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Abstract

In human adults the auditory representation of others' actions is capable to activate specific areas of the motor and premotor cortices. Nonetheless, basic information regarding sensorimotor activation in response to action-related sounds are still lacking in developmental samples. In the present study, sensorimotor activity, as indexed by µ rhythm suppression, was measured using electroencephalography in 14-month-old infants who listened to hand- and foot-produced action sounds (i.e., footsteps and clapping) and to mechanical sounds (i.e., blender). Footstep sounds elicited activation at the midline electrode cluster over the foot area (Cz), and not in correspondence of lateralized clusters over the hand areas (C3 and C4). Greater activation in response to clapping compared to blender and footstep sounds was also recorded at electrodes in the left central cluster, over the hand sensorimotor cortex (i.e., C3), but extended to some extent over the midline central electrode cluster. Furthermore, our results underscore the role of natural locomotor experience in shaping sensorimotor system activation, since infants who gathered more walking experience exhibited stronger sensorimotor activation for footstep sounds over left central electrodes. Taken together, current results provide the first evidence that action sounds produced by another person are capable to elicit sensorimotor activation during infancy.

Keywords:

Sensorimotor cortex; sounds; action perception; infancy; motor experience

Humans can hear sounds and respond to them from as early as 25 weeks of gestational age, when the auditory system is structurally developed and becomes functional (Birnholz & Benacerraf, 1983; Draganova et al., 2018; Graven, & Browne, 2008; Shahidullah and Hepper, 1994). Indeed, very early in life auditory information plays a crucial role in infants' ability to process and organize the world around them (Lewkowicz, Leo, & Simion, 2010; Sai, 2004). Among the many sounds that constitute the acoustic environment in which infants grow, action sounds are present in many daily activities and are fundamental to everyday social life. However, despite demonstrations that, from about the age of 5 months, infants are capable to extract people's intentions from watching their actions (e.g., Geangu, Senna, Croci, & Turati, 2015; Natale et al., 2014; Saylor, Baldwin, Baird, & LaBounty, 2007; Southgate, Johnson, El Karoui & Csibra, 2010; Woodward, 2009), evidence about how the sounds contribute to action understanding is still very limited (Geangu, Quadrelli, Lewis, Macchi Cassia & Turati, 2015). Indeed, most studies using auditory stimuli in infancy are mainly interested in the examination of the development of cerebral specialization for the human voice (Blasi et al., 2011; Grossmann, Oberecker, Koch & Friederici, 2010; Lloyd-Fox, Mercure, Elwell & Johnson, 2011). The current study aims to expand our current knowledge of infants' neurocognitive processing of their surrounding auditory social environment by providing evidence of their neural activation to human action sounds. In light of evidence demonstrating the recruitment of the human (e.g., Galati et al., 2008) and non-human (e.g., Kohler et al., 2002) adult primates' motor system in response to the sounds of others' actions, we investigate whether listening to action sounds can elicit sensorimotor activation in human infants, and whether this activation is organized in a somatotopic manner. **Specifically, we recorded infants' sensorimotor activation in response to auditory information which is naturally inherent to the moving human body (i.e., clapping and footstep).**

Several studies demonstrated that, in human adults, motor and premotor areas are activated while seeing (e.g., Buccino et al., 2001; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006) and hearing (e.g., Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; D'Ausilio, 2007) an action performed by others, as well as during the execution of that action. This multimodal system is referred to as the mirror neuron system (MNS) (Rizzolatti & Craighero, 2004; Pineda, 2005). Evidence shows that in monkeys, a set of neurons in area F5 of the frontal cortex have these mirroring properties (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992) and are responsive to action-related sounds (Kohler et al., 2002; Keysers et al., 2003). Evidence exists that also in human adults, brain areas known to be part of the MNS (e.g., premotor and inferior parietal regions) are responsive to action perception via auditory information (e.g., Bangert et al., 2006; Lahav, Saltzman, & Schlaug, 2007). Comparisons between congenitally blind and sighted participants of brain activation during presentations of hand actions demonstrated that areas of the MNS are activated by visual and auditory cues in the sighted group and that the same areas are activated by auditory cues in congenitally blind individuals (Ricciardi et al., 2009). Thus, existing literature indicates that listening to action sounds elicits neural activity in areas of the adult MNS and might have a role in recognizing and understanding others' actions. Importantly, action listening is something that happens almost automatically and takes part in many of our daily activities. We can often recognize the action of another individual even if we can only hear it (e.g., listening to door knocking or finger snapping) (Lahav et al., 2007). Using different techniques, several studies explored the processing of action sounds in healthy adults. Their findings converge to suggest that specific cortical areas in the fronto-parietal network are selectively activated by action-related sounds (Aglioti & Pizzaglia, 2010; Galati et al., 2008; Giusti, Bozzacchi, Pizzamiglio & Di Russo, 2010). Specifically, imaging studies showed that areas known to be part of the human MNS (i.e., premotor and parietal cortices) are active while adults listen to sounds generated by human actions (Gazzola, Aziz-Zadeh & Keysers, 2006), sounds generated by tools (Lewis et al., 2005), and spoken sentences about actions (Tettamanti et al., 2005). Notably, action execution and observation of similar actions elicited the activation of the same cortical areas. Furthermore, greater motor activation was recorded from hand muscles when participants listened to hand action sounds as compared to control sounds (Aziz-Zadeh et al., 2004).

It is widely known that specific regions of the motor and premotor cortices are responsible for the control of specific body parts, namely they follow a somatotopic organization. Crucially, several studies in adults determined that action execution and observation induce an effector-specific somatotopic activation, with hand and mouth actions producing greater neural activity respectively in the dorsal and ventral parts of the contralateral premotor cortex (Buccino et al., 2001; Schubotz, von Cramon, & Lohmann, 2003). Within the auditory domain, results are still controversial. Some functional magnetic resonance imaging (fMRI) investigations in adult participants showed that passively listening to sounds generated by hand or mouth actions activates somatotopically the left hemisphere. Specifically, hand action sounds elicit greater activation in the dorsal premotor cortex, and sounds of mouth actions generate greater activation in the ventral premotor cortex (Gazzola et al., 2006; Hauck et al., 2006; but see also Galati et al., 2008).

