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

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Abstract

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6 Measuring changes in sensorimotor alpha band activity in nine-month-old infants we sought to
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8 understand the involvement of the sensorimotor cortex during observation of the Point-Light (PL)
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10 animation of a grasping hand. Attenuation of alpha activity was found both when the PL display
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12 moved toward the to-be-grasped object and when the object was deleted from the video. Before the
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14 beginning of the movement of the PL stimuli, only in the presence of the object evoked attenuation
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16 of sensorimotor alpha activity was documented, possibly interpreted either as movement prediction
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18 or as graspable object perception. Our main findings demonstrate that, during observation of stimuli
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20 moving with biological kinematics, the infants' sensorimotor system is activated when the pictorial
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22 information is absent or highly reduced, and independently of the presence of the goal-directed
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24 object. The possible compensatory function of the sensorimotor system during observation of
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26 highly degraded moving stimuli is discussed.
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37 **Keywords.** *Visual perception, biological motion, sensorimotor activation, mu rhythm, EEG*
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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 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 (Zoja 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

1 crucial role that this mechanism plays in effectively integrating individuals within their social
2 milieu justifies the evidence that even more abstract forms of actions, those that have lost almost all
3 the hallmarks of action, may activate the sensorimotor system. Some examples are given by
4 transcranial magnetic stimulation (TMS) experiments showing that the observation of static
5 snapshots representing a mimicked grasping action induces a corticospinal activation (Urgesi et al.,
6 2010; Urgesi, Moro, Candidi, & Aglioti, 2006), as well as the observation of a handled object out of
7 reach for participants provided that it was ready to an avatar's hand (Cardellicchio, Sinigaglia, &
8 Costantini, 2013). Therefore, the sensorimotor system seems to be involved when the observed
9 movement is taking place, when it is known that it will be carried out, and when it is probable to
10 occur. The necessity to understand and predict what others are doing can even become vital in
11 situations where visibility is reduced due to obscurity or to the presence of obstacles. The possibility
12 to recognize gender, actions, intentions, and emotions of an agent in the absence of pictorial
13 information is well known (Blake & Shiffrar, 2007), as you can check at the following link
14 [www.biomotionlab.c a/Demos/BMLwalker.html](http://www.biomotionlab.ca/Demos/BMLwalker.html) (Troje, 2002). The trick to experimentally study
15 this issue was invented by Gunnar Johansson (Johansson, 1976, 1973) who devised the technique
16 known as point-light (PL) animation of biological motion: he attached small point lights to the main
17 joints of a person's body and filmed the scene so that only the lights were visible on a dark
18 background. Static frames of the resulting animation typically appear as meaningless assemblages
19 of dots, but the rapid succession of consecutive PL frames is immediately experienced as an
20 apparent motion of a human form engaged in a specific activity. Johansson's work was an
21 outgrowth of his applied research on traffic safety: putting lights or reflective tape on pedestrians
22 can allow drivers to instantaneously recognize them as human beings at night (Wood, Tyrrell, &
23 Carberry, 2005). Indeed, Johansson used the term biological motion in the title of his seminal article
24 (Johansson, 1973) to separate the perception of human movement from other motion, and ten years
25 later Viviani (Viviani & Terzuolo, 1982) proposed the two-thirds power law that characterises the

1 velocity of a point on a moving animal projected onto a plane with respect to the curvature of the
2 projected arc at that point, and demonstrated that our perceptual system is very well attuned to this
3 relation between velocity and curvature (Viviani, Baud-Bovy, & Redolfi, 1997; Viviani & Stucchi,
4 1992).

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

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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; Meary et al., 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

