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Abstract:

Contemporary active-EEG and EEG-imaging methods show particular promise for studying the development of action planning and social-action representation in infancy and early childhood. Action-related mu suppression was measured in eleven 3-year-old children and their mothers during a 'live,' largely unscripted social interaction. High-density EEG was recorded from children and synchronized with motion-captured records of children's and mothers' hand actions, and with video recordings. Independent Component Analysis (ICA) was used to separate brain and non-brain source signals in toddlers' EEG records. EEG source dynamics were compared across three



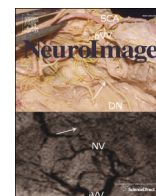
kinds of epochs: toddlers' own actions (execution), mothers' actions (observation), and between-turn intervals (no action). Mu (6–9 Hz) power was suppressed in left and right somatomotor cortex during both action execution and observation, as reflected by independent components of individual children's EEG data. These mu rhythm components were accompanied by beta-harmonic (~16 Hz) suppression, similar to findings from adults. The toddlers' power spectrum and scalp density projections provide converging evidence of adult-like mu-suppression features. Mu-suppression components' source locations were modeled using an age-specific 4-layer forward head model. Putative sources clustered around somatosensory cortex, near the hand/arm region. The results demonstrate that action-locked, event-related EEG dynamics can be measured, and source-resolved, from toddlers during social interactions with relatively unrestricted social behaviors.

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EEG imaging of toddlers during dyadic turn-taking: Mu-rhythm modulation while producing or observing social actions

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ABSTRACT

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Introduction

Action interpretation is central to many social-cognitive skills that develop within the first 2–3 years of life. Perspective taking, imitation, joint attention and cooperation all require some awareness and knowledge of other people's actions. Single neuron recordings from monkey cortex indicate that action observation activates a subset of neurons that also fire during action execution. These are sometimes called 'mirror neurons' (Di Pellegrino et al., 1992; Rizzolatti and Craighero, 2004). Mirror neuron activity also has been found in human brains using imaging methods (Rizzolatti, 2005). Notably, electroencephalographic (EEG) studies of human adults have found suppression of 8–13 Hz oscillatory power, and concurrent suppression of the beta-range harmonic (18–26 Hz), during action execution and action observation (e.g., Hari and Salmelin, 1997). This desynchronization, called mu-suppression, is related to sources around central sulcus encompassing primary somatosensory and motor cortices (Babiloni et al., 2002; Forss and Silén, 2001; Kilner and Frith, 2008; Makeig et al., 2004; Ritter et al., 2009). Because it is elicited by action observation as well as execution, it is considered

an EEG signature of the 'mirror-neuron' systems (Pineda et al., 2000; Iacoboni et al., 2005).

EEG power suppression in the 5–9 Hz range also has been found in older infants and children while watching a hand produce an action (Lepage and Théoret, 2006; Nyström et al., 2011). This suggests that by one year of age, cortical networks might have learned to represent patterns of biological motion related to human action. A next step is to determine whether and how these representations are activated during everyday social interactions. A recent study found 6–9 Hz power suppression in 14-month-olds during action observation in a social context (Marshall et al., 2011). Unlike previous studies that examined only electrode sites over sensorimotor cortex, 6–9 Hz power was analyzed across several distant scalp regions. Unlike typical mu suppression, however, the authors found a much broader distribution of suppression over all scalp regions. The results might therefore reflect a general effect of attention and arousal (Coull, 1998), rather than action-related mu-suppression. Moreover, because the specific frequency range was predefined as 5–9 Hz and other ranges were not analyzed, it is unclear whether suppression was specific to the mu spectrum. These ambiguities are largely unresolved by more recent reports (Marshall et al., 2013; Saby et al., 2013). Consequently, the nature of action-based mu-suppression in young children during real social interactions remains largely unexplored.

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Other EEG indices of social-action processing have not yet been explored in young children. For example, a beta-range harmonic of mu-suppression is consistently observed in adults during action processing (Hari and Salmelin, 1997). However, beta-band modulation has been described in only a single report of infant/child action processing (Van Elk et al., 2008). One possible explanation is that beta modulation undergoes later development, because the EEG power distribution shifts towards higher frequencies (beta and gamma) throughout childhood (e.g., Benninger et al., 1984; Gasser et al., 1988), especially during early childhood when social-cognitive skills show profound development. However, because only one study has reported beta-modulation in toddlers, in response to videos of other infants, we cannot yet make inferences about how beta modulation develops in response to action processing.

Finally, previous studies of infants and children have not used contemporary EEG methods to model the cortical sources of mu-suppression. Although we might presume that action-related mu-suppression in children originates in somatomotor cortex, as it does in adults, this has not been demonstrated. More generally, there have been few efforts to extend contemporary EEG source imaging methods to young children, despite considerable advances in modeling methods (e.g., Michel and Murray, 2012) and application of these methods to data from infants and children (e.g. Sperli et al., 2006; Bathelt et al., 2013). Current optimal methods include boundary-element and finite-element models, constrained by conductivity estimates of interposed tissues (Acar and Makeig, 2010). Using an age-appropriate anatomical model, it should be possible to estimate the source locations of coherent EEG activity in toddlers. This would represent an advance in documenting the early cortical substrate of social action processing.

Optimal methods for processing EEG data, including source localization, include a biologically plausible approach to un-mixing cortical sources (Makeig et al., 2002). Channel-level analyses are inappropriate because each channel represents an unknown mixture of cortical and non-cortical electrical sources. Also, because cortical sources project

tangentially from both gyral and sulcal surfaces, it is difficult to infer a specific vector from scalp to cortex based on channel-level activity. A preferable approach is to utilize all information (frequency, amplitude, and phase) to mathematically separate maximally independent sources of coherent activity in an EEG record (Onton et al., 2006; Delorme et al., 2012). Nyström et al. (2011) used this 'un-mixing' approach to increase signal-to-noise ratio in infant mu-suppression data, but the authors did not conduct source localization.