Similar to fMRI studies, evidence exists, in adults and in infants, of a somatotopic distribution of sensorimotor µ rhythm suppression, in response to the observation and execution of actions with different effectors (e.g., de Klerk, Johnson & Southgate, 2015; Pfurtscheller, Brunner, Schlogl & Da Silva, 2006; Saby, Meltzoff & Marshall, 2013). Mu rhythm suppression or desynchronization is an electroencephalographic (EEG) measure which is recorded at central electrode sites and is considered to be an index of neural activation of the underlying sensorimotor cortex (Muthukumaraswamy, Johnson & McNair, 2004; Pineda et al., 2013; Thorpe, Cannon & Fox, 2016). Suppression of EEG oscillations in the µ frequency range measured at central scalp regions appears to be correlated with activation recorded through fMRI in motor areas – i.e., inferior parietal lobule and dorsal premotor cortex – when performing and observing actions (Arnstein et al., 2011). When adult participants are presented with action (i.e., hand- or mouth-produced), environmental (i.e., water dripping or howling wind) and control (i.e., scrambled versions of action sounds) sounds, greater sensorimotor activation is recorded in response to action compared to non-action sounds. Importantly, results highlighted the presence of an effector-specific organization of the sensorimotor activation, with greater µ rhythm desynchronization over the hand area in response to hand- versus mouth action sounds (Pineda et al., 2013). These results add to those obtained by Pizzamiglio and collaborators (2004), employing EEG with source analysis and showing the existence of a somatotopically organized lateralized activation of the left posterior superior temporal and premotor areas occurring in response to action-related sounds (i.e., hand or mouth actions) (Pizzamiglio et al., 2004). Thus, an increasing number of studies provides insights on the somatotopic organization of µ rhythm desynchronization in response to action sounds in adults.

From a developmental perspective, several studies report the existence of a somatotopic organization of the neural activation elicited by action observation. For example, in an EEG study with 14-month-old infants, participants observed a live experimenter performing a button-pressing action by using the foot or the hand (Saby et al., 2013). Results demonstrated that infants observing the hand action displayed more µ rhythm suppression at the C3 electrode position, over the hand areas, while infants observing the foot action showed more suppression at the Cz electrode location, over the foot area. Another study with a group of adults and 12-month-old infants aimed to compare the organization of µ rhythm desynchronization during the execution and observation of actions implemented with different effectors (i.e., arm or leg) (de Klerk et al., 2015). Adults displayed a somatotopic activation both during action execution and observation, while infants showed a somatotopically-organized suppression during action execution only. Furthermore, it has been shown that active and observational experiences with the perceived actions are responsible for shaping the gradual specialization of motor representations (Sommerville, Woodward & Needham, 2005; Cannon & Woodward, 2012; see Quadrelli & Turati, 2016). Indeed, both infants (Gerson, Bekkering, & Hunnius, 2015; Stapel, Hunnius, Meyer, & Bekkering, 2016) and adults (Calvo-Merino et al., 2006; Cross, Hamilton, & Grafton, 2006; Gerson, Meyer, Hunnius, & Bekkering, 2017; Haslinger et al., 2005) acquiring more experience performing specific actions show enhanced motor activation when they perceive the same action performed by someone else. For instance, infants with more crawling experience display greater μ suppression in response to observation of videos of crawling as compared to walking infants, thus suggesting that our own motor skills affect how we perceive actions performed by others already at 14 months of age (van Elk, van Schie, Hunnius, Vesper & Bekkering, 2008).

While a considerable amount of evidence is accumulating about sensorimotor activation in response to action observation in the first years of life, available literature on the response of infants' sensorimotor cortex at the presentation of action sounds is extremely poor and mainly focused on artificially produced associations between an action and the auditory effect generated by an actively manipulated object (Paulus, Hunnius, van Elk, & Bekkering, 2012; Gerson, Bekkering, & Hunnius, 2015). Research examining infants' ability to represent the causal sequence of an action – e.g., a hand manipulating an object to produce a specific sound – demonstrated that it is by the end of the first year of life that infants start encoding the relation between human actions and their acoustic outcomes (Baumgartner & Oakes, 2011; Perone, Madole, & Oakes, 2011). However, it is to note that already by the age of 7 months infants are capable to discriminate between auditory information related to human actions compared to other human and non-human sounds (Geangu et al., 2015). Using event-related potentials (ERPs), this study revealed that human action sounds (e.g., clapping and footsteps) generate enhanced neural processing, as highlighted by larger activation at anterior left temporal locations, compared to the other types of sounds (i.e., human vocalizations, environmental and mechanical sounds). Basic information regarding sensorimotor responsiveness to action sounds in developmental samples is still scarce. To our knowledge a single case study using intracranial EEG in a 12-year-old epileptic child, investigated the presence of μ rhythm suppression in response to hand action sounds (i.e., finger clicks) and reported a specific suppression occurring over the hand area of the motor cortex (Lepage et al., 2010). Additionally, one recent study demonstrated that infants' perception of a rattle's sound activates the motor program involved in the production of that sound (i.e., hand action) and that it is capable to create an association between a motor program and its sensory effect by using auditory information (Paulus et al., 2012). Specifically, it was proven that 8-month-old infants undergoing a training in which they learned to actively produce a rattle sound, showed a stronger suppression of the μ frequency band in electrodes over the hand representation areas in both hemispheres when subsequently presented with the rattle sound as compared to two novel sounds. **Similarly, Gerson and colleagues (2015) recorded μ rhythm suppression after providing 10-month-old infants with a short active training in which they learned a motorically unfamiliar action resulting in a novel sound effect and a passive training in which they observed someone performing a novel action which resulted in a different sound. Results showed greater sensorimotor activation in response to the sound that was used during the active training as compared to the one used during the observational training. Hence, active experience was crucial for modulating the sensorimotor activation in response to the auditory perception of the action effect (Gerson et al., 2015). Thus, to our knowledge only**

two investigations have examined the relationship between µ rhythm suppression and action-related sounds in infancy and they all explored sensorimotor activation elicited by the artificial association between a hand action and a sound (Paulus et al., 2012; Gerson et al., 2015). Moreover, in both studies, the auditory stimuli were generated by an external and novel object which was manipulated by participants throughout a training.