1 kicking person, infants of this age exhibit larger positive ERP amplitude over the right parietal
2 cortex at a latency of 200-300 ms (Reid, Hoehl, & Striano, 2006). ().
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5 Despite the rich behavioral literature and the few electrophysiological studies, to date there is a
6 sizable lack of studies specifically examining whether during infancy and childhood biological
7 motion observation determines the involvement of the sensorimotor cortex as occurs in adults,
8 evident in the suppression of the alpha SMR (Ulloa & Pineda, 2007). Like in adults, infants and
9 children demonstrate alpha SMR desynchronization during action observation and action execution,
10 which indirectly reflects the early emergence of action-perception coupling (Marshall, Bar-Haim, &
11 Fox, 2002; Marshall & Meltzoff, 2011). SMR desynchronization occurs in the frequency range of
12 6-9 Hz in the first two years of life, compared with the 8-13 Hz range that characterizes it in adults,
13 and increases from infancy to adulthood (Thorpe, Cannon, & Fox, 2016), being in nine-month-olds
14 around 10% when executing an action, and around 5% when observing an action (Southgate,
15 Johnson, Osborne, & Csibra, 2010).
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33 In the present study, for the first time, we used EEG to measure changes in SMR alpha band activity
34 in nine-month-old infants during observation of PL animation moving with biological kinematics.
35 Furthermore, stimuli were not PL displays depicting human total body movements such as walking
36 or running, but consisted in a PL display in which the velocity and motion profile of the PL markers
37 followed the typical velocity profile of human goal-directed hand actions, which is characterized by
38 a fast-velocity initial phase and a low-velocity final phase (Jeannerod, 1984). According to the
39 biological motion hypothesis of action anticipation (Elsner, Falck-Ytter, & Gredeback, 2012), the
40 observation of this biological kinematics is sufficient to automatically implement in the observer the
41 motor programs equivalent to those used in action (Iacoboni et al., 1999; Rizzolatti & Craighero,
42 2004; Rizzolatti, Fogassi, & Gallese, 2001), such as proactive-gaze (Flanagan & Johansson, 2003;
43 Rotman, Troje, Johansson, & Flanagan, 2006). Unlike PL displays of walkers which are
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1 immediately and easily recognized as such, those of a grasping hand are recognized as hands only
2 by few adult participants, both when markers are attached on the major joints of the hand (Elsner et
3 al., 2012), and when they are placed along the contour of the hand (Craighero, Iacono, et al., 2016;
4 Craighero, Lunghi, et al. 2016). Nevertheless, Elsner et al. (2012) reported that no gaze behavior
5 differences were observed between participants who recognized the hand and those who did not,
6 indicating that participants' performance was not affected by the familiarity of the observed
7 movement. The difference in the ability to recognize PL animations of walkers in comparison with
8 PL animations of a grasping hand may depend from the different type of information the two
9 kinematics provide to the observer. The first kinematics is formalized by the two-third-power law of
10 motion generation and perception (Viviani & Terzuolo, 1982), which defines the dynamic
11 regularities that reflect the structure and the control schemes of the musculo-skeletal system, and it
12 is explained by the rules of biomechanics (Gribble & Ostry, 1996). The second one concerns the
13 typical biological kinematics of a hand reaching for an object, which depends from the central
14 programming of the relationship between velocity of the hand and position of the to-be-reached
15 object (Jeannerod, 1984). Therefore, walking is a cycling movement whose regularities are strictly
16 linked to the shape of the body that limits the biomechanical possibilities, and, probably for this
17 reason, the shape of the body results immediately evident when the rapid succession of consecutive
18 PL frames are presented, but static frames appear as meaningless assemblages of dots. Instead,
19 reaching-grasping is a goal-directed action specifically programmed according to the distance and
20 the intrinsic properties of the to-be-grasped object, and the typical accelerated-decelerated
21 kinematics of the reaching phase is not necessarily restricted to the hand effector but it is common
22 to every biological effector or tool used to reach the same goal (Quinlan & Culham, 2015; Zheng &
23 MacKenzie, 2007), and it is also common to monkeys' actions (Roy, Paulignan, Farnet, Jouffrais, &
24 Boussaoud, 2000). The absence of a direct inference from the kinematics to the identity of the
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2 effector may be the reason for the lack of precise recognition of the original hand effector when
3 observing the relative PL animation.
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5 The decision to use hand PL displays instead of walkers PL displays lies in the possibility to
6 specifically investigate transitive goal-directed actions and verify whether the presence of a
7 graspable object at the end of the movement influences SMR alpha band activity in three phases of
8 the observed movement: an anticipatory phase, in which the PL animation is still in its initial
9 position, a reaching phase, corresponding to the accelerating period of the reaching movement, and
10 a grasping phase, corresponding to the decelerating period of the reaching phase in which the
11 movement ends.
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21 22 23 24 25 26 27 1. Methods

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29 No part of the study procedures or analyses was pre-registered prior to the research being
30 conducted.
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35 We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria
36 established prior to data analysis, all manipulations, and all measures in the study.
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39 Study data and digital study materials have been archived in the following publicly accessible
40 repository: <https://osf.io/cjmr7/>
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51 *1.1. Participants*