To investigate modulation of mu power and its cortical sources in toddlers during live social interactions, synchronized high-density EEG and body motion were recorded while toddlers played a turn-taking "bubble popping" game with their mothers (Fig. 1). This allowed us to lock toddlers' EEG to their own and their parents' game-related movements. This is therefore the first study to use mobile brain-and-body imaging (MoBi; Makeig et al., 2009) to investigate toddlers' social cognition. The MoBi approach capitalizes on methodologies that permit a relatively natural range of behavior, in relatively naturalistic task contexts (compared to typical neurodevelopmental studies), while capturing high-density, action-locked physiological data. MoBi studies typically use EEG, which is the only brain imaging method that allows both freedom of head and body movement, and time-locking physiology with behaviors.

We predicted that high-density EEG could separate ICs in toddlers related to mu suppression and localize them to somatomotor cortex. We also predicted that toddlers would show somatomotor mu suppression both while taking turns and while watching their mother take turns. Finally, we predicted parallel results for beta desynchronization. We also tested whether mu and beta suppression would be greater for execution than for observation. Finally, we tested whether mu suppression was sensitive to 'local' turn-taking dynamics; that is, whether there is more suppression when the current actor 'matches' their partner's last action (i.e., touches the same bubble), than when the actor makes a non-matching action (i.e., touches the other bubble). If mirroring effects are sensitive to the recent context of a partner's actions, this

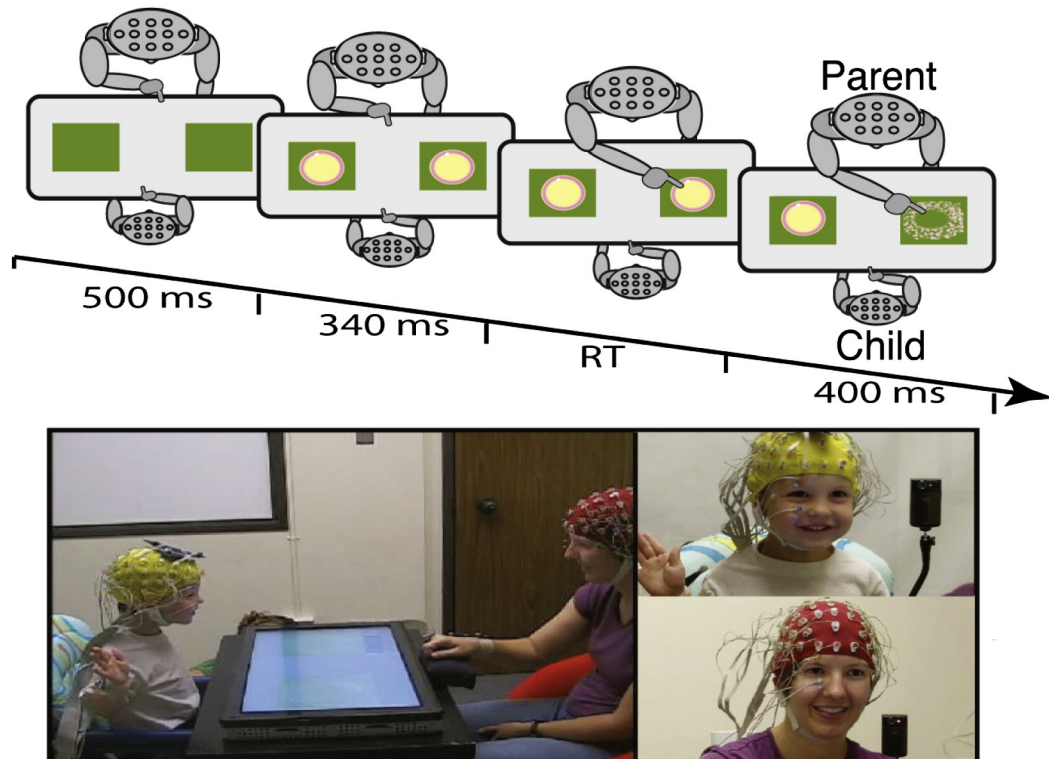


Fig. 1. Top: Experiment game paradigm and event time line for a single action observation trial (i.e., mother's turn) in the game. Bottom: Camera views for video recordings. Note that the current report focuses only on toddlers' EEG records.

variable might modulate mu suppression. This possibility has not been tested in children.

Methods

Participants

Twenty-one mother–toddler dyads participated in testing. One dyad was dropped from dyadic behavioral analysis because they finished only one block of the game. The final sample for EEG analysis included 11 toddlers (mean age 41 ± 4 months, 7 females) who received the final protocol and provided sufficient EEG data for effective ICA decomposition. Participants were recruited through local playgroups, parenting classes, and word-of-mouth. All had previously participated in a longitudinal study beginning at 3 months of age. Mothers averaged 35.5 years of age (range: 26 to 43 years) with an average of 16.7 years of formal education (range: 14 to 19 years). All procedures were approved by the University's IRB.

Experimental procedure

Each toddler–mother dyad sat facing each other across a table-mounted 66-cm capacitive touch screen monitor (Elo, California, USA). Both participants wore 64-channel EEG caps with active Ag/AgCl electrodes (Biosemi, The Netherlands), and motion-capture markers (NaturalPoint, Oregon, USA) on their heads and right wrists. EEG data were sampled at 256 Hz (24-bit). Custom software processed participants' head and right hand positions in real time by calculating the distance and angle of the markers from two pre-defined left and right target regions. When a participant-specific head or wrist marker entered a target region, custom software recorded a 'reach-to-target' event programmed to cause a specific game event. Thus, the program responded to each participant's specific reaching action in real time.

Mother–child dyads participated in a turn-taking 'bubble popping' game on the touch screen. As shown in Fig. 1, each trial began with two background images (approximately 12×12 cm² cartoon lawns) appearing on the left and right sides of the touch screen, approximately 35 cm apart, for 500 ms. Subsequently, identical animations of an enlarging bubble synchronously appeared on each background image for 340 ms.