The current study aims to capitalize on the lack of knowledge related to the processing of naturally produced human action sounds in infancy. Indeed, the first aim of the current research is to determine whether infants' sensorimotor activation can be selectively generated in response to action sounds experienced in natural contexts compared to other naturally experienced non-action related sounds. **Morevover, existing research has typically explored infants' processing of action sounds by recording sensorimotor activation in response to the auditory perception of the action effect generated by a manual action performed with a tool (e.g. rattle or other toys). Rather, we sought to explore cortical activation elicited by auditory information which is naturally inherent to the moving human body in the absence of object manipulation.** Furthermore, this study is aimed at exploring whether µ rhythm oscillations are somatotopically organized for the auditory perception of hand- or foot-produced actions in 14-month-old infants. Similar to existing studies investigating the response of the infant µ rhythm desynchronization to action observation, we hypothesize that listening to hand and foot action sounds would generate greater µ rhythm desynchronization as compared to the control sound category at central electrode clusters over the sensorimotor cortex. Should a somatotopically organized activation be found, greater activation for clapping and footstep sounds will be found respectively over the hand (C3, C4) and foot (Cz) electrode clusters. Finally, based on findings showing that motor experience might influence µ rhythm suppression over the sensorimotor areas (e.g., Cannon et al., 2014; van Elk et al., 2008; Yoo, Cannon, Thorpe, & Fox, 2016), we will also explore the relation between infants' locomotor experience and sensorimotor activation. We predict that greater locomotor experience will be associated with greater µ rhythm desynchronization in response to footstep sounds in correspondence to the electrode cluster over the foot area.

Methods

Participants

Thirty 14-month-old infants and their families were recruited from a diverse urban environment including the metropolitan and suburban areas of XXX. 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 for their age. The final sample consisted of seventeen 14-month-old infants (10 females, mean age = 439.2 days; SD = 8.4; range 421-453 days). An additional 13 infants were tested but excluded from final analysis due to fussiness (n= 4), excessive artifacts (n=8), or technical problems with data collection (n=1). The proportion of excluded infants is similar to other EEG studies investigating µ rhythm with infants this age (e.g., Saby, Meltzoff & Marshall, 2013). The procedure followed the ethical standards (the Declaration of Helsinki, BMJ 1991; 302:1194) and was approved by the ethical committee of the University of XXX (Protocol number: 236 XXX – Title of study: "I correlati neurofisiologici del riconoscimento di oggetti sociali e non sociali nella prima infanzia"). Parents filled out a consent form for their infants' participation and a questionnaire on their infants' motor development prior to the study.

Locomotor experience questionnaire

Parents were asked to fill in a questionnaire about their infants' motor development. The questionnaire was specifically developed for the current study and consisted of few questions about infants' locomotor abilities. Parents were asked whether their child was able to walk freely or with assistance and since when their child had begun to show this behavior. All participants were reported to be able to independently walk. Overall, the infants of our sample had an average walking experience of 2.64 months (SD = 1.15 month), with 10 infants who had started walking within 2 months preceding the testing, and 8 infants who had experience with walking for longer than 2 months. **Furthermore, parents were asked two questions about their child manual dexterity. Specifically, whether their child was able to pass an object from one hand to another and whether their child was able to clap spontaneously or to imitate someone else clapping. All participants were reported to be able to clap and pass an object from hand to hand.**

Stimuli

Infants were presented in a random order with three sound categories: footsteps (FOO) and clapping (CLA) sounds, representing the category of sounds produced by humans, and blender (BLE) sounds, representing the control category of sounds produced by automated mechanical devices. Each category included 5 different exemplars which were used in a previous study (Geangu et al., 2015) or downloaded from the internet and successively screened and chosen by 5 adult listeners based on ease of recognition. All the sound stimuli were edited to 1000 ms duration, matched for the total Root Mean Square (RMS) power and with a 25 ms ramped onset/offset using Praat software (Boersma & Van Heuven, 2001). Sounds were controlled for pitch and loudness and, in order to avoid any binaural spatial cues, they were also converted to one channel (mono, 44.1 kHz, 16 bits) and presented to both ears via two speakers.

Procedure

EEG was recorded while infants sat on their parent's lap at a distance of approximately 60 cm from a 24-inch monitor in a dimly lit, audiometric and electrically shielded cabin. Sound stimuli were randomly presented using E-Prime software v2.0 (Psychology Software Tools Inc., Pittsburgh, PA) over two speakers placed to the left and right of the monitor. Parents were instructed to remain as still as possible and to keep silence during the experimental session in order to avoid any acoustic interference. The whole experiment was recorded through an infrared camera, hidden over the monitor, which fed into the data acquisition computer, located outside the testing cabin. In order to minimize infant movements and to sustain their quiet attention, a looping and silent animation of soap bubbles floating against a black background was presented temporally unrelated to the acoustic presentation throughout the entire experiment. Stimuli were presented randomly to each infant, with the only constraint that sounds from the same category could not occur more than two times consecutively. A trial consisted of 1000 ms stimulus presentation and the interstimulus interval varied randomly between 1300 and 1500 ms.

