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Mirror neuron activation as a function of explicit learning: changes in mu-event-related power after learning novel responses to ideomotor compatible, partially compatible, and non-compatible stimuli

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Abstract

Questions regarding the malleability of the mirror neuron system (MNS) continue to be debated. MNS activation has been reported when people observe another person performing biological goal-directed behaviors, such as grasping a cup. These findings support the importance of mapping goal-directed biological behavior onto one's motor repertoire as a means of understanding the actions of others. Still, other evidence supports the Associative Sequence Learning (ASL) model which predicts that the MNS responds to a variety of stimuli after sensorimotor learning, not simply biological behavior. MNS activity develops as a consequence of developing stimulus-response associations between a stimulus and its motor outcome. Findings from the ideomotor literature indicate that stimuli that are more ideomotor compatible with a response are accompanied by an increase in response activation compared to less compatible stimuli; however, non-compatible stimuli robustly activate a constituent response after sensorimotor learning. Here, we measured changes in the mu-rhythm, an EEG marker thought to index MNS activity, predicting that stimuli that differ along dimensions of ideomotor compatibility should show changes in mirror neuron activation as participants learn the respective stimulus-response associations. We observed robust mu-suppression for ideomotor-compatible hand actions and partially compatible dot animations prior to learning; however, compatible stimuli showed greater mu-suppression than partially or non-compatible stimuli after explicit learning. Additionally, non-compatible abstract stimuli exceeded baseline only after participants explicitly learned the motor responses associated with the stimuli. We conclude that the empirical differences between the biological and ASL accounts of the MNS can be explained by Ideomotor Theory.

Introduction

The mirror neuron system is a frontal-parietal cortical network that is active while observing goal-directed behaviors that are part of one's motor repertoire. Initially, neurons with mirror properties were observed in the F5 region and inferior parietal lobe of the macaque monkey when the monkey performed an action, such as grasping a piece of food, as well as when the monkey observed an experimenter or conspecific performing a similar, meaningful behavior (Fogassi *et al.*, 2005; Gallese *et al.*, 1996; Murata *et al.*, 1997; Rizzolatti *et al.*, 1996; Umilta *et al.*, 2001). PET and fMRI neuroimaging data revealed a human homolog to the monkey mirror system in Broca's area (inferior frontal gyrus, IFG) and the inferior parietal lobe (Grafton *et al.*, 1996; Grézes *et al.*, 1998; Iacoboni *et al.*, 1999; Grézes & Decety, 2001). Also, other neuroimaging techniques such as EEG (Electroencephalography; Altschuler *et al.*, 1997, 2000; Cochin *et al.*, 1999, 2001), MEG (Magnetoencephalography; Hari *et al.*, 1998), and rTMS/TMS (repetitive Transcranial Magnetic Stimulation; Fadiga *et al.*, 1995; Gangitano *et al.*, 2001; Maeda *et al.*, 2002) show mirror neuron activity in humans. Historically, investigations of the mirror neuron system have focused on action recognition of goal-directed biological behavior, assuming that mirror neurons have developed as a result of evolution in primates and humans to facilitate understanding of the intentions and meanings of others' actions (for a review, see Rizzolatti & Craighero, 2004). However, there is evidence to support an alternative account, the associative sequence learning model (ASL) which assumes that mirror neurons are nothing more than motor neurons that become responsive to specific stimulus-response associations through sensorimotor learning and experience over an organism's life span (see Heyes, 2010; Catmur, 2013). We suggest that these conflicting accounts can be reconciled by Ideomotor Theory, which

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assumes that the more perceptually similar (i.e., ideomotor compatible) a stimulus is with a response, the more strongly the response is activated (Brass *et al.*, 2000). Here, we provide empirical support that (i) mirror neurons can be activated by both ideomotor compatible and partially compatible stimuli prior to learning explicit stimulus-response associations, (ii) ideomotor non-compatible stimuli take on mirror-like properties after explicit learning, and (iii) even after learning, ideomotor-compatible stimuli activate the mirror system more robustly than non-compatible stimuli; however, the activation for ideomotor-compatible stimuli was no different than that for partially compatible stimuli.