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53 Thirty-eight 9-month-old infants and their families were recruited from a diverse urban environment
54 including the metropolitan and suburban areas of Milan by using mailing lists. In order to
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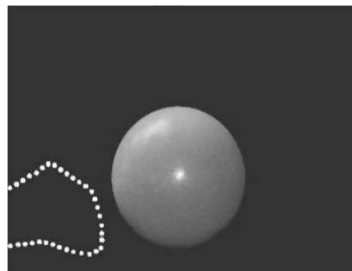
1 participate, infants had to be born at term (37-42 weeks gestation), had a normal birth weight
2 (>2500 g), did not suffer of any neurological or other medical conditions, and were observed to
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4 have normal vision and hearing. The EEG analyses were carried out for nineteen 9-month-old
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6 infants (10 females, mean age= 281.47 days; S.D. = 8.55; range 269-292 days). The remaining
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8 infants were excluded due to fussiness (n=10), excessive artifacts (n=7), or technical problems with
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10 data collection (n=2). The proportion of excluded infants is similar to other EEG studies
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12 investigating SMR alpha activity with infants this age (e.g., Southgate, Johnson, El Karoui, &
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14 Csibra, 2010). Our sample size is in line with that of previous research measuring alpha activity
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16 across several scalp locations in infants (e.g., Cannon, Simpson, Fox, Vanderwert, Woodward, &
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18 Ferrari, 2016). Moreover, an a priori power analysis indicated that 19 participants would be needed
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20 in order to have 80% probability of detecting a significant three-way interaction ($\alpha = .05$) with a
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22 medium effect size ($r = .25$) (Cohen, 1992) in the repeated measures ANOVA. The procedure has
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24 been carried out in accordance with The Code of Ethics of the World Medical Association (the
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26 Declaration of Helsinki, BMJ 1991; 302:1194) for experiments involving humans , and was
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28 approved by the University ethical committee. Parents filled out an informed consent form for their
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30 infants' participation and a questionnaire on their infants' motor development prior to the study.
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43 2.2 *Stimuli and procedure*

44 EEG activity was recorded while infants observed stimuli presented using E-Prime software v2.0
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46 (Psychology Software Tools Inc., Pittsburgh, PA). Stimuli were the same PL animations previously
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48 used both in a TMS experiment in adults (Craighero, Iacono, et al., 2016), and in an infant-control
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50 preferential looking technique study on 2-day-old newborns (Craighero, Lunghi, et al., 2016), with
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52 the only exception that they were shortened to 2000 ms by cutting the initial static part of the video
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54 in order to adapt them to the EEG procedure. PL animations were obtained by the graphic
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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 naive 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 naive 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.

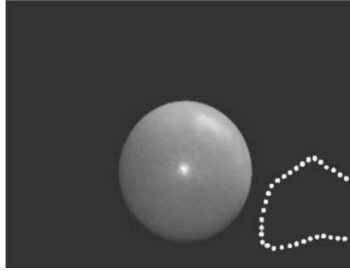
1 In the present experiment, each video lasted 2000 ms, and it was mirrored to obtain PL animations
2 coming both from the left (**Video 1; Video 2**) or the right side (**Video 3; Video 4**) of the monitor,
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4 so that the movement direction was counterbalanced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



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9 **Video 2** - PL animation showing only the dots (NoBall stimulus) in which the dots move from the left



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20 **Video 3** - PL animation showing the dots and the ball (Ball stimulus) in which the dots move from the right



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30 **Video 4** - PL animation showing only the dots (NoBall stimulus) in which the dots move from the right

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35 *2.3. Electroencephalogram collection and processing*