Participants were instructed to take turns using their right hands to touch one of the bubbles, causing it to 'pop'. Touching a bubble triggered different 400-ms feedback animation sequences, depending on who touched a particular bubble. A mother's touch always triggered a popping animation accompanied by a popping sound. A toddlers' touch triggered the same animation only when he or she touched the same bubble (left or right) that the mother had touched in the previous trial. This is a 'matching' response. However, if the toddler touched the other (contralateral) bubble (a 'mismatch' response), a different 400-ms animation was triggered in which the bubble distorted but did not pop, accompanied by another sound effect. In each trial a small colored bar, visible to the mother, reminded her whose turn was next.

Feedback animations were triggered when the appropriate participant's wrist marker moved into a region containing one or the other bubble. However, the program ignored multiple successive touches by either participant. Thus, if a toddler failed to take turns, the game did not advance.

Before data acquisition began, the participants practiced the game until they were familiar with its rules. Mothers were asked to occasionally switch their choice of bubble (left/right), so that touches would be fairly evenly distributed between targets. However, mothers were not given any other guidance or feedback about which bubble to press.

Each game block included 20 mother turns and 20 toddler turns. Mothers' turns were designated as toddlers' action observation trials, and toddlers' own turns were designated as action execution trials. Dyads completed an average of 4.7 game blocks (range: 3 to 6) for an

average total of 182 valid trials (range: 120 to 240). Blocks of the bubble-popping game were interspersed with blocks of another game (to be reported elsewhere). Each session lasted 70 to 90 min, including 25 to 40 min of preparation and 30 to 50 min of data recording.

Data acquisition

Synchronous EEG and body motion capture

Customized software synchronized and recorded data from all sources, including both participants' EEGs, locations of all motion-tracked markers, motion-triggered events, touch-screen events and locations, and programmed game events. Toddlers' EEGs were recorded from 64 scalp channels plus four bipolar H/V EOG electrodes and two active reference electrodes on the mastoid bones.

Hand motions were tracked using a 6-camera NaturalPoint Optitrack system that registers the position of pre-calibrated rigid bodies in real time (100 Hz sampling). Reflective three-marker rigid frames were placed on participants' heads (affixed to the EEG cap) and on a soft band on participants' right wrists.

EEG and motion-tracking data were resampled online to 256 Hz and synchronized by DataRiver software (Delorme et al., 2011).

Video recording

Three video cameras captured HD videos (30 Hz) from three perspectives: a side view of both participants, and close-up views of each participant's head and upper body (see Fig. 1). Videos were synchronized to game events in post-processing.

EEG analysis

Data preprocessing and independent component analysis (ICA)

Toddlers' EEG data were analyzed using custom MATLAB scripts in the EEGLAB toolbox (Delorme and Makeig, 2004). First, channels with grossly abnormal patterns were removed, leaving an average of 49 channels ($SD = 4$) out of the 70 total EEG, EOG, and reference channels. After re-referencing to the average of the remaining channels, the EEG data were band-pass filtered from 1–35 Hz. Data intervals containing (by visual inspection) extreme peak-to-peak deflections or large bursts of high frequency EMG activity were identified by visual inspection and removed. Intervals containing traces from eye blinks, eye movements, or other muscle activity were not removed at this stage.

Artifact-rejected data for each subject were separately decomposed by independent component analysis (ICA), specifically, Adaptive Mixture ICA (AMICA) (Palmer et al., 2008). ICA decomposition of EEG data separates the recorded activity into maximally independent (i.e., spatially fixed; temporally distinct) activity sources, and increases the signal-to-noise ratio of cortical sources. The final EEG dataset length used for ICA decomposition ranged from 20 to 48 min (mean = 33.7 min), with a mean of 518 k ($SD = 122$ k) data points for ICA decomposition. This provided a mean of over 300 time points per AMICA learned-matrix weight – a favorable basis for ICA decomposition.

Equivalent dipole model fitting of IC scalp maps

To fit cortical ICs to an equivalent neuroanatomical source dipole model, we used a database (Sanchez et al., 2012a,b) of tissue-segmented structural MRI scans of 3- and 4-year-old children ($N_s = 22$ and 19 respectively) to generate age-specific head models. Three-layer finite element method (FEM) head meshes using tetrahedral elements (Acar and Makeig, 2010) were used to generate 3-year-old and 4-year-old template head models. A 64-channel Biosemi EEG electrode location template with six EXG ocular reference channels was used to co-register electrode locations to the scalp mesh of the head models. Assumed scalp conductivity was 0.33 S/m (Geddes and Baker, 1967). Because errors in assumed skull conductivity can significantly affect EEG source location estimates (Akalin Acar and Makeig, 2013), skull conductivity was estimated using an age-based sc function adopted from BESA (Besa GmbH,

Graefelfing, Germany, www.besa.de): $sc = 0.064 * \exp(-0.195 \times [\text{years of age}])$. This yielded an *sc* estimate of 0.0357 s/m and brain-to-skull conductivity ratio of 9.2 for 3-year-olds, and 11.3 for 4-year-olds. Dipoles for each participant were fitted to either the 3-year-old or 4-year-old head model, depending on which was closer to the participant's age.

Brain component selection

IC activity time series for each subject were categorized by two of the authors (YL and SM) as reflecting brain or non-brain source activity, based on two objective criteria: (1) only the first 35 ICs were considered; on average these accounted for 94.6% (SD = 4.2%) of variance in total channel power; (2) only ICs with dipoles within the brain (based on scalp distribution and dipole fit) were considered. The remaining (dipolar within-brain) ICs were further restricted to those with less than 12% residual variance (RV) between the scalp map and best-fitting projection of a single model equivalent dipole within the template brain volume. The number of these ICs retained for group level analyses averaged 16 per subject (SD = 6; range = 9 to 31). The mean RV of the selected ICs across subjects was 5.6% (SD = 0.6%).