The ASL model is supported by evidence suggesting that the mirror system is malleable in response to sensorimotor training and experience. For example, after explicit sensorimotor training, mirror neurons responded to observed, incompatible finger movements (Catmur *et al.*, 2007). Additionally, mirror neurons fired in response to abstract, non-biological stimuli associated with motor responses via sensorimotor learning (Behmer & Jantzen, 2011; Landmann *et al.*, 2011; Press *et al.*, 2012). These findings support ASL model predictions (Heyes, 2010), which assumes that mirror neurons develop as the result of forming a predictive relationship between an observed action and its goal outcome. More specifically, the ASL theory assumes that mirror neurons start off as regular motor neurons that weakly code for action observation and the more co-occurrences between a motor stimulus and a response, the more sensitive motor neurons become to the frequency of these stimulus-response pairings. As a result, these motor neurons that end up coding for a specific action and its outcome take on 'mirror-like' properties.

Interestingly, some studies showed that observing and/or imitating biological behavior activates the mirror neuron system more robustly than when observing or responding to an abstract stimulus (Iacoboni *et al.*, 1999; Heiser *et al.*, 2003). One possible explanation for these findings may be that the mirror system has a bias for biological goal-directed behavior because observers directly map the observed action onto an existing action that is a part of their motor repertoire (Rizzolatti & Craighero, 2004). Another explanation, offered by the ideomotor literature, is that stimuli that are ideomotor compatible with a response facilitate automatic response activation (e.g., Greenwald, 1972; Shin *et al.*, 2010). For example, Brass *et al.* (2000) showed that individuals were faster when responding to finger flexions as opposed to symbolic and spatial cues, as well as when responses were compatible vs. incompatible with the observed action. This suggests that responses that are ideomotor compatible between type and movement may be faster because such a sensorimotor transformation is easier to process (i.e., there are more features contained in the stimulus that map on to the actual response) when compared to responding to a stimulus that is only partially compatible, or non-compatible.

This study investigated how mirror neuron activity changes while learning response associations with stimuli that varied in ideomotor compatibility. We used EEG to measure changes in mu-event-related power over the motor cortex. EEG is well suited for investigating the mirror neuron system. First, suppression of mu-activity observed over the motor cortex is thought to be an EEG correlate of mirror neuron activity, reflecting downstream activation of the IFG (Pineda, 2005; however, see Vigneswaran *et al.*, 2013 regarding mirror neurons in the primary motor cortex). Second, a decrease in spectral power from baseline is interpreted as an increase in event-related cortical activity or arousal (ERD; also known as mu-suppression), whereas an increase in spectral power from baseline indicates a resting state or idling of cortical neural activity (ERS; Neuper *et al.*, 2006; Pfurtscheller & Lopes da Silva, 1999; Pfurtscheller *et al.*, 1996). Third, differences in EEG amplitude reflect increased brain activation (Babilonni *et al.*, 2009; Babilonni *et al.*, 2010; Grabner *et al.*, 2004; Neubauer *et al.*, 2005; Neubauer & Fink, 2009). Finally, dipole-fitting procedures can be used to fit individual components of motor activity over M1, minimizing the effects of volume conductivity associated with investigating electrodes in sensor space (Kavanagh *et al.*, 1978).

In this study, participants viewed three different types of stimuli (*Hands* executing a sequence of keypresses on button boxes, *Dot* animation sequence of keypresses on button boxes, and *Abstract* image of a colored pound sign and asterisk) across three sessions over 2 days. The *Hands* stimuli were ideomotor compatible in terms of both type (hands) and movement (up/down). The *Dot* stimuli were partially compatible in terms of movement (up/down). Finally, the *Abstract* stimuli were not ideomotor compatible (non-compatible). During the first and third sessions, participants observed the stimuli and did not execute any responses. During the second session, participants observed and responded to the stimuli. Below, we lay out the specific predictions, comparing changes in mu-event-related power in response to the *Hands*, *Dot*, and *Abstract* stimuli across and within sessions.

Predictions

Consistent with past research, we predict that mu-suppression during *Hands* should be greater than baseline for all three sessions because participants observed and/or responded to a biological goal-directed stimulus (Rizzolatti & Craighero, 2004), and because the *Hands* stimuli were ideomotor compatible for both type and movement (Greenwald, 1972; Brass *et al.*, 2000; Shin *et al.*, 2010). As a consequence, mu-suppression should be greater for *Hands* during the pre- and post-learning sessions compared the ideomotor non-compatible, *Abstract* stimuli.

The ideomotor (Jansson *et al.*, 2007) and mirror neuron literatures [Saygin *et al.*, 2004, 2010 (fMRI); Ulloa & Pineda, 2007 (EEG/mu-suppression)] predict that mu-suppression for the *Dot* stimuli should be greater than baseline across all three sessions, because participants should be able to easily infer the action goal for the *Dot* stimuli. Additionally, given that the *Hands* and *Dot* stimuli are identical in terms of movement, Ideomotor Theory predicts that there should be no difference between RTs and error rates for *Dot* and *Hands* during the learning/execution session.