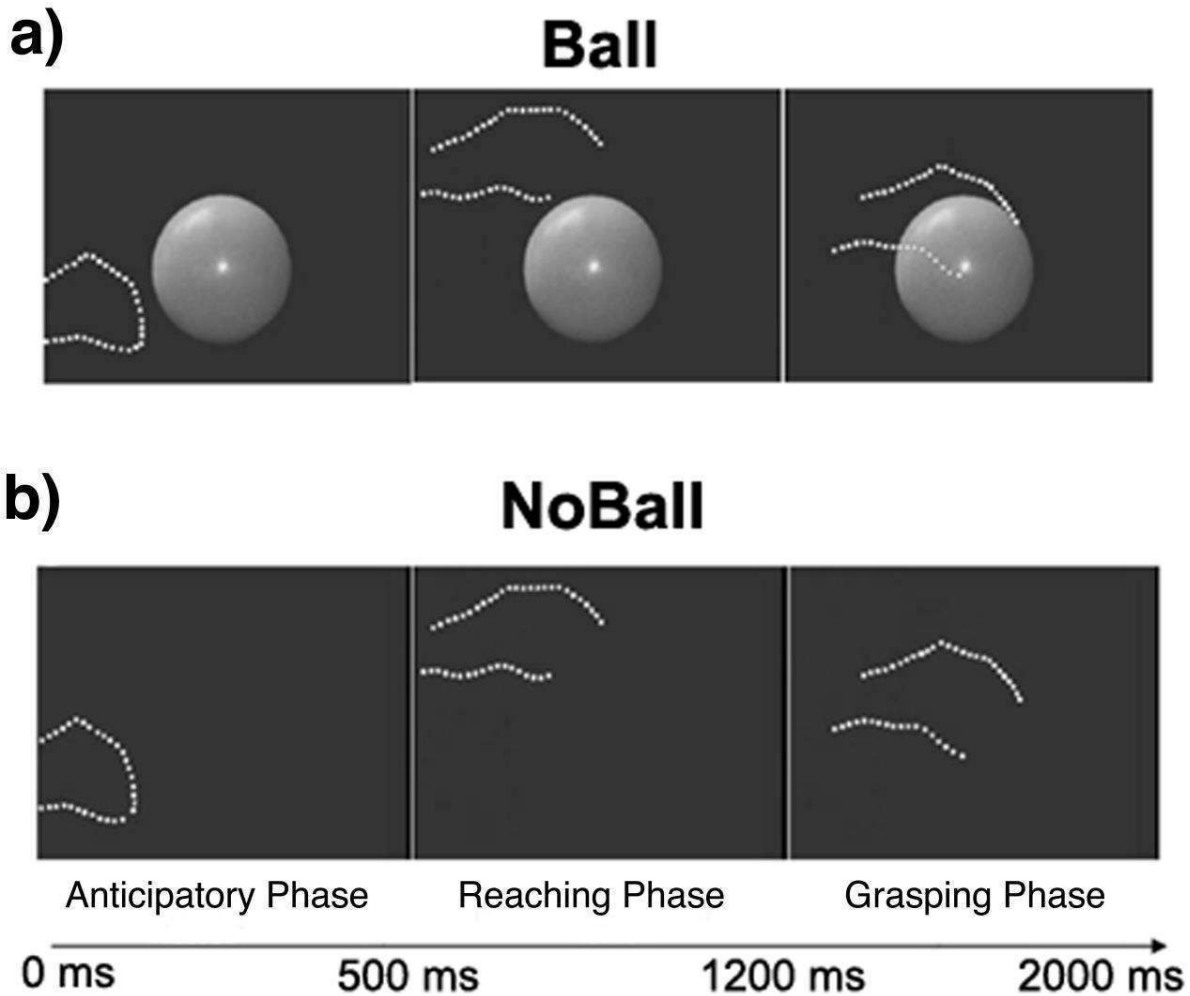
36 EEG was recorded using a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic In.,
37 Eugene, OR) and sampled at 500 Hz by means of an EGI NetAmps 300 amplifier. The signal was
38 recorded with respect to the vertex electrode and re-referenced to the average reference. A bandpass
39 filter of .1 to 100 Hz was applied online and impedances were checked prior to the beginning of
40 each session and considered acceptable if lower than 50 **Kn**. EEG data were further high-pass
41 filtered offline (0.3 Hz) and segmented into 3400 ms epochs beginning 1000 ms before and ending
42 2400 ms after stimulus onset. Trials were excluded if more than eighteen bad channels were
43 detected (e.g., Halit, de Haan, & Johnson, 2003). Of the remaining trials, individual bad channels
44 were replaced using spherical spline interpolation. To ensure that we measured sensorimotor
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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 $\pm 200 \mu\text{V}$ 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, $t(18) = 0.578$; $p = .57$.

Time-frequency analyses were performed on each artifact-free trial using continuous wavelet transform with Morlet wavelets at 1 Hz intervals in the 3 to 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, in press) 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 ms of each epoch were removed and a 200 ms baseline period starting 300 ms 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 & Meltzoff, 2011; Marshall, Bar-Haim, & Fox, 2002), we averaged activity over this range. Averaged activity in the 6-9 Hz range during the 200 ms 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 ms) in which the dots are still in their initial position, a Reaching Phase (RP: 500-1200 ms) in which the PL animation is in the accelerating period of the reaching movement, and a Grasping Phase (GP: 1200-2000 ms) in which the PL animation is in the decelerating period of the reaching and concludes its movement (**Figure 1**).



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

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44 EEG data were recorded, pre-processed using Netstation v4.6.4, and analysed using WTools (see
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47 Parise & Csibra, 2013). All statistical tests were conducted on a .05 level of significance (two-
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49 tailed), and pairwise comparisons were performed by applying t-tests and the Fisher's least
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52 significant difference procedure (Howell, 1987), and Holm-Bonferroni correction was used where
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54 appropriate (Abdi, 2010). The Greenhouse-Geisser correction for non-sphericity has been used to
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56 adjust degrees of freedom as appropriate. Effect sizes were estimated using the partial eta square
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measure (r), and the data are reported as the mean and the standard deviation (S.D.). 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, $F(2,36) = 26.00; p < .001, r = .59$, and a main effect of Region $F(2,36) = 16.82; p < .001, r = .48$. These results were qualified by the significant interactions Phase x Condition, $F(2,36) = 12.54, p < .001, r = .41$, and Phase x Region, $F(1.82, 32.67) = 12.25, p < .001, r = .44$. A significant three-way Phase x Condition x Region interaction, $F(2.42, 43.53) = 3.99, p = .02, r = .18$, was also revealed, which was inspected by means of paired samples comparisons within each region (**Figure 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 = $-0.22 \mu\text{V}$, S.D. = $.27 \mu\text{V}$) than during the GP (mean = $-0.07 \mu\text{V}$, S.D. = $.19 \mu\text{V}$), $t(18) = -24.99; p = .02, d = .57$, and attenuation was greater during the RP (mean = $-0.31 \mu\text{V}$, S.D. = $.32 \mu\text{V}$) than during the GP, $t(18) = -38.71; p = .001, d = .89$.