Eliminating movement artifact

Because toddlers' ability to inhibit movement impulses is immature, it is critical to rule out deliberate actions (e.g., reaches) during both 'no-action' epochs (i.e., –200 ms to 1000 ms from the background onset in execution trials, while neither participant was reaching) and during action-observation epochs (i.e., –1000 ms to 200 ms from the mother's screen touch). Two methods were used to eliminate action artifacts from these epochs:

1. Frame-by-frame video coding: Synchronized videos were coded using Interact software (Mangold International, Arnstorf, Germany). Two experienced coders recorded, frame-by-frame, any deliberate hand or body movements, or speech. All no-action or action-observation epochs with deliberate toddler actions were excluded from final analysis. Two researchers independently coded all videos. Inter-coder reliability (Cohen's Kappa) averaged $\kappa = .79$.
2. Motion records of toddler's right hand were analyzed using EEGLAB's MoBiLAB toolbox (Ojeda et al., 2014). All no-action or action-observation epochs in which hand velocity exceeded 0.45 mm/s were excluded from final analysis.

After applying these criteria, an average of 32.5 (SD = 14.7) no-action epochs, 45.6 (SD = 22.5) action-execution epochs, and 28.1 (SD = 16.7) observation epochs remained per participant. Execution epochs included an average of 24.3 (SD = 16.1) trials in which toddlers' action (i.e., left or right bubble touch) matched their mother's last action, and 21.1 (SD = 14.8) trials in which toddlers' action mismatched the mother's last action (i.e., switched sides). Observation epochs included means of 11.2 (SD = 10.1) trials in which the mother matched the toddler's last action, and 17.4 (SD = 13.1) in which she mismatched the toddler's last action.

Component power spectral density (PSD)

Mean PSDs from 3 to 35 Hz for the identified brain ICs in no-action, observation, and execution epochs were calculated using fast Fourier transforms.

Component event-related spectral perturbations (ERSPs)

For each IC included in the analysis, mean ERSPs (Makeig, 1993) for each of the three epoch types were computed using three-cycle Morlet wavelets in the 3 to 35 Hz range.

IC clustering across participants

To identify categories of functionally equivalent ICs across participants, retained ICs from all subjects were submitted to a clustering algorithm. Features of each IC, including scalp topography, equivalent dipole position, log mean power spectral density, average ERSP, and Inter-Trial

Coherence (ITC, which indexes phase locking at each frequency relative to time-locking events; Delorme and Makeig, 2004), were entered as variables for clustering classification. All parameters excepting dipole locations were first compressed by principal component analysis (PCA) into a 10-dimensional vector. The dipole location measures were inherently three-dimensional, but for scaling purposes they were weighted by a factor of 10. The PCA-reduced information was combined into a single matrix and further reduced by PCA to 10 principal dimensions. ICs were classified based on pairwise distances in this 10-dimensional space, using a K-means algorithm (Delorme and Makeig, 2004). This yielded 15 clusters. Two of these were left- and right-hemisphere somatomotor mu IC clusters, identified as such based on: characteristic mean power spectra, scalp maps, and equivalent dipole locations. In addition, three more clusters that seemed to capture central, parietal and occipital sources, respectively, were identified for further analysis.

Cluster PSDs and ERSPs

After IC clustering, separate cluster-average PSDs and ERSPs were calculated for the left somatomotor mu and right somatomotor mu-related IC clusters. Mu power (6–9 Hz) was compared across the three epoch types by repeated-measure ANOVAs. The 6–9 Hz range was chosen based on the peak range of mu clusters reflected in our spectrum analysis, but is consistent with numerous previous studies of mu-rhythms in children (e.g., Saby et al., 2013). Analogous ANOVAs for each cluster were performed to compare integrated power differences among epoch-types in the beta range (i.e. 15–18 Hz). Separate comparisons were run for the left and right IC clusters.

Results

Behavioral results

None of the 20 mothers in the analyses showed a side preference: their mean proportion of left (in reference to toddler's position) bubble touches was 55% (SD = 5%). However, toddlers showed a right side bias (mean right touches = 59%, SD = 15%; range: 14% to 68%; $p < .01$), possibly because participants used their right hands. However, the total number of trials was large enough that this bias is not problematic for further analyses.

Mothers matched their child's previous action (i.e., popped the same bubble) on an average of 57% of turns (SD = 10%), significantly more than expected by chance (50%): $t(19) = 3.39, p < .01$. Mothers matched more often after the child mismatched her previous action (51%, SD = 16%) than after the child matched her action (32%, SD = 13%), $t(19) = 3.79, p < .01$. Thus, mothers' decisions were not independent of the child's last action. Toddlers, by contrast, matched their mother's last turn more often if she had just matched their action (63%, SD = 23%) than if she did not (32%, SD = 22%), $t(19) = 5.15, p < .001$. Thus, toddlers' decisions also were dependent on the mother's last action. These patterns indicate that the game elicited reciprocity and mutual influence.

EEG results

Mu-rhythm clusters and their sources

As shown in Fig. 2A, the left somatomotor mu cluster included 11 IC's, one from each child. Each IC showed a similar scalp maps with a characteristic polarity reversal over left somatomotor cortex and a corresponding tangential equivalent dipole consistent with an origin near central sulcus, generally at a dorsoventral position consistent with the hand/arm receptive field (Forss and Silén, 2001; Makeig et al., 2004). The location of the average equivalent dipole centroid for ICs in the cluster, projected onto the age-based head models, was $x = 50, y = 84$, and $z = 85$. This is consistent with somatomotor mu source locations reported from adult brains (Ritter et al., 2009; Mizuhara, 2012).