Because the *Abstract* stimuli have no inherent motor associations, mu-event-related power should not exceed baseline levels during the pre-learning session. During the learning/execution session, mu-suppression should be greater than baseline, reflecting the normal increases in mu-suppression associated with motor planning and responding (Pfurtscheller & Lopes da Silva, 1999). Both ASL (Heyes, 2010) and ideomotor theories (Brass & Heyes, 2005) predict that after participants explicitly learn the responses to the *Abstract* stimuli, mu-suppression for *Abstract* should be greater during the post- compared to the pre-learning session. Finally, mu-event related power for the *Abstract Control* stimulus introduced during the post-learning session should not exceed baseline and should not differ from mu-power levels observed for the *Abstract* stimuli during the pre-learning session.

Methods

Participants

Sixteen undergraduates from Washington State University participated in the experiment over 2 days (eight females; 18–30 years old, $M = 20.4$, $SD = 3.5$). This study was approved by the Institutional Review Board, and participants received optional extra credit in their psychology courses. Participants were right-handed (Oldfield, 1971), had at least 20/40 visual acuity, and correctly identified the colors red and green on a Snellen chart.

Stimuli

Figure 1 shows an example of the two different events (Event A and Event B) for each of the four different stimuli. Event A was a 2000-ms video clip that was presented 3 × 4 inch box centered at 2° above a white fixation cross. Event B was a 50-ms video clip that was presented 3 × 4 inch box centered at 2° below a white fixation cross. All participants observed the *Hands, Dot,* and *Abstract* stimuli during Sessions 1, 2 and 3, and an additional *Abstract Control* stimulus during the post-learning session (session 3). The general paradigm was modified from a previous task (Stoet & Hommel, 1999). The four different stimuli are described below.

Hands

Event A

Video clips of the *Hands* stimuli were ideomotor compatible across type and movement. The video clips showed two hands resting above two keypads with the hands in the same orientation as the participants (see Fig. 1, *Hands* for Event A). Each keypad had three vertically oriented keys. The actor in the videos executed four different responses, each requiring three individual key presses. The index finger of the left hand pressed either the 'center, up, center' or 'center, down, center' keys on the left keypad, or the index finger of the right hand pressed either the 'center, up, center' or 'center, down, center' keys on the right keypad. The video clips were digitally edited so that the actor pressed the center key immediately after the onset of the video clip for 500 ms, followed by a second key press above or below the center key, for 500 ms and a third key press back to, and remaining at, the center key for 1000 ms.

Event B

The video clips contained the same keypads as the Event A video clips. The actor executed two rapid key presses on the center buttons of the left keypad with the left index finger or on the right keypad with the right index finger. The video clips were constructed using a picture of either the left or right index finger pressing the center key for 50 ms. Because the video clips for Event B were so short in duration, only the hand that executed the key presses were visible in the videos in order to ensure that the participants could determine which hand was being used to execute the key presses (See Fig. 1, *Hands* for Event B).

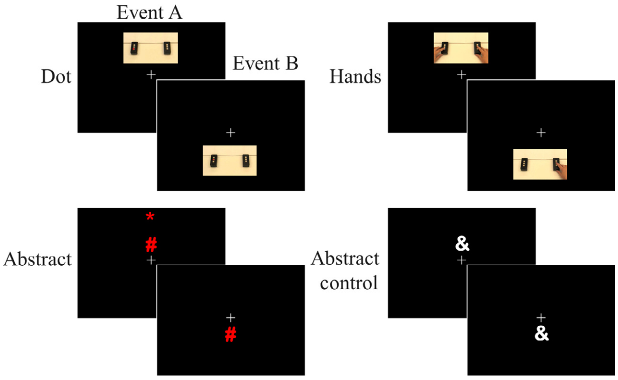

FIG. 1. Examples of stimuli used for Event A and Event B for the *Hands*, *Dot*, *Abstract*, and *Abstract, Control* stimuli.

Dot

Event A

Video clips of the *Dot* stimuli were ideomotor compatible for movement. The video clips used the same keypads from the *Hands* videos described above. A sequence of three red dots briefly appeared over the 'center, up, center' or 'center, down, center' keys on either the left or right keypad representing one of the same four possible sequences described in the *Hands* section above (see Fig. 1, *Dot* for Event A). No more than one red dot was displayed at a time, and dot sequences were presented exclusively on either the left or right keypads. The video clips were digitally edited so that the red dot appeared over the center key immediately at the onset of the video clip for 500 ms, followed by a second red dot over either the up or down key for 500 ms and a third red dot over the center key for 1000 ms.