Electroencephalogram collection and processing

EEG was recorded using a 128-electrode HydroCel Geodesic Sensor Net (Electrical Geodesic In., 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 to 100 Hz was applied online and impedances were checked prior to the beginning of each session and considered acceptable if lower than 50 KΩ. EEG data were further high-pass filtered offline (0.3 Hz) and segmented into 2400 ms segments, beginning 1000 ms before and ending 1400 ms after stimulus onset. For eliminating artifacts, segmented data were automatically rejected whenever the signal exceeded ± 200 µV at any electrode. **Further visual inspection of the video recorded throughout the experiment checked for any trials in which the infant did not attend to the screen or made any gross or fine limb or head movements in order to subsequently exclude those trials in which eye-movements, eye-blinks and any other body movement artifacts not detected by the automated algorithm. Trials were excluded if more than eighteen (i.e., 15%) bad channels were detected.** Of the remaining trials, individual bad channels were replaced using spherical spline interpolation. Only infants with at least 10 artifact-free trials were included in the analyses. The mean number of artifact-free trials contributing to analyses was 22.71 (FOO: 22.44, SD = 8.85; CLA: 21.94, SD = 7.97; BLE: 23.75, SD = 8.71). There were no significant differences between the three conditions in the number of artifact-free trials F(2,34)= 2.60; *p* = .089. Time-frequency analyses were performed on each artifact-free trial using continuous wavelet transform with Morelet wavelets at 1 Hz intervals in the 3 to 20 Hz range. In order to eliminate distortion created by the wavelet transform, the first and the last 400 ms of each segment were removed and a 500 ms baseline period starting 600 ms before stimulus onset was selected. Based on previous work showing that in infants of this age, the peak frequency band most reactive to movement is the 7-8 Hz band (Marshall & Meltzoff, 2011; Marshall, Bar-Haim, & Fox, 2002), we averaged activity over this range. Averaged activity in the 7-8 Hz range during the 500 ms baseline was then subtracted from averaged activity recorded during stimulus presentation. Average wavelet coefficients within infants were calculated by taking the mean across the trials. As in previous studies investigating the somatotopic organization of sensorimotor suppression in infancy (de Klerk et al., 2015; Saby et al., 2013), activity over a cluster of electrodes disposed over the left-hemisphere (30, 36, 37, and 42), the right-hemisphere (87, 93, 104, and 105) and over the midline (7, 31, 55, 80, 106 and Cz) were analyzed (Figure 1). The scalp locations of these left lateral, medial, and right lateral electrode clusters correspond to the locations of C3, Cz, and C4 in the international 10–20 system of electrode placement. The medial cluster is located over the leg representation area of the sensorimotor cortex, while the left and right electrode clusters are located over the bilateral arm/hand representation areas. The average activity in the 7-8 Hz range was extracted for statistical analyses from these three regions in the 100-400 ms time window. **This time window, corresponding to the interval when the action sounds effectively began, was chosen based on the visual examination of the peak activation elicited across participants by the employed sounds, and also based on existing studies suggesting an early activation of motor areas in response to action perception (Hauk, Shtyrov, & Pulvermuller, 2006; Lepage et al., 2010).** In addition, because we wanted to know whether sensorimotor suppression while infants listened to each sound category was specific to the central region or extended to the frontal and occipital regions (Cuevas, Cannon, Yoo, & Fox, 2014), 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. EEG data was recorded and pre-processed using Netstation v4.6.4 and analysed using WTools (see Parise & Csibra, 2013). All statistical tests were conducted on a .05 level of significance (two-tailed). When the ANOVAs yielded significant effects, pairwise comparisons including ≤ 3 means were performed by applying t tests and the Fisher's least significant difference procedure (Howell, 2012), and Holm-Bonferroni correction was used where appropriate (Abdi, 2010).

Results

An initial 5 x 3 repeated measures analysis of variance (ANOVA) was conducted with Category (clapping, footsteps, blender) and Electrode Cluster (C3, Cz, C4,

Occipital, Frontal) as within-subject factors. The ANOVA revealed only a significant Category x Electrode Cluster interaction, *F*(8,128) = 2.15; *p* = .04, η_p^2 = .118 (all other *p*s > .44).

In order to compare the scalp distribution of sensorimotor alpha suppression over central electrode sites during the listening of hand and foot movements in 14-month-old infants, we used a 3 x 3 repeated measures analysis of variance (ANOVA) with electrode cluster (C3, Cz, C4) and sound category (clapping, footsteps, blender) as within-subject factors.

The ANOVA yielded a significant main effect of Category, *F*(2,32) = 3.57; *p* = .04, η_p^2 = .182. The pairwise comparisons revealed that clapping sounds (M = -.11 µV, SD = .23 µV) elicited greater suppression than blender (M = .05 µV, SD = .21 µV; *p* = .017) and footsteps sounds (M = -.01 µV, SD = .18 µV; *p* = .049).

The main effect was qualified by a significant Cluster x Category interaction, *F*(4,64) = 3.69; *p* = .009, η_p^2 = .187, which was due to a different pattern of sensorimotor activation over central electrode sites as a function of the sound categories (Figure 2). In order to disentangle this interaction, post-hoc comparisons were conducted separately for each of the three electrode clusters. There was significantly more suppression for clapping sounds (M = -.21 µV; SD = .33 µV) compared to blender sounds (M = .21 µV, SD = .40 µV), *t*(16) = -3.30; *p* = .004, *d* = .80, and compared to footstep sounds (M = .06 µV, SD = .25 µV), *t*(16) = -2.23; *p* = .04, *d* = .54 over the C3 electrode cluster (i.e., left-lateralized hand representation area). Furthermore, footstep sounds (M = -.11 µV, SD = .12 µV) elicited a marginally greater sensorimotor suppression compared to blender sounds (M = .02 µV, SD = .19 µV), *t*(16) = -1.90; *p* = .07, *d* = .46 but not compared to clapping sounds (M = -.13 µV, SD =

.27 µV), *t*(16) = .26; *p* = .80, *d* = .06 over the Cz electrode cluster (i.e., foot representation area). All other differences were not significant (*p* > .42).

Additionally, one sample *t*-tests were performed to investigate which electrode cluster displayed the strongest sensorimotor suppression during the listening of action sounds. During the listening of footstep sounds, only the suppression over the foot representation area (i.e., Cz electrode cluster) was significantly different from zero, *t*(16) = -2.26; *p* = .04, *d* = .55 while during the listening of clapping sounds, sensorimotor suppression was significantly different from zero over the left-lateralized hand representation area (i.e., C3 electrode cluster), *t*(16) = -2.63; *p* = .02, *d* = .64 and was marginally significantly different over the foot representation area, *t*(16) = -1.94; *p* = .07, *d* = .47.

In order to explore the relation between motor experience and sensorimotor activation elicited by action sounds we calculated the correlation between the amount of walking experience and µ rhythm desynchronization elicited by footstep sounds over central electrode sites. The amount of walking experience was significantly correlated with the activation elicited by footstep sounds over the C3 electrode cluster, *r* = -.53; *p* = .03, while no significant correlations were found over the Cz and C4 electrode clusters nor for the other sound categories (all *p*s > .25). Similarly to van Elk and colleagues (2008), in order to check for possible maturational effects due to age of participants at the time of testing, partial correlation was performed. The correlation between µ rhythm desynchronization elicited by footstep sounds over the C3 electrode cluster and walking experience remained high even when taking into account age of participants at the time of testing, *r* = -.52; *p* = .03 (Figure 3).