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- In the NoBall condition, attenuation was greater during the RP ((mean= $-.33 \mu\text{V}$, S.D. = $.32 \mu\text{V}$) compared to the AP (mean= $-.06 \mu\text{V}$, S.D. = $.19 \mu\text{V}$), $t(18) = 41.16; p < .001, d = .94$, and to the GP (mean= $-.07 \mu\text{V}$, S.D. = $.14 \mu\text{V}$), $t(18) = -36.44; p = .002, d = .84$.

Furthermore, only in the AP a statistically significant difference, $t(18) = -2.312; p = .033$, was present between the Ball condition (mean = $-.22 \mu\text{V}$, S.D. = $.27 \mu\text{V}$) and the NoBall condition (mean = $-.06 \mu\text{V}$, S.D. = $.19 \mu\text{V}$). 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 = $-.39 \mu\text{V}$, S.D. = $.31 \mu\text{V}$), $t(18) = 3.42; p = .003, d = .79$, and the GP (mean = $-.36 \mu\text{V}$, S.D. = $.32 \mu\text{V}$), $t(18) = 2.75; p = .01, d = .63$, compared to the AP (mean= $-.18 \mu\text{V}$, S.D. = $.31 \mu\text{V}$).

- Similarly, in the NoBall condition attenuation was significantly greater during the RP (mean = $-.39 \mu\text{V}$, S.D. = $.31 \mu\text{V}$), $t(18) = 6.67; p < .001, d = 1.53$, and the GP (mean= $-.36 \mu\text{V}$, S.D. = $.32 \mu\text{V}$), $t(18) = 6.55; p < .001, d = 1.50$, compared to the AP (mean= $-.18 \mu\text{V}$, S.D. = $.31 \mu\text{V}$). 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, $t(18) = -4.45; p < .001, d = 1.03$.

