mechanisms: A neuroconstructivist framework. *British Journal of Developmental Psychology*, 34(1), 6–23. <https://doi.org/10.1111/bjdp.12110>.
- Quinlan, D. J., & Culham, J. C. (2015). Direct comparisons of hand and mouth kinematics during grasping, feeding and fork-feeding actions. *Frontiers in Human Neuroscience*, 9, 580. <https://doi.org/10.3389/fnhum.2015.00580>.
- Raos, V., Umiltà, M. A., Murata, A., Fogassi, L., & Gallese, V. (2006). Functional properties of grasping-related neurons in the ventral premotor area F5 of the macaque monkey. *Journal of Neurophysiology*, 95(2), 709–729. <https://doi.org/10.1152/jn.00463.2005>.
- Reid, V. M., Hoehl, S., & Striano, T. (2006). The perception of biological motion by infants: An event-related potential study. *Neuroscience Letters*, 395(3), 211–214.
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey - II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71, 491–507. <https://doi.org/10.1007/BF00248742>.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27(1), 169–192. <https://doi.org/10.1146/annurev.neuro.27.070203.144230>.
- Rizzolatti, G., & Fogassi, L. (2014). The mirror mechanism: Recent findings and perspectives. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 369(1644), 20130420. <https://doi.org/10.1098/rstb.2013.0420>.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, 2, 661–670. <https://doi.org/10.1038/35090060>.
- Rizzolatti, G., & Sinigaglia, C. (2007). Mirror neurons and motor intentionality. *Functional Neurology*, 22(4), 205–210. <https://doi.org/10.1038/2622>. PMID: 18182127.
- Rotman, G., Troje, N. F., Johansson, R. S., & Flanagan, J. R. (2006). Eye movements when observing predictable and unpredictable Actions. *Journal of Neurophysiology*, 96, 1358–1369. <https://doi.org/10.1152/jn.00227.2006>.
- Roy, A. C., Paulignan, Y., Farnè, A., Jouffrais, C., & Boussaoud, D. (2000). Hand kinematics during reaching and grasping in the macaque monkey. *Behavioural and Brain Research*, 117(1–2), 75–82.
- Saby, J. N., Marshall, P. J., & Meltzoff, A. N. (2012). Neural correlates of being imitated: An EEG study in preverbal infants. *Social Neuroscience*, 7, 650–661. <https://doi.org/10.1080/17470919.2012.691429>.
- Saby, J. N., Meltzoff, A. N., & Marshall, P. J. (2013). Infants' somatotopic neural responses to seeing human actions: I've got you under my skin. *PLoS One*, 8, e77905. <https://doi.org/10.1371/journal.pone.0077905>.
- Saygin, A. P. (2007). Superior temporal and premotor brain areas necessary for biological motion perception. *Brain*, 130, 2452–2461. <https://doi.org/10.1093/brain/awm162>.
- Saygin, A. P., Wilson, S. M., Hagler, D. J., Bates, E., & Sereno, M. I. (2004). Point-light biological motion perception activates human premotor cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 24(27), 6181–6188. <https://doi.org/10.1523/JNEUROSCI.0504-04.2004>.
- Schmitz, J., Bartoli, E., Maffongelli, L., Fadiga, L., Sebastian-Galles, N., & D'Ausilio, A. (2018). Motor cortex compensates for lack of sensory and motor experience during auditory speech perception. *Neuropsychologia*. pii: S0028-3932(18)30007–30011. <https://doi.org/10.1016/j.neuropsychologia.2018.01.006>.
- Schmuckler, M. A., & Fairhall, J. L. (2001). Visual-proprioceptive intermodal perception using point light displays. *Child Development*, 72, 949–962. <https://doi.org/10.1111/1467-8624.00327>.
- Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences*, 105(2), 809–813. <https://doi.org/10.1073/pnas.0707021105>.
- Soken, N. H., & Pick, A. D. (1992). Intermodal perception of happy and angry expressive behaviors by seven-month-old infants. *Child Development*, 63, 787–795. <https://doi.org/10.1111/j.1467-8624.1992.tb01661.x>.
- Sommerville, J. A., Woodward, A. L., & Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition*, 96(1), B1–B11. <https://doi.org/10.1016/j.cognition.2004.07.004>.
- Southgate, V., Johnson, M. H., Karoui, I. El, & Csibra, G. (2010). Motor system activation reveals infants' on-line prediction of others' goals. *Psychological Science*, 21, 355–359. <https://doi.org/10.1177/0956797610362058>.
- Southgate, V., Johnson, M. H., Osborne, T., & Csibra, G. (2009). Predictive motor activation during action observation in human infants. *Biology Letters*, 5, 769–772. <https://doi.org/10.1098/rsbl.2009.0474>.
- Sparling, J. W., Van Tol, J., & Chescheir, N. C. (1999). Fetal and neonatal hand movement. *Physical Therapy*, 79(1), 24–39. <https://doi.org/10.1177/088307389300800103>.
- Sparling, & Wilhelm. (1993). Quantitative measurement of fetal movement. *Physical and Occupational Therapy in Pediatrics*, 12, 97–114. https://doi.org/10.1080/J006v12n02_06.

- Stapel, J. C., Hunnius, S., van Elk, M., & Bekkering, H. (2010). Motor activation during observation of unusual versus ordinary actions in infancy. *Social Neuroscience*, 5, 451–460. <https://doi.org/10.1080/17470919.2010.490667>.