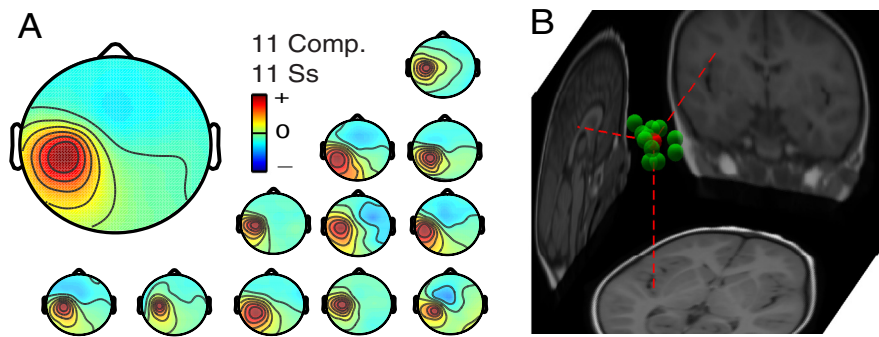


Fig. 2. (A) Scalp maps for each contributed independent component (small), and the mean map for the cluster (large). (B) Equivalent dipole location for each IC in the cluster (green points), and the centroid location (red).

The right somatomotor mu cluster (Fig. 3A) included 10 ICs from 9 toddlers. IC scalp maps showed a characteristic polarity reversal over right somatomotor cortex. The average centroid of the dipoles was in right somatomotor cortex ($x = 110$, $y = 94$, $z = 102$) (Fig. 3B).

The PSDs of both left and right clusters conformed to those expected for somatomotor mu, with peaks in the 7–9 Hz range (Hari and Salmelin, 1997; Berchicci et al., 2011), and smaller beta (16–18 Hz) harmonic peaks. See Table 1.

Event-related mu suppression

As shown in Fig. 4A, mu suppression for the left cluster was time-locked to screen touches during both execution and observation epochs, compared to a mean baseline (i.e., 500 ms before movement began in execution trials). Notably, although mu and beta suppression were induced in both conditions as the hand approached the target, they persisted after the touch only in the execution condition, presumably while the child was withdrawing his/her hand.

Power differences for the left somatomotor mu cluster across the three epoch types are shown in Fig. 4B (also see Table 1). Mu power differed significantly across epoch types, $F(2, 20) = 10.92$, $p < 0.01$, $\eta^2 = 0.52$. Pairwise comparisons revealed significant mu suppression in execution epochs ($p < .01$) and in observation epochs ($p < .01$) compared to no-action epochs. There was also significantly more suppression in execution than observation epochs, $p < .05$. Also, beta power differed significantly between epoch types, $F(2, 20) = 4.532$, $p = .045$, and $\eta^2 = 0.31$. Pairwise comparisons revealed significantly lower power in execution epochs ($p < .05$) and marginally lower power in observation epochs ($p = .07$), than in no-action epochs. Beta power did not differ reliably between execution and observation epochs ($p = .13$).

The right somatomotor mu cluster ERS image also shows both mu and beta suppression (Fig. 3C). Mu power differed significantly among epoch types, $F(2, 16) = 10.02$, $p < 0.01$, and $\eta^2 = 0.56$. Pairwise comparison revealed significantly lower power in execution and observation epochs (both $ps = .01$) than in no-action epochs. Mu power did not

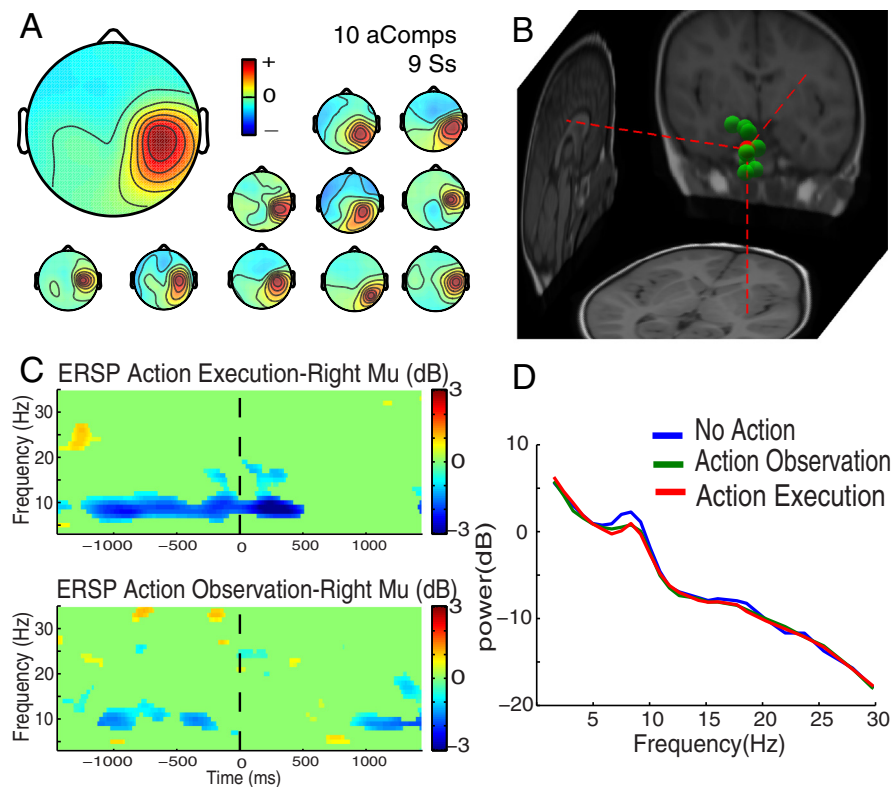


Fig. 3. Right somatomotor cortex mu-rhythm cluster profile. (A) Scalp maps of each contributing IC (small maps) and the mean map for the cluster (large map); (B) dipole location of each contributing IC (green) and centroid location (red). (C) Significant ERS differences ($p < .05$) from baseline (0 to 500 ms after the background onset) displayed as warm or cool colors. T = 0 is locked to when the player's hand-marker crosses a boundary around a bubble. (D) Group-averaged PSDs for the right somatomotor mu-rhythm IC cluster, for the three epoch types.

Table 1

Mean and Standard Deviation (SD) for Mu and Beta Frequency Power Spectral Density (in $\mu V^2/Hz$).