Event B

The video clips used the same keypads as Event A. The video clips were constructed using a picture of the red dot on either the left or right center key for 50 ms. As with Event A, the Event B red dot was presented exclusively on either the left or right button box (see Fig. 1, *Dot* for Event B).

Abstract

Event A

Video clips of the *Abstract* stimuli were ideomotor-non-compatible. The video clips contained a static image of a green or red pound sign (#, 0.63° visual angle) with an asterisk (*,0.53° visual angle) located above or below the pound sign (0.74° visual angle; see Fig. 1, *Abstract* for Event A).

Event B

The video clips contained a static image of a red or green pound sign (0.67° visual angle; see Fig. 1, *Abstract* for Event B).

Abstract control (Session 3 only)

Event A

The video clips contained a static image of a white ampersand (&; 0.63° visual angle; see Fig. 1, *Abstract Control* for Event A).

Event B

The video clips contained a static image of a white ampersand identical to Event A (0.63° visual angle; see Fig. 1, *Abstract Control* for Event B).

Procedure

Participants completed the pre-learning and learning/execution sessions on the first day and the post-learning session on the following day. All instructions and stimuli were presented on a 17-inch computer screen. E-prime software (version 2.0) generated the stimuli for all three sessions and recorded the behavioral data during the learning/execution session.

The pre-learning session (Session 1)

After participants' handedness and visual acuity were assessed, they were fitted with an EEG cap and electrodes. Participants sat in front of the computer and were instructed to observe the different stimuli (*Hands, Dot*, and *Abstract*). Figure 2 (left panel) shows the trial order for the pre-learning session. To initiate each trial, participants pressed the space bar on a computer keyboard. The trial began with a fixation cross for 1250 ms, which served as a baseline for the EEG recordings. This was followed by the presentation of Event A for 2000 ms, the fixation cross for 1250 ms, and then the presentation of Event B for 50 ms. To prevent mu- activity from becoming entrained to the stimuli, a jitter screen ranging randomly between 1500 and 3000 ms was added after each trial. This was followed by the initiation screen for the next trial.

Participants viewed 12 blocks of 26 trials. Each stimulus (*Hands, Dot*, and *Abstract*) appeared in a random order, eight times within a block. Within each trial, Event A and B were always from the same stimuli. The four different Event A stimuli were equally paired with the two different Event B stimuli across trials within each block. To ensure that participants were paying attention to the stimuli, each block contained two catch trials. During the catch trials, participants were instructed to press the '1' key on the 10-key keypad when the initial fixation cross turned from white to blue. There were mandatory 30-s breaks after every third block, and participants were encouraged to take short breaks between trials if they felt fatigued. The pre-learning session required approximately 30–40 min to complete. After the pre-learning session, all participants took a 5-min break before starting the learning/execution session.

The learning/execution session (Session 2)

The apparatus and procedure were the same as the pre-learning session except for the following. Events A and B always required the participant to execute a sequence of key presses on the button boxes in response to the stimuli. Two keypads were placed on a table in front of the participants (6 cm in front of the computer screen and 10.5 cm from the table edge) with one keypad 11 cm to the left and the other 11 cm to the right of the participant's body midline. Each keypad had three vertically oriented keys (1 cm × 1 cm in size, separated by 0.2 cm), and were identical to the keypads used in the *Hands* and *Dot* videos. Participants rested their index fingers on the center keys, and pressed both center keys simultaneously to initiate each trial. The keypads recorded responses made with the index fingers. Left-hand responses were executed on the left keypad and right-hand responses on the right keypad.

During the instructions, participants learned how to execute the key presses associated with the stimuli they observed during the pre-learning session. During the *Hands* trials, participants were to imitate the movements observed in the video for Event A and Event B. For example, if participants observed an Event A sequence where the left hand was used to press the center, upper, and center buttons on the left keypad, participants imitated that same action on the left-side keypad in front of them. Additionally, if Event B consisted of two, center key responses with the right hand on the right keypad, participants responded by pressing the center key on the right-side keypad twice. During the *Dot* trials, participants were instructed to press the keys in the order corresponding to the dot movements in the video for Event A and Event B. For example, if participants observed an Event A sequence in which a red dot appeared on the center, lower and center buttons on the right keypad, participants responded by pressing the same buttons in the same order on the right-side keypad in front of them. Additionally, if the Event B video consisted of a red dot appearing on the center key on the right keypad, participants responded by rapidly pressing the center key on the right-side keypad twice. Finally, during Event A for the *Abstract* trials, the color of the pound sign (red or green) indicated the response hand (left or right respectively), and the asterisk (above or below the pound sign) indicated the initial movement direction of the index finger relative to the center key on the keypad. For example, a red pound sign with an asterisk above it required participants to use their right hand to execute a center, upper and center response on the right-side keypad. During Event B, participants pressed the left center key twice with their left hand in response to the red pound sign or the right center key twice with their right hand in response to the green pound sign.