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

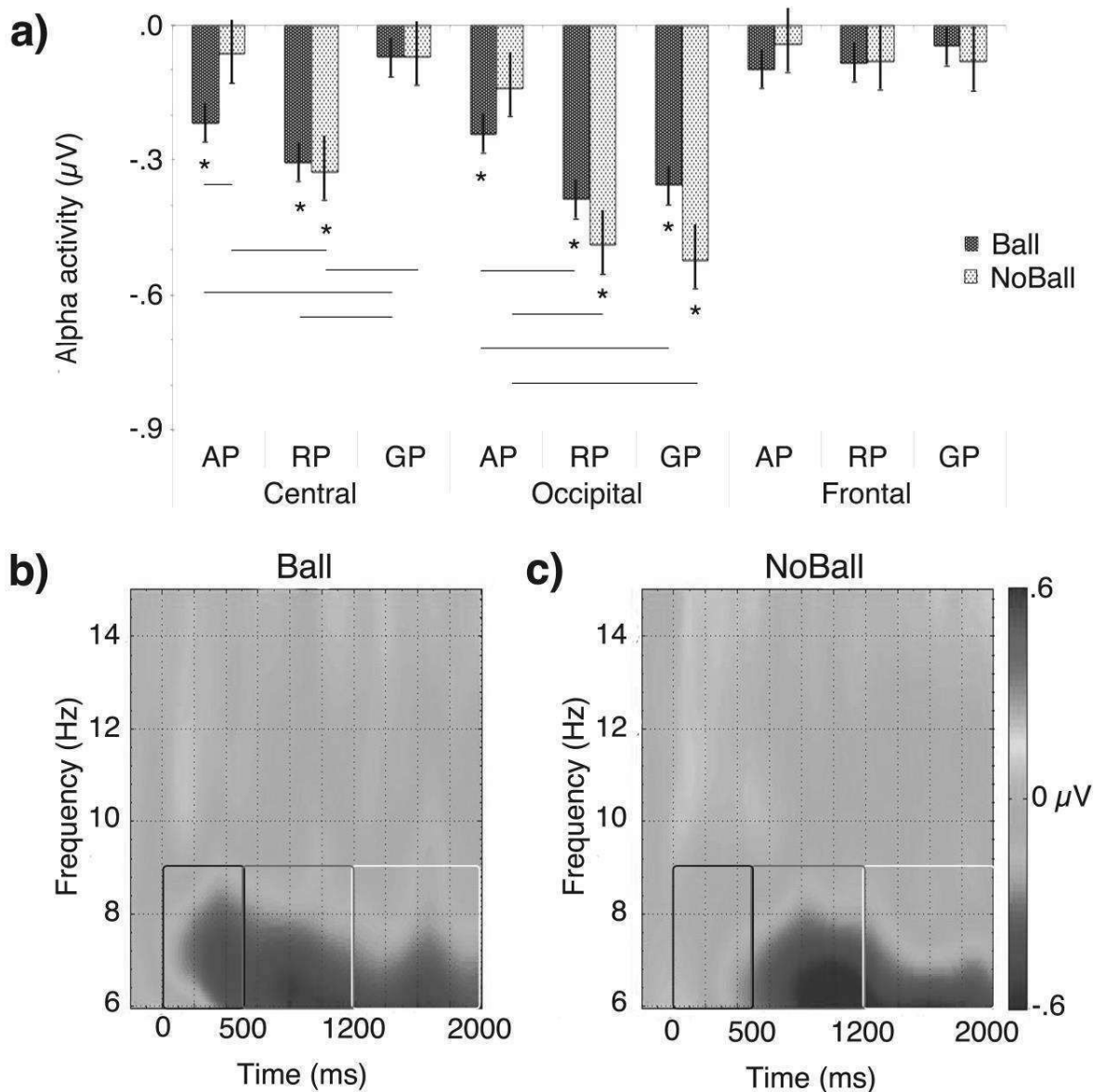


Fig. 2 - The upper panel (a) displays alpha activity(μV) over the selected electrode clusters (Central, Occipital, Frontal) averaged over the Anticipatory Phase (0-500 ms), the Reaching Phase (500-1200 ms), and the Grasping Phase (1200-2000 ms) for the Ball (black bars) and NoBall (grey bars) conditions. 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.

4. Discussion

1 We measured changes in SMR alpha band activity in nine-month-old infants, in order to survey the
2 involvement of the sensorimotor cortex during observation of a PL animation of a hand grasping an
3 object and during observation of the same PL animation after deletion of the object. Sensorimotor
4 activity was recorded both prior to the onset of the PL display movement and during it.
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9 We found a stronger attenuation of alpha activity during the observation of the accelerating period
10 of the PL stimuli movement compared to the observation of the PL stimuli still in their initial
11 position. However, during this anticipatory phase, a significant decrease in activity was evident in
12 trials in which the to-be-grasped object was present. No alpha activity attenuation was present
13 during the decelerating period of the movement, a result in agreement with EEG studies in adults
14 reporting that SMR rebounds at the end of the observed reaching-grasping movement (Avanzini,
15 Fabbri-Destro, Dalla Volta, Daprati, Rizzolatti, & Cantalupo, 2012; Lapenta, Ferrari, Boggio,
16 Fadiga, & D'Ausilio, 2018).
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31 Present results for the first time indicated that in infants, as in adults (Ulloa & Pineda, 2007), the
32 observation of point-light biological motion displays produced SMR alpha activity suppression
33 relative to baseline. Our findings demonstrate that observation of biological kinematics in the
34 absence of pictorial information related to the real hand is able to determine SMR alpha activity
35 suppression in nine-month-old infants, as it happens in children of the same age during grasping
36 execution and during the mere observation of a real hand grasping an object (Southgate et al.,
37 2009), and as it happens in adults when subjects move, imagine movement, observe movements
38 (Babiloni et al., 1999; Cochin et al., 1998; Gastaut & Bert, 1954; Pineda et al., 2000), or when they
39 observe point-light biological motion animation videos of jumping jacks and kick (Ulloa & Pineda,
40 2007).
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56 Importantly, the stimuli used here were not the transformation in PL animation of walkers, but of a
57 hand that grasps an object. This type of stimuli was used only in three previous studies,
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1 investigating gaze performance in adults (Elsner et al., 2012) and infants (Craighero, Lunghi, et al.
2 2016), and corticospinal excitability in adults (Craighero, Jacono, et al., 2016). It is interesting to
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4 note that all three studies reported that the PL views of a moving hand, even after substantial
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6 repetition, are recognized precisely and immediately only by some observers, unlike the detection
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8 of whole body movement that is constantly rapid and precise (Troje, 2002). Despite the lack of
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10 recognition of the action behind PL animation, all three studies were able to replicate findings
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12 obtained during observation of a real moving hand: the presence of anticipatory gaze shifts towards
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14 the goal in adults (Elsner et al., 2012), of orienting of attention toward the final part of the observed
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16 movement in newborns (Craighero, Lunghi, et al. 2016), and of motor resonance in adults
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18 (Craighero, Iacono, et al., 2016), excluding that these effects merely depend on the recognition of
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20 an acting hand. In line with these studies, here, in a preliminary experiment, we found that adults
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22 were not capable to reliably recognize a grasping hand from the PL stimuli we used. Also , the
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24 presence of a ball at the end of the PL movement did not increase adults' ability to recognize the
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26 grasping hand as source stimulus of the animation. Nonetheless, our study shows that, during the
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28 reaching phase, 9-months-old infants' sensorimotor system was recruited during the observation of
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30 the moving PL displays, suggesting that, regardless of the presence of a graspable object, kinematic
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32 information is sufficient to engage the activation of the sensorimotor cortex. The only study
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34 partially investigating this same issue in infants, investigated real hand observation and reported
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36 different results (Southgate et al., 2010). In the study, to verify whether infants can generate online
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38 predictions about action outcomes, nine-month-old infants were presented either with a real hand in
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40 a grasping posture disappearing behind an occluder, or the same mimed action without any
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42 occluder. Results showed a significant attenuation of SMR alpha activity from baseline only for
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44 movements disappearing behind the occluder. This was interpreted as evidence that sensorimotor
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46 activity is present only if the observed action permits infants to infer a likely outcome (i.e. that the
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48 hand is likely grasping for an occluded object), an interpretation supported by the presence of
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1 higher desynchronization of the SMR alpha in eight-month-old infants during observation of a goal-
2 directed action than of a spatially similar non-goal-directed movement (Nystrom, Ljunghammar,
3 Rosander, & Von Hofsten, 2011). However, it has been shown that greater suppression of alpha
4 activity is also present in response to unusual actions compared with ordinary ones (Stapel,
5 Hunnius, van Elk, & Bekkering, 2010) and explained by the authors as evidence that, since the
6 motor system is used to generate predictions about actions, when we observe actions that deviate
7 from what expected, additional predictions have to be generated, resulting in a stronger motor
8 activation. Indeed, while the totally visible hand shown by Southgate and colleagues (Southgate et
9 al., 2010) requires no prediction, the disappearing hand, more attractive and interesting, probably
10 involves some predictive activity. This may represent a possible alternative explanation for the
11 difference in alpha attenuation between the two conditions, without strictly attributing it to the
12 inference of the presence of a hidden object. In addition, in adults the motor system is assigned a
13 compensatory role when it is necessary to compensate for the noisy or missing sensory input
14 (D'Ausilio, Bufalari, Salmas, Busan, & Fadiga, 2011; D'Ausilio, Bufalari, Salmas, & Fadiga, 2012;
15 D'Ausilio, Jarmolowska, Busan, Bufalari, & Craighero, 2011), when we lack related sensorimotor
16 experience (Schmitz et al., 2018), and when we need to refine a sensorimotor skill-set (Aglioti,
17 Cesari, Romani, & Urgesi, 2008; Bangert & Altenmüller, 2003; Calvo-Merino, Glaser, Grezes,
18 Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006). The results of the present
19 experiment support the hypothesis of a compensatory role of the sensorimotor system by showing a
20 strong involvement of the sensorimotor cortex during observation of highly degraded moving
21 stimuli, not modulated by the presence of a graspable object.