Somatomotor IC clusters	Condition	Mu (6–9 Hz) Mean (SD)	Beta (15–18 Hz) Mean (SD)
Left	No action	1.67 (1.16)	0.20 (0.17)
	Action observation	1.32 (0.94)	0.16 (0.11)
	Action execution	1.01 (0.69)	0.13 (0.09)
Right	No action	1.53 (0.86)	0.19 (0.11)
	Action observation	1.12 (0.57)	0.16 (0.86)
	Action execution	1.16 (0.63)	0.16 (0.77)

significantly differ between execution and observation epochs, $p = .56$. Beta power showed no significant differences across epoch types.

To test the specificity of mu/beta suppression, EEG power was also compared across epoch types in three additional clusters, located at central, parietal and occipital regions, respectively. We did not predict differential power from ICs in these regions. The results therefore will indicate whether desynchronization during action execution and observation was specific to somatomotor networks. As shown in Fig. 5, a central cluster of 13 ICs contributed by 10 toddlers had a mean PSD with an alpha range peak (7–9 Hz) and a small beta peak (16–18 Hz), which suggests mu rhythm activity. However, unlike the somatomotor mu clusters, power did not significantly differ across epoch types. A parietal cluster (12 ICs from 9 toddlers) and an occipital cluster (14 ICs from 8 toddlers) each showed alpha range PSD peaks around 7–9 Hz each, with no beta harmonic. Again, power difference between epoch types were not significant. These results support the hypothesis that mu suppression associated with manual action observation and execution originate selectively in left and right somatomotor cortex.

Further, a 2 (Match/Mismatch) \times 2 (Observation/Execution) repeated ANOVA was performed to investigate if mu power in somatomotor ICs was modulated by matching versus mismatching the partner's previous actions (see Supplementary Fig. 1 for plots of the four conditions). For the left mu cluster, consistent with the results described above, there was a main effect of observation/execution condition, $F(1, 10) = 4.93$, $p < 0.05$, and $\eta^2 = 0.33$. However, there was no main effect or interaction involving match/mismatch trials ($ps > .67$). The right mu

cluster also showed no effect of match/mismatch. This suggests that mu power suppression was not modulated by whether the actor matched the last action (i.e., touched the same bubble) or mis-matched it (i.e., touched the other bubble).

Verification by motion analysis

To verify that mu suppression during action–observation epochs was not an artifact of incidental task-irrelevant motor activity, toddlers' hand movement velocity profiles were compared across epochs (recall that observation and no-action epochs with gross motor activity were already excluded). As shown in Fig. 4C, toddlers' mean right hand velocity increased and then decreased during execution epochs, with lowest average velocity of 66 ms after touching the screen. By comparison, hand velocity was minimal (mean < 0.075 m/s) during observation and no-action epochs, with no significant changes during the epochs. A repeated-measure ANOVA with Greenhouse–Geisser correction shows that velocity differed significantly between epoch types, $F(1, 318) = 1268.28$, $p < 0.0001$, and $\eta^2 = 0.81$. LSD post hoc tests revealed significantly more hand movement during execution than observation or no-action epochs (both $p < .0001$), but no difference between the latter ($p = .63$).

Discussion

This study investigated the neural generators and spectral properties of mu rhythm perturbations related to action perception in young children. High-density EEG was measured from toddlers during a 'live,' unscripted turn-taking game in which children alternately chose a manual action and watched their mother choose an action. Our analyses identified bilateral Independent Components of cortical activity with spectral power peaks at 7–9 Hz, and secondary (harmonic) peaks at 16–18 Hz. The ICs showed all spectral and spatial properties of somatomotor mu-suppression that have been reported in adults. Locations of the IC sources were imputed from age-specific 3D head models. As predicted, all ICs fell within a region centered near the sulcal walls of somatomotor cortex. The ICs were not "cherry-picked" for these clusters, but were machine-classified by an algorithm that did not select any particular a priori features of mu-suppression. Rather, the algorithm incorporated

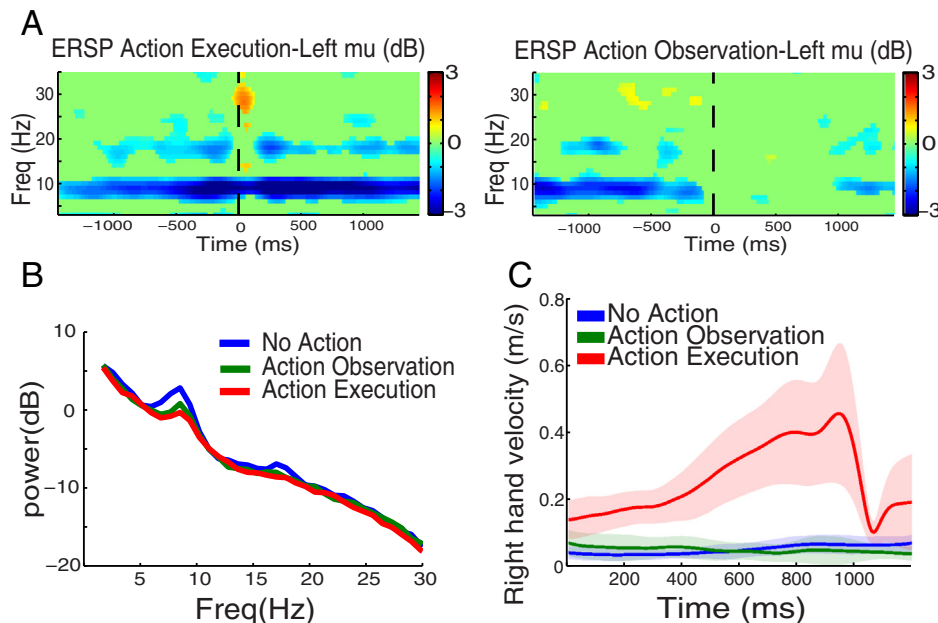


Fig. 4. (A) Group-averaged time-frequency distribution of mean event-related spectral perturbations (ERSPs) for the left somatomotor mu-rhythm IC cluster. Significant ERSP differences ($p < .05$) from baseline (0–500 ms after the background onset in execution trials) are displayed as warm or cool colors. T = 0 is the moment when the player's hand-marker crosses the virtual boundary around one of the bubbles. (B) Cluster-mean power spectral densities (PSDs) for the left somatomotor mu-rhythm IC cluster. (C) Group-averaged toddler's right hand-movement velocity changes during time windows corresponding to the three EEG epoch types.