Finally, to determine whether sensorimotor suppression was specific to central sites, we performed a repeated measures ANOVA with Category (clapping,

footsteps, blender) as within subject factor on activation over occipital and frontal electrodes. The analysis of occipital cluster did not yield a significant effect, *F*(2,32) = .19; *p* = .83, η_p^2 = .018. Moreover, activation of occipital regions during perception of each sound category was not significantly different from baseline activation (clapping: M = -.03, SD = .41; footsteps: M = -.11, SD = .37; blender: M = -.16, SD = .72; all *p*s > .34). Similarly, the analysis of frontal cluster did not highlight a significant effect, *F*(2,32) = .36; *p = .*69, η_p^2 = .022. Moreover, activation of frontal regions during perception of each sound category was not significantly different from baseline activation (clapping: M = .02, SD = .14; footsteps: M = -.01, SD = .24; blender: M = -.06, SD = .35; all *p*s > .46). Thus, while there was a significant sensorimotor suppression at central channels, no difference in occipital and frontal activation was found between categories or as compared to baseline.

Discussion

Very little is known about the electrophysiological responses to action-related sounds (Geangu et al., 2015) and few studies have examined whether and how these sounds are capable to generate a sensorimotor activation in infancy (Gerson et al., 2015; Paulus et al., 2012). **The present research investigated whether naturally experienced human action sounds elicit sensorimotor cortex activation and whether the spatial distribution of the sensorimotor µ rhythm is linked to the different effectors used to produce those sounds in 14-month-old infants. Differently from previous research exploring sensorimotor activation elicited by the auditory perception of an action effect generated by a manual action in infancy (Gerson et al., 2015; Paulus et al., 2012), 14-month-old infants in the current study were presented with naturally experienced human action sounds generated by hands (i.e., clapping) and feet (i.e., footsteps), as well as with a mechanical sound category (i.e., blender).** Our results provide evidence that 14-month-old infants' listening to action sounds produced by another person is associated with an increased sensorimotor activation, as indexed by the µ rhythm suppression over central electrode sites. We observed a significant and a marginally significant event-related µ rhythm desynchronization over central sites respectively in response to hand and foot action sounds as compared to the control sound category. These results suggest that 14-month-old infants manifest a sensorimotor sensitivity to action related sounds. This is generally consistent with evidence provided by previous adult studies comparing sensorimotor activation elicited by action sounds (i.e., mouth and hand sounds such as crunching chips and ripping a sheet of paper) with non-action related sounds (e.g., environmental sounds) using EEG and fMRI (Gazzola et al., 2006; Pineda et al., 2013; Pizzamiglio et al., 2005). In particular, results from Gazzola et al. (2006), and Pineda et al. (2013), showed that action sounds produced more µ desynchronization and recruited the premotor and somatosensory cortex more than control sounds. Consistent with these findings, our results indicate that already by the age of 14-months human action sounds are capable of eliciting sensorimotor activation, similarly to what occurs while watching and executing actions (Fox et al., 2016; Marshall & Meltzoff, 2015).

Additionally, we investigated whether sensorimotor activation in response to hearing human action sounds is somatotopically organized. Based on a growing number of studies reporting a somatotopic distribution of µ desynchronization recorded in infants in response to visually observing actions performed by feet and hands (de Klerk et al., 2015; Saby, Meltzoff & Marshall, 2013; Marshall, Saby & Meltzoff, 2014), we tested the possibility that hand and foot action sounds elicit greater µ rhythm desynchronization as compared to baseline and to other sounds at electrodes located over the hand (C3, C4) and foot (Cz) areas of the sensorimotor cortex. **Greater µ rhythm desynchronization was found in response to footsteps as compared to blender sounds at the midline electrode**

cluster (i.e., Cz) over the foot sensorimotor cortex, but the difference only approached significance. The lack of a fully significant difference between footstep and control sounds over Cz might be due to the use of footstep sounds recorded from adults. Indeed, the difference in walking rhythmicity between how infants and adults perform and experience their own walking, might have rendered more difficult for infants to represent the footstep sounds into their own motor system. Despite this limitation, we found that footstep sounds elicited a significant activation as compared to baseline only in the midline electrode cluster Cz, corresponding to foot area, and not in lateralized clusters C3 and C4 corresponding to the hand areas. Thus, listening to foot-related action sounds appears to specifically recruit the foot area as indicated by the somatotopically organized activation of the sensorimotor μ rhythm. **Recently, cortical motor activation has been reported in response to sounds produced by manual actions (Gerson et al., 2015; Paulus et al., 2012), however, infants were not presented with sounds produced by other effectors. Our study is the first to provide electrophysiological evidence of a specific pattern of sensorimotor activation elicited by foot related action sounds in infancy.** Similar to previous studies exploring μ rhythm desynchronization in response to the visual observation of foot actions in 14-month-old infants (Saby et al., 2013; Marshall et al., 2014), current results show that sensorimotor activation is greater over the foot area. This finding is also in line with evidence from adult studies using fMRI to investigate the neural correlates of hearing foot-related sentences (Tettamanti et al., 2005) and observing foot actions (Buccino et al., 2001), which elicited a somatotopic activation of the premotor cortex (i.e., dorsal premotor cortex).

Fourteen-month-old infants in our study showed also greater activation in response to clapping compared to blender as well as to footstep sounds at electrodes in the left hemisphere, over the hand sensorimotor cortex (i.e., C3).