22 Therefore, object presence did not affect our results during observation of PL moving stimuli
23 (Reaching Phase). Nonetheless, the presence of the ball induced attenuation of alpha activity during
24 the observation of the PL stimuli still in their initial position (Anticipatory Phase), not evident when

1 the object was absent. So, it seems that when a graspable object is present, the sensorimotor system
2 is activated even before the action actually begins, possibly in an independent fashion from its
3
4 actual execution. This finding is similar to what Southgate and colleagues (Southgate et al., 2009)
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6 found in nine-month-old infants during the observation of actions presented in a live setting: the
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8 infants were seated in front of a puppet stage with the curtains closed, and when infants were still
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10 and attentive, curtains opened to reveal a graspable object that after a while a hand grasped and
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12 removed from the scene. Their findings showed an attenuation of the alpha rhythm prior to the
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14 onset of the observed action. This sensorimotor activity was interpreted as a predictive motor
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16 activation evoked by the learning that a hand would appear after the curtains were opened. A
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18 similar interpretation can be adopted for current results, arguing that the presence of the object
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20 stronger suggests that a movement will occur and therefore the attenuation of alpha activity during
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22 the observation of the PL stimuli still in their initial position in the presence of the ball could reflect
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24 a prediction process.
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31 However, in the current study Ball and NoBall stimuli have been mixed up, and following the
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33 repeated observation of the stimuli, either the presence or the absence of the object had the
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35 possibility to suggest the incoming movement. Moreover, the PL animation was a degraded
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37 stimulus not easily recognized as a grasping hand, and it was already present at the beginning of the
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39 video. Furthermore, during the reaching phase the presence of the object did not modulate results.
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41 Therefore, a possible alternative interpretation is that the attenuation of SMR alpha activity prior to
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43 PL movement can be attributed to the presence of the object that could be the target of an action
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45 rather than to a learning process occurring during the testing session. This interpretation requires
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47 that our nine-month-old participants were able to use pictorial depth cues to infer three-dimensional
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49 structure in the presented two-dimensional depiction of the ball, and the results of a series of
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51 habituation-dishabituation and preferential-looking studies are in favor of this possibility, showing
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2 that the ability to extract pictorial 3D information emerges at about 6 months (see, Kavsek, Yonas,
3 Granrud, 2012).