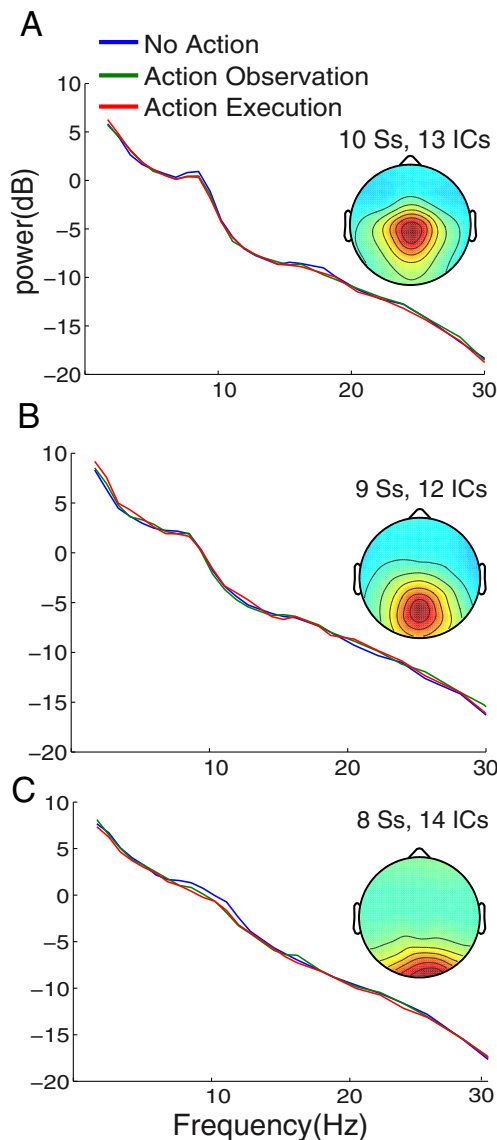


Fig. 5. Group-averaged PSDs and cluster scalp maps for central (A), parietal (B), and occipital region ICs, across the three epoch types.

unbiased PSD, ERSP, ITC, and spatial properties. Although there is currently no conventionally agreed-upon method for classifying EEG ICs, and variables like the weighting of feature types in a clustering algorithm would likely affect the results, in this case the strong resemblance of ICs in each cluster render it likely that a wide range of classification methods would yield the same clusters.

In adults, somatomotor mu power and its beta harmonic are suppressed by either making a deliberate action or watching another's action (Pineda, 2005). Likewise, toddlers showed left somatomotor mu-suppression both when executing actions and when watching their parent act. Most toddlers showed a parallel source in right hemisphere. These sources also showed beta-power suppression (in left hemisphere) when executing actions, and a marginal trend when observing actions. There are several possible reasons why the pattern was less consistent in right hemisphere, but a likely factor is that participants used their right hands to play the game. It is intriguing that even in this unimodal task, mu suppression was found in the ipsilateral hemisphere (i.e., serving the inactive hand). Hari et al. (1998), for example, found desynchronization only in the left (contralateral) somatomotor cortex of adults using their right hand or watching another person use their right hand. However, there are many differences between that

study and ours, in task and measurement and in participants' age, so the difference in results is hard to interpret. For example, some possibly influential factors include the fact that stimuli in our paradigm appeared approximately equally in both visual hemifields, that toddlers reached to both ipsilateral and contralateral targets, and that lateralization of handedness is not complete by 4 years of age (Sacrey et al., 2013). In general, lateralization and regionalization of somatomotor mu-suppression remains little studied in infants and toddlers (see Saby et al., 2013).

Assessing social brain activity in toddlers

Testing brain-behavior correspondences in young children poses particular challenges. Because toddlers enjoy moving around and interacting with people and objects, rather than sitting still and watching simple repetitive stimuli (e.g., experimental stimuli), they tolerate only brief testing periods using traditional methods, and tend to produce many task-irrelevant movements. It is therefore difficult to acquire EEG data sets that permit powerful analyses. The same limitations make other functional imaging techniques like MEG or MRI even less feasible. For these reasons, it has not been considered possible to study the brain activity of toddlers during social interactions. Our paradigm demonstrates, however, that contemporary EEG approaches make it feasible to study toddlers' brain activity during social interactions, and even to lock specific brain responses to specific spontaneous social actions. Engaging toddlers in socially interactive tasks or games can maintain their interest, allowing for longer data acquisition periods. The bubble game, a controlled turn-taking paradigm, is suitable for participants as young as two years: toddlers in this sample completed 150–250 trials after being capped for high-density EEG, and completed a second social game (to be reported elsewhere) in the same session as well. As wireless and dry-electrode EEG technology improves (e.g., Fonseca et al. 2007; Lin et al., 2008) and EEG capping becomes faster and more pleasant, even more extensive and naturalistic data sets will be obtainable during social interactions.

ICA unmixing of cortical sources is an underutilized method in EEG studies of infants and children, particularly for unmixing signal from extraneous motion (i.e., 'squirminess'). The current study demonstrates that this approach can be enhanced and validated through converging robust measures of movement: motion tracking, video, or (hypothetically) EMG. We detected, coded and quantified movement artifacts using two methods: frame-wise analysis of synchronized video, to identify periods of gross motor activity, and motion-capture of arm movements, to measure continuous, fine-grained velocity changes. These methods offer complementary benefits: video allows for rich qualitative characterization of actions, including verbalizations, but does not permit high temporal or spatial accuracy. Motion capture can detect movements with high spatial and temporal precision, but requires further processing to integrate data into discrete action types or bounded events. In any event, combination of methods allowed thorough detection and, when appropriate, removal of motion-related EEG activity. Notably, some previous studies that claimed to find observational mu suppression in infants did not control for infants' own motor activity during periods of putative action observation, so it is not actually known whether mu-suppression was due to the infant's own actions or to observation of another person's actions (e.g., Meyer et al., 2011; Reid et al., 2011).