Based on results from previous studies with 14-month-old infants exploring sensorimotor activation in response to action observation and execution (e.g., Saby et al., 2013) and on the fact that the production of clapping sounds involves the use of both hands, we might have expected to find increased desynchronization also over the right-lateralized electrode cluster (i.e., C4). However, no significant difference was found between activation elicited by clapping as compared to blender sounds over the right hemisphere. The lack of significant desynchronization over the right hemisphere in response to bimanual hand action sounds is at odds with evidence showing sensorimotor activation upon hearing hand-related action sounds at electrodes positioned over sensorimotor areas of the right hemisphere (Lepage et al., 2010; Paulus et al., 2012). Nevertheless, our results are congruent with other studies with adult and infant samples using auditory stimuli and displaying an activation pattern that is lateralized over a left temporal electrode cluster in response to human action sounds (e.g., Geangu et al., 2015; Pizzamiglio et al., 2005). **This lateralization may be related to hand preference. Previous studies have shown that in the case of bimanual actions, such as clapping, there is usually a dominant or preferred hand which, at the group level, is considered to be the right hand. Studies exploring the neural correlates of hand preferences for clapping behaviors in non-human primates, highlighted the presence of a predominant right-handedness pattern linked to a specific left-lateralized activation of the planum temporale (Meguerditchian, Gardner, Schapiro, & Hopkins, 2012). Infants' hand preference is usually acquired between 6 and 14 months of age and stabilizes by 2 years of age (Nelson, Campbell, & Michel, 2013). It is thus possible that the observed lateralization to the left hemisphere occurring in response to clapping sounds may be related to the emergence of right hand dominance in late infancy. Future research should specifically investigate the issue of the lateralization of sensorimotor activation elicited by hand action sounds, possibly by comparing the**

cortical responses to uni- and bimanual actions, and also by assessing hand preference patterns and testing different age groups.

Overall, our results seem to support the hypothesis that listening to human action sounds elicits an effector-specific sensorimotor activation already in 14-month-old infants. Remarkably, however, clapping sounds not only elicited a significant activation over the left-lateralized hand area, but also elicited a marginally significant activation over the midline foot area. A possible explanation for the presence of an extended activation occurring over the hand and foot sensorimotor areas generated by clapping sounds is that the sensorimotor processing of hand action sounds involves the recruitment of a broader cortical area early in development, possibly exceeding the brain regions known to be specialized for the processing of hand-related action sounds in adults (Gazzola et al., 2006; Hauck et al., 2006). **One alternative level of interpretation takes into account potential differences in terms of active motor experience between clapping and walking in 14-month-old infants. Indeed, infants' perceptual experience with clapping and footstep sounds can be assumed to be equivalent at the group level. On the contrary, it is possible that 14-month-old infants acquired a more prolonged firsthand motor experience performing clapping as compared to walking, since imitation of clapping hands typically develops by 8 months (Jones, 2007), while attainment of independent walking is reported to occur at 13 months (Størvold, Aarethun, & Bratberg, 2013).**

Finally, in the current study we explored the relation between infants' natural variability in locomotor development and the sensorimotor activation elicited by the auditory perception of others' actions. Similar to previous studies exploring the role of motor experience in shaping motor system activation in adults (Calvo-Merino et al., 2006; Yang, 2015; Zhang et al., 2018) and infants (Cannon et al., 2014; van Elk et al., 2008; Yoo et al., 2016), stronger μ rhythm desynchronization was found for footstep sounds at the left-lateralized electrode cluster (i.e., C3) in those infants who acquired more walking experience. Contrarily to our expectations and despite the fact that group results revealed that hearing foot-related sounds elicits a specific activation of the foot area, the expertise-related effect was not found over the foot but over the left-lateralized electrode cluster. An explanation for this finding may be that, for those infants that acquired more walking experience, activation generated by footstep sounds does not involve only the foot area of the sensorimotor cortex, but also extends to the adjacent electrode cluster. This result is consistent with previous studies in adults and children demonstrating the experience-driven plasticity of the structural and functional organization of the sensorimotor cortex (e.g., Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Gaser, & Schlaug, 2003; Hyde et al., 2009). For example, motor practice gained by expert musicians is known to lead to the recruitment of an enlarged portion of the motor cortex compared to that recruited in non-musicians (Krings et al., 2000). It is possible that motor experience gained during sensitive periods of brain maturation is responsible for the functional enlargement of the representative sensorimotor area underlying a specific motor skill such as learning to play an instrument (Hyde et al., 2009) or walking. **An additional explanation takes into account the link between the transition from crawling to walking. When infants begin to walk, their hands previously involved in locomotion gain more freedom to perform more effector specific actions (e.g., manipulate objects, interact with others - Adolph, Vereijken, & Shrout, 2003; Kubo, & Ulrich, 2006). Thus, it is possible that the observed correlation between infants' walking experience and activation elicited by footstep sounds over the hand area might be due to the qualitative changes in how infants use their hands once they start walking (Karasik, Tamis-LeMonda, & Adolph, 2011).**

To date little is known about the development of µ rhythm somatotopic pattern in response to action observation and execution in early infancy (de Klerk et al., 2015;

Marshall & Meltzoff, 2015; Saby et al., 2013). It also appears evident from existing literature that even less is known about the mechanisms allowing the developmental trajectory of the somatotopic organization generated by the auditory representation of others' actions from early infancy to late childhood and adulthood. **The current study established that the mere listening of action sounds determines the activation of the sensorimotor cortex. These results suggest the activation of the mirror neuron system to human action sounds in 14-month-old infants. However, a definitive word to claim that the observed activation in response to hand and foot action sounds reflects a mirroring process can be provided only comparing the listening to an execution condition (Cuevas, 2014; Marshall, & Meltzoff, 2011). Further research is thus needed to corroborate the presence of perception-action matching system that responds to the sounds of actions.** Moreover, as the current study used natural variation in infants' walking skills, a question that future research might address concerns the investigation of the effects of experimentally-controlled amount of experience on the sensorimotor activation elicited by action sounds perception. Few studies examined the neural correlates of action perception after manipulating the amount of walking experience (Reid, Kaduk, & Lunn, 2017), as well as the amount of visuomotor contingency experienced during walking (de Klerk et al., 2015), in pre-walking infants. These studies provide evidence of a role of visuomotor experience, and especially of the strength of the experienced contingency during the walking training, in shaping the link between action perception and execution.

Taken together, results from the current study provide evidence of sensorimotor activation in response to human action sounds in 14-month-old infants and also speak in favor of a role a motor experience in shaping μ rhythm desynchronization response patterns. Additionally, our findings suggest the existence of a neural somatotopic organization of the sensorimotor cortex in response to auditory stimulation early in development, which however should be further explored by future research. Importantly, given the big transformations in motor and perceptual skills occurring within the first years of life (e.g., object manipulation, crawling, and walking), this age range appears crucial to investigate the effects of motor and perceptual experience on the organization of the neural somatotopy to others' action perception across different sensorial modalities, such as visual, auditory and tactile stimulations.