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5 Indeed, it is known that the mere observation of objects that have the potential for being
6 manipulated is effective in modulating the activity of the motor system in both monkeys and
7 humans. In monkeys, a set of premotor neurons known as "canonical neurons" discharges during
8 the presentation of graspable objects (Murata et al., 1997; Raos, Umilta, Murata, Fogassi, &
9 Gallese, 2006; Rizzolatti et al., 1988; Umilta, Brochier, Spinks, & Lemon, 2007), and in humans,
10 both brain imaging studies (Chao & Martin, 2000; Grezes, Armony, Rowe, & Passingham, 2003;
11 Grezes, Tucker, Armony, Ellis, & Passingham, 2003; Mruzec, von Loga, & Kastner, 2013), and
12 electrophysiological and psychophysical investigations (Craighero, Fadiga, Rizzolatti, & Umilta,
13 1998; 1999; Craighero, Fadiga, Umilta, & Rizzolatti, 1996; Craighero, Zorzi, Canto, & Franca,
14 2014; Ellis & Tucker, 2000; Makris, Hadar, Yarrow, 2011; Symes, Ellis, Tucker, 2007; Tucker &
15 Ellis, 1998) showed that the observation of graspable objects recruits the same sensorimotor
16 representations involved in their actual manipulation.
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35 Several studies have evidenced that SMR alpha activity in adults is sensitive to mere object
36 observation (Proverbio, 2012; Wamain, Gabrielli, & Coello, 2016; Wamain, Saha*"*i, Decroix, Coello,
37 & Kalenine, 2018). In Proverbio (2012), the level of manipulability of the object affected the
38 amplitude of alpha suppression. In Wamain et al. (2016), manipulable objects induced a stronger
39 suppression when they were presented in peripersonal space in comparison to extrapersonal space,
40 and in Wamain et al (2018), SMR alpha activity was extinguished when the observed object
41 afforded simultaneously different structural and functional gesture representations, suggesting that
42 it may have a role in action selection processes during object perception. Present findings showing
43 that the presence of an object induced attenuation of alpha activity during the observation of not
44 moving PL stimuli suggest that even in infants object sight may recruit the sensorimotor cortex.
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1 However, further investigation is necessary to discriminate between the two alternative

2 interpretations of these results, specifically testing in infancy the presence of sensorimotor

3 involvement during the mere observation of graspable objects.

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8 Importantly, modulation of alpha attenuation differed in the central, occipital and frontal regions. In

9 particular, alpha attenuation was completely absent in the frontal region. It was present in the

10 occipital region, but significantly greater in both the reaching and grasping phase as compared to

11 the anticipatory phase. Conversely, in the central region, SMR desynchronization was modulated

12 differently both as a function of the three selected phases of the action and the presence of the ball.

13 Specifically, SMR desynchronization was absent in the grasping phase, it was not affected by the

14 presence of the ball in the reaching phase, and it was significantly different in the ball and no ball

15 condition in the anticipatory phase. Our findings are consistent with previous reports showing that

16 in infants (Filippi et al., 2016) and in adults (Marshall, Bouquet, Shipley, & Young, 2009) SMR

17 desynchronization over central regions is accompanied by alpha desynchronization at occipital

18 regions during action observation. Occipital alpha is known to be linked to visual attention

19 (Warreyn et al., 2013; Debnath, Salo, Buzzell, Yoo, & Fox, 2019). In this vein, the occipital alpha

20 attenuation we have found regardless of the presence of the object (i.e., ball) might reflect the

21 involvement of an attentional component during observation of a moving stimulus as compared to

22 observation of a static one. A further interpretation, not necessarily alternative to the previous one,

23 is that the observed occipital alpha desynchronization in response to PL animations moving with the

24 accelerated-decelerated kinematics of goal-directed hand actions might be due to an ongoing

25 canalization process responsible for the development of a specialized sensorimotor mechanism

26 involved in the processing of others' actions (Quadrelli & Turati, 2016). Indeed, as demonstrated in

27 a previous study (Yoo, Cannon, Thorpe, & Fox, 2016), observation of goal-directed actions elicited

28 the recruitment of occipital regions to a greater extent in 9-month-olds as compared to 12-month-

1 olds. Thus, from a developmental perspective, it is possible that action observation requires the
2 recruitment of broader cortical areas within the first months of life and that acquired active and
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4 observational experiences with actions are responsible for shaping the gradual specialization of
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6 sensorimotor representations (Sommerville, Woodward & Needham, 2005; Cannon & Woodward,
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9 2012). Future infant research should further explore the relation between occipital and central alpha
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11 attenuation, possibly investigating the role of kinematics specificity by comparing accelerated-
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13 decelerated biological kinematics with constant velocity non-biological kinematics across
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16 development.
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23 5. Conclusions

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

The authors declare no competing financial interests.

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