- Symes, E., Ellis, R., & Tucker, M. (2007). Visual object affordances: Object orientation. *Acta Psychologica*, 124, 238–255. <https://doi.org/10.1016/j.actpsy.2006.03.005>.
- Thorpe, S. G., Cannon, E. N., & Fox, N. A. (2016). Spectral and source structural development of mu and alpha rhythms from infancy through adulthood. *Clinical Neurophysiology*, 127, 254–269. <https://doi.org/10.1016/j.clinph.2015.03.004>.
- Troje, N. F. (2002). Decomposing biological motion: A framework for analysis and synthesis of human gait patterns. *Journal of Vision*, 2, 371–387. <https://doi.org/10.1167/2.5.2>.
- Tucker, M., & Ellis, R. (1998). On the relations between seen objects and components of potential actions. *Journal of Experimental Psychology: Human Perception and Performance*, 24(3), 830–846. <https://doi.org/10.1037/0096-1523.24.3.830>.
- Ulloa, E. R., & Pineda, J. A. (2007). Recognition of point-light biological motion: Mu rhythms and mirror neuron activity. *Behavioural Brain Research*, 183(2), 188–194. <https://doi.org/10.1016/j.bbr.2007.06.007>.
- Umiltà, M. A., Brochier, T., Spinks, R. L., & Lemon, R. N. (2007). Simultaneous recording of macaque premotor and primary motor cortex neuronal populations reveals different functional contributions to visuomotor grasp. *Journal of Neurophysiology*, 98, 488–501. <https://doi.org/10.1152/jn.01094.2006>.
- Urgesi, C., Maieron, M., Avenanti, A., Tidoni, E., Fabbro, F., & Aglioti, S. M. (2010). Simulating the future of actions in the human corticospinal system. *Cerebral Cortex*, 20(11), 2511–2521. <https://doi.org/10.1093/cercor/bhp292>.
- Urgesi, C., Moro, V., Candidi, M., & Aglioti, S. M. (2006). Mapping implied body actions in the human motor system. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 26(30), 7942–7949. <https://doi.org/10.1523/JNEUROSCI.1289-06.2006>.
- Vaina, L. M., Solomon, J., Chowdhury, S., Sinha, P., & Belliveau, J. W. (2001). Functional neuroanatomy of biological motion perception in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 98(20), 11656–11661. <https://doi.org/10.1073/pnas.191374198>.
- Vanderwert, R. E., Fox, N. A., & Ferrari, P. F. (2013). The mirror mechanism and mu rhythm in social development. *Neuroscience Letters*, 540, 15–20. <https://doi.org/10.1016/j.neulet.2012.10.006>.
- van Kemenade, B. M., Muggleton, N., Walsh, V., & Saygin, A. P. (2012). Effects of TMS over premotor and superior temporal cortices on biological motion perception. *Journal of Cognitive Neuroscience*, 24, 896–904. https://doi.org/10.1162/jocn_a_00194.
- Viviani, P., Baud-Bovy, G., & Redolfi, M. (1997). Perceiving and tracking kinesthetic stimuli: Further evidence of motor-perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance*. <https://doi.org/10.1037/0096-1523.23.4.1232>.
- Viviani, P., & Stucchi, N. (1992). Biological movements look uniform: Evidence of motor-perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 1232–1252. <https://doi.org/10.1037/0096-1523.18.3.603>.
- Viviani, P., & Terzuolo, C. (1982). Trajectory determines movement dynamics. *Neuroscience*, 7, 431–437. [https://doi.org/10.1016/0306-4522\(82\)90277-9](https://doi.org/10.1016/0306-4522(82)90277-9).
- Wamain, Y., Gabrielli, F., & Coello, Y. (2016). EEG μ rhythm in virtual reality reveals that motor coding of visual objects in peripersonal space is task dependent. *Cortex*, 74, 20–30. <https://doi.org/10.1016/j.cortex.2015.10.006>.
- Wamain, Y., Sahaï, A., Decroix, J., Coello, Y., & Kalénine, S. (2018). Conflict between gesture representations extinguishes μ rhythm desynchronization during manipulable object perception: An EEG study. *Biological Psychology*, 132, 2012–2211. <https://doi.org/10.1016/j.biopsycho.2017.12.004>.
- Warreyn, P., Ruyschaert, L., Wiersema, J. R., Handl, A., Pattyn, G., & Roeyers, H. (2013). Infants' mu suppression during the observation of real and mimicked goal-directed actions. *Developmental Science*, 16(2), 173–185.
- Wood, J. M., Tyrrell, R. A., & Carberry, T. P. (2005). Limitations in drivers' ability to recognize pedestrians at night. *Human Factors: The Journal of the Human Factors and Ergonomics Society*, 47, 644–653. <https://doi.org/10.1518/001872005774859980>.
- Yoo, K. H., Cannon, E. N., Thorpe, S. G., & Fox, N. A. (2016). Desynchronization in EEG during perception of means-end actions and relations with infants' grasping skill. *British Journal of Developmental Psychology*, 34(1), 24–37.
- Zheng, B., & MacKenzie, C. L. (2007). Kinematics of reaching and grasping with a tool. *Human Factors and Ergonomics Society Annual Meeting Proceedings*, 51(19), 1353–1357. <https://doi.org/10.1177/154193120705101917>.
- Zoia, S., Blason, L., D'Ottavio, G., Bulgheroni, M., Pezzetta, E., Scabar, A., et al. (2007). Evidence of early development of action planning in the human foetus: A kinematic study. *Experimental Brain Research*, 176(2), 217–226. <https://doi.org/10.1007/s00221-006-0607-3>.