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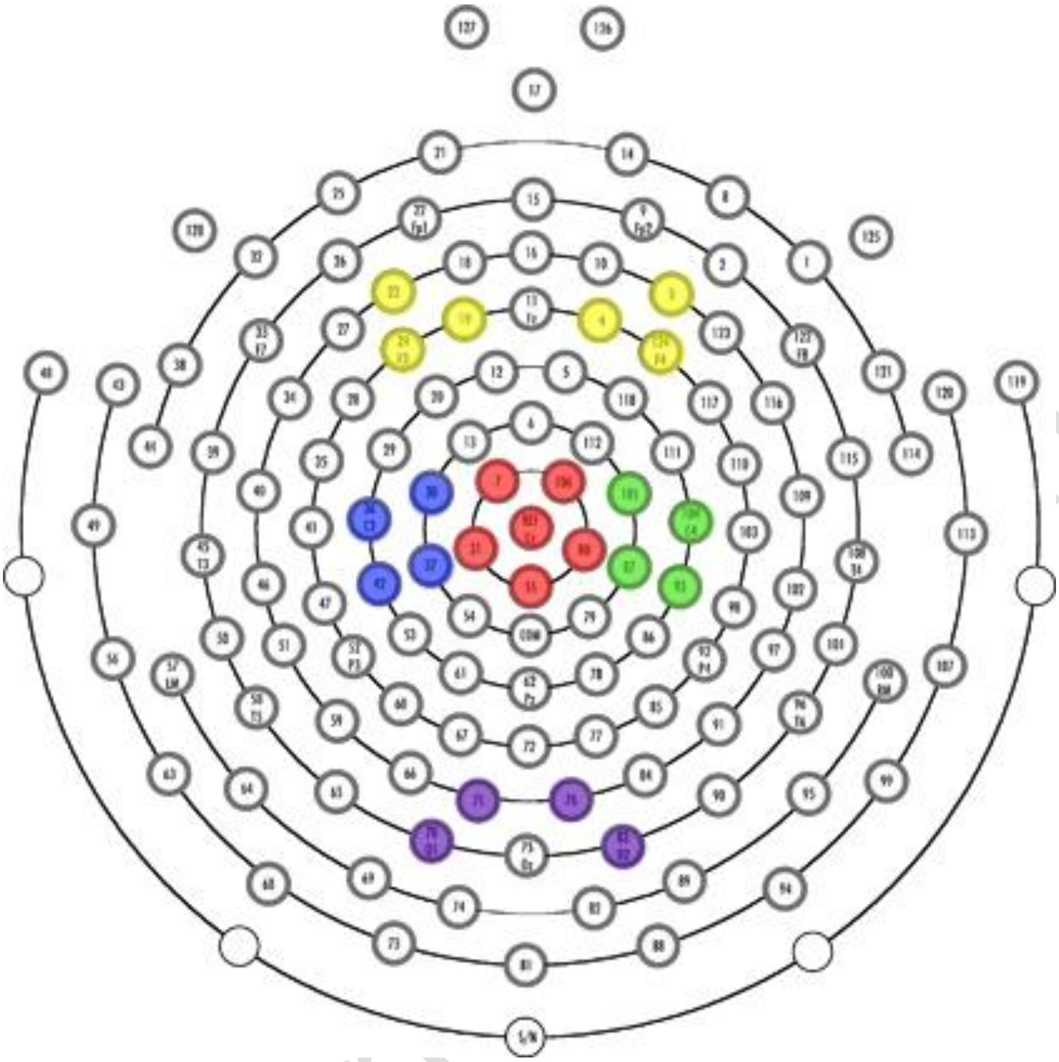

Figure 1. Schematic diagram of the 128-channels sensor layout showing the three clusters of electrodes located over the left hand (blue; channels 30, 36, 37, 42), the leg (red; channels 7, 31, 55, 80, 106, Cz), and the right hand (green; channels 87, 93, 104, 105) areas of the sensorimotor cortex, along with the occipital (purple; channels 70, 71, 76, 83) and frontal (yellow; channels 23, 24, 19, 3, 4, 124) electrode clusters.