Mu desynchronization in children

The current findings are consistent with findings from EEG and MEG studies of mu suppression in adults (Cochin et al., 1998; Pineda et al., 2000; Babiloni et al., 2002; Caetano et al., 2007; Kilner and Frith, 2008). Several prior studies (Southgate et al., 2009; Marshall et al., 2011; Saby et al., 2013) also reported mu-suppression in toddlers during action observation. The current study goes further not only by

employing a socially interactive paradigm and by precisely quantifying and controlling for toddlers' motor activity, but also by (1) locking toddlers' EEG to the onset and offset of their own or their mother's actions; (2) identifying mu suppression using multiple criteria including ERS, PSD, scalp maps and source locations; and (3) comparing EEG power profiles across a wide range of frequencies and channel locations. Some previous reports of mu suppression only examined power in the 6–9 Hz range (e.g., *Lepage and Théoret, 2006*), and/or examined only 1–2 channels. Yet without examining a broad frequency band and multiple channels, somatomotor mu suppression cannot be inferred – for example, desynchronization might be broad-band or broadly distributed (as in *Marshall et al., 2011*), and this cannot be ruled out when analysis is limited to a narrow frequency range or channel selection. Moreover, using channel-level analyses without unmixing non-cortical and cortical sources, as in all previous studies, permits only allows gross inferences about mu source locations. The current approach allowed us to identify and characterize IC sources in various cortical regions (e.g., parietal, occipital), and document differences between these sources and the sources of somatomotor mu suppression. Important, only the latter sources were selectively modulated by action execution or observation. These comparisons lend credence to the results, and should be standard practice in EEG studies of infants and children (see *Cuevas et al., 2014*, for related arguments).

The results showed, like previous studies (*Berchicci et al., 2011*), mu frequency peaks in toddlers of 7–9 Hz, slightly lower than in adults (8–13 Hz). The results also showed a small beta peak, a distinct feature of adult somatomotor mu activity that has not been investigated in toddlers (but see *van Elk et al., 2008*). Previous studies suggest that beta-modulation might be more related to action production (e.g., probability gating, or sensorimotor dynamics) than to observation of others' actions (*Jenkinson and Brown, 2011; Quandt et al., 2012*). Our finding that left somatomotor beta suppression was greater in execution than observation epochs is consistent with this hypothesis; however, results from the right cluster were equivocal. This therefore remains an open question.

These results are the first to localize mu-rhythm sources in toddlers to somatomotor cortex, potentially near the hand/arm homunculus in central sulcus. This reflects recent advances in signal analysis that allow considerably improved EEG source localization (*Buzsáki et al., 2012; Grech et al., 2008*). ICA decomposition can yield highly dipolar scalp maps of brain sources, with localization error medians as low as 4.1 mm if accurate head models and skull conductivity estimates are used (*Acar and Makeig, 2013*). By using age-specific head models and conductivity values, we found somatomotor mu-source locations consistent with those predicted by simultaneous fMRI–EEG studies of adults (*Pfurtscheller and Neuper, 1997; Ritter et al., 2009; Mizuhara, 2012*).

An unaddressed question is whether mu suppression in children is modulated by the similarity of an executed or observed action to a previously seen or performed action. However, mu power suppression was not affected by whether the current action matched (i.e., touched the same bubble) or mis-matched the previous action. A possible explanation is that matching and mismatching responses in the current task were all fairly similar, and each bubble was touched many times. Perhaps any effects of matching was 'washed out' by the repetition of this paradigm. It remains unknown how repetition and predictability of actions might influence mu power changes, and how this might change with age.

In sum, the results suggest that cortical sources that desynchronize during deliberate action execution or observation are adult-like in all known properties by 3 years of age. Of course, skilled control of action is still far from mature: preschoolers' deliberate actions are more variable, slower, less precise, and less inhibited than adults' (*Adolph and Berger, 2006*). Toddlers' perception and knowledge of human action is also immature (e.g., *Liao and Deák, 2011*). Thus, these results provide a benchmark for further research on the neurological resources that serve children's growing action control, and growing understanding of other people's actions.

Behavioral and brain dynamics of social interactions

Decision analyses showed that mothers' and toddlers' bubble choices formed a dynamically reciprocal system. The results therefore suggest that mu suppression is a measurable signature of toddlers' action processing during complex, reciprocal social interactions.

Most 'social neuroscience' studies use experimental paradigms with no social interaction. Often, participants watch videos but do not interact with real social partners (e.g., *Cochin et al., 1998; Caetano et al., 2007; Iacoboni, 2009*). Recent studies have begun to examine real-time brain activity during social interactions (*Makeig et al., 2002; Dumas et al., 2010, 2011; Konvalinka and Roepstorff, 2012*). However, observational mu suppression has been studied almost exclusively using disembodied, non-social stimuli. The current results show that mobile brain/body imaging (MoBI; *Makeig et al., 2009*) methods can capture this phenomenon during social interactions. This has implications for future studies of social development. Infants and young children spend most of their waking hours embedded in face-to-face social interactions. Their experiences are structured by other people, especially caregivers, who act as 'gatekeepers' for infants' social activities, and engage infants and toddlers in a widening variety of social interactions. Through these interactions, the developing brain is trained for several years in a daily immersive 'social boot camp'. To understand human social development, we must investigate how the developing brain responds to these social experiences. By studying brain activity in 'live' social interactions, we can learn how the capacity to participate in everyday social experiences develops.

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