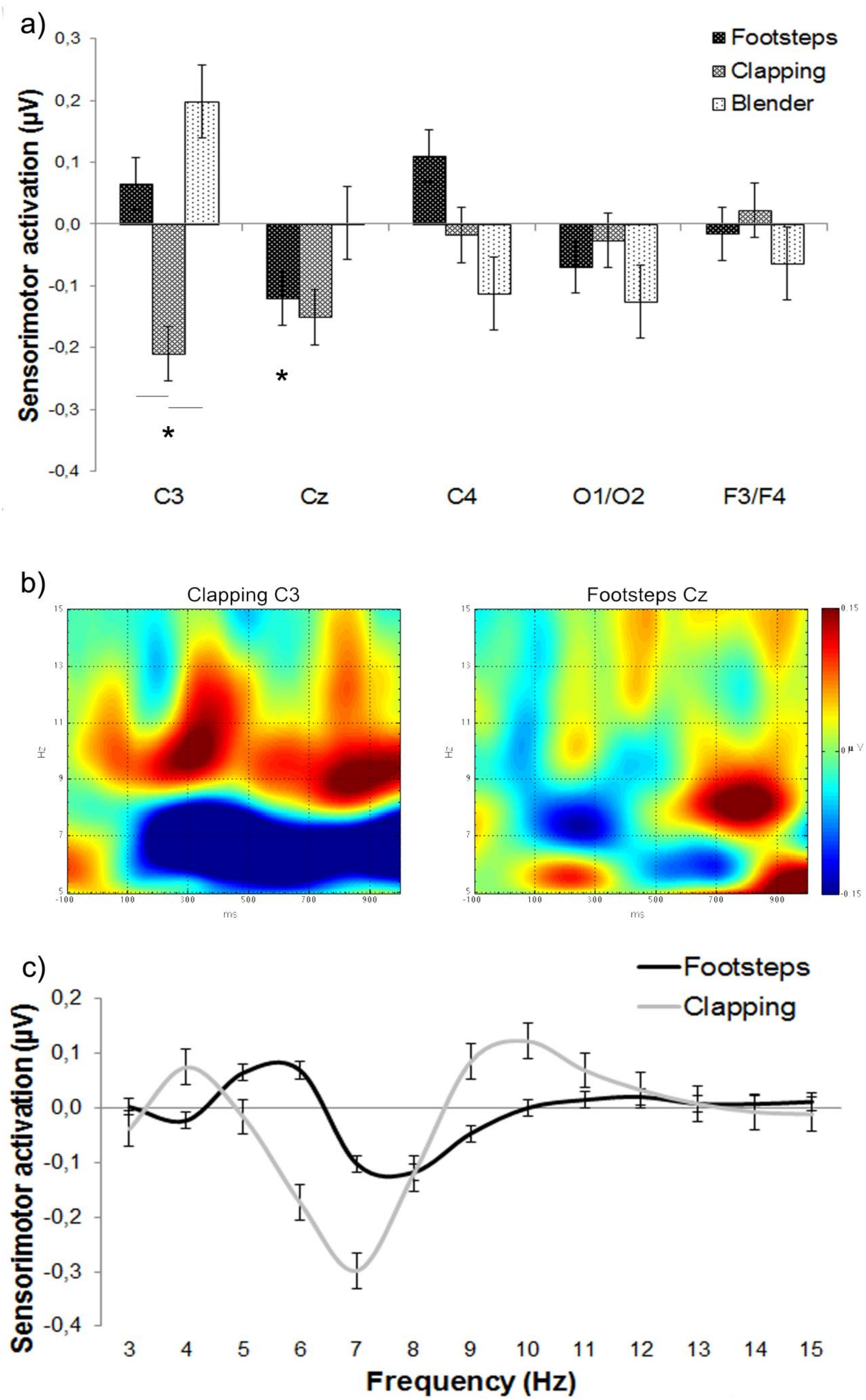
a)
Sensorimotor activation (µV)
0,3
0,2
0,1
0,0
-0,1
-0,2
-0,3
-0,4
Footsteps
Clapping
Blender
*
*
C3
Cz
C4
O1/O2
F3/F4
b)
Clapping C3
Footsteps Cz
Hz
15
13
11
9
7
5
-100
100
300
500
700
900
ms
0.15
0 µ V
-0.15
c)
Footsteps
Clapping
Sensorimotor activation (µV)
0,2
0,1
0,0
-0,1
-0,2
-0,3
-0,4
3
4
5
6
7
8
9
10
11
12
13
14
15
Frequency (Hz)

Figure 2. The top panel (a) displays mean sensorimotor activation over the medial leg area (Cz), bilateral hand (C3, C4) and occipital (O1/O2) areas during the presentation of foot (i.e., footsteps), hand (i.e., clapping), and mechanical (i.e., blender) sounds (a). Significant suppression from baseline and significant comparisons between conditions are illustrated, * *p* < .05. The middle panel (b) show time-frequency results for the listening of clapping and footstep sounds respectively in correspondence of C3 and Cz electrode clusters. The bottom panel (c) represents frequency modulation over C3 and Cz respectively during infants' auditory perception of clapping (light grey) and footstep (black) sounds from 3 to 15 Hz. Error bars represent +/- 1 standard error.

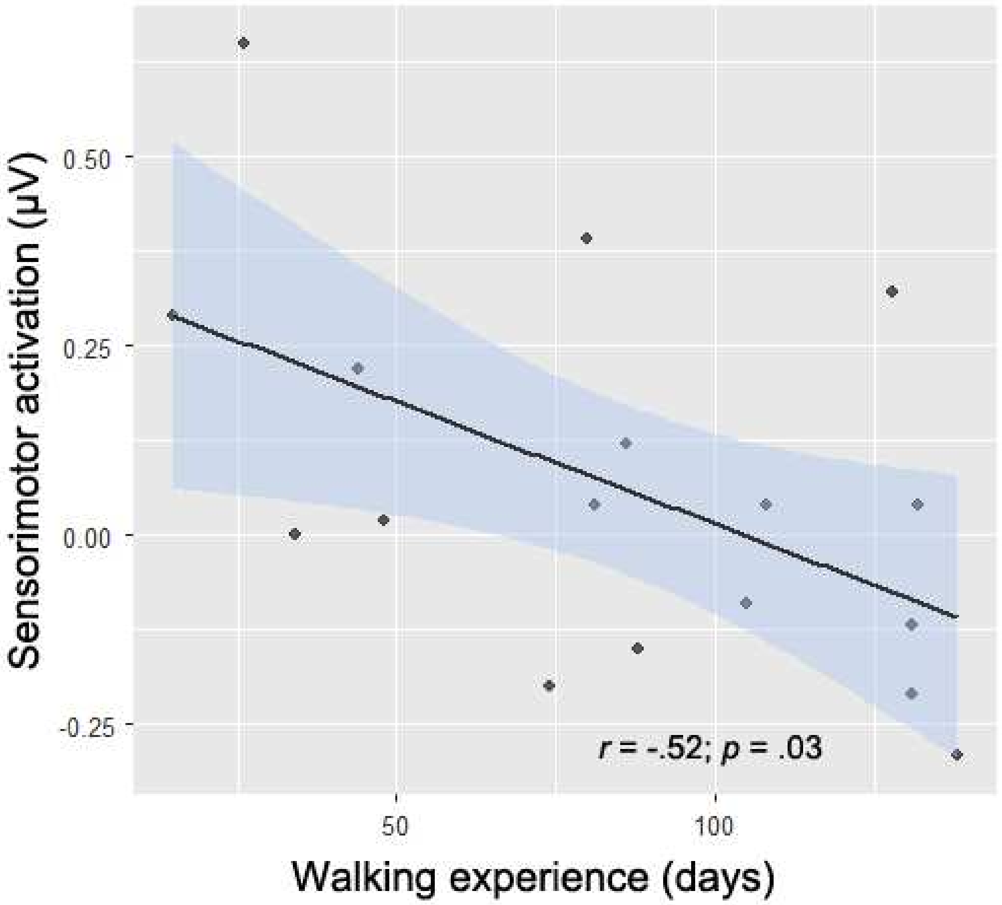

Figure 3. Correlation between walking experience and sensorimotor activation elicited by footstep sounds over the C3 electrode cluster. Pearson's *r* represents the partial correlation between the sensorimotor activation and the walking experience after controlling for age of participants at testing.