The trial sequence for the learning/execution session (Session 2) is shown in Fig. 2 (right panel). Participants initiated each trial by simultaneously pressing the center left and right keys on the keypad. When Event A appeared, participants planned a response to Event A, and held that response in memory. When Event B occurred, participants executed their response to Event B quickly and accurately, and then recalled the response to Event A by executing the correct

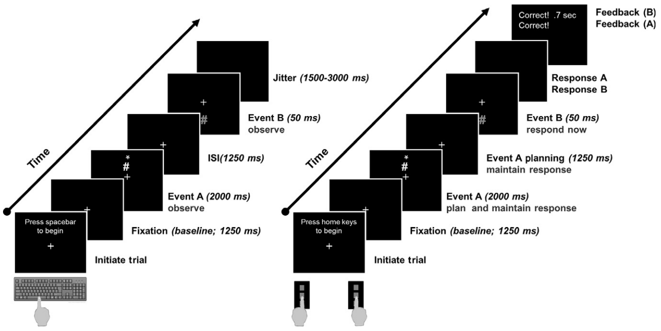

FIG. 2. Trial sequence. The left panel shows the trial sequence for Sessions 1 and 3. Participants observed the stimuli for Events A and B. The right panel shows the trial sequence for The learning/execution session. After observing Event A participants formed an action plan for Event A and maintained that action plan in memory. After observing Event B, participants responded to Event B as quickly and accurately as possible, and then executed the response to Event A held in memory. Participants received performance feedback at the end of each trial.

sequence of key presses for Event A on the keypad. Participants were instructed to emphasize accuracy, not speed, when executing the response corresponding to Event A. Following the response to Event A, feedback indicating Event B RT, Event B accuracy and Event A accuracy was presented together for 1450 ms.

Participants completed 12 blocks of 24 trials, which took approximately 30–40 min. Afterwards, participants were administered a questionnaire about strategies they employed while doing the task. At the conclusion of the learning/execution session, the EEG cap and electrodes were removed, and participants were instructed to get a good night's sleep and return the next day for the post-learning session at the scheduled time.

The post-learning session (Session 3)

Figure 2 (left panel) shows the trial sequence for the post-learning session, which was identical to the pre-learning session with the following exceptions. An additional *Abstract Control* stimulus was added which appeared in a random order, eight times within a block. Participants completed 12 blocks of 34 trials, including two catch trials that participants accurately identified 100% of the time. The post-learning session required 50–60 min to complete.

Electrophysiology measures

During all three sessions, EEG signals were continuously recorded from 32 Ag/AgCl active electrodes (Biosemi, Active Two), mounted in an elastic head-cap according to the 10–20 configuration. The Active Two system uses two separate electrodes in lieu of a ground, which form a feedback loop designed to decrease effective impedance with a factor of 100 at 50 Hz. Signals were conducted using a saline-based conductive gel (Signa Gel), and all offsets were maintained below 20 uV. Unreferenced signals were digitized at a sampling rate of 2048 Hz using Biosemi Active Two amplifiers and acquisition software.

Processing and visualization was accomplished using the EEGLab toolbox (v13.4.5b) and Matlab 7.8.0 software. Continuous data from each participant were downsampled to 256 Hz, before bandpass filtering at 1 Hz. In lieu of 50 Hz low-pass filtering, sinusoidal artifact was removed from each channel using the CleanLine plug in (Mullen, 2012), default setting of 2 Hz in each 4-s sliding window. EEG channels were rejected if activity was 3 *SD* larger than the mean of each channel. Data were referenced to the average potential of all electrodes. Prior to ICA, short epochs were extracted between −1000 and 2000 ms around the onset of each trial, stimulus presentation, and/or response for Sessions 1 and 2. Noisy epochs were automatically rejected based on extremely large fluctuations (a ±500 microV threshold limit) and improbable activity (6 SD per channel and 2 SD probability threshold for all channels with a 5% maximum number of trials being rejected per iteration). Additionally, trials where participants committed an error were removed from the learning/execution session. ICA was then performed using the remaining epochs (Delorme & Makeig, 2004).

The main epochs for analysis were extracted between −1500 and 5000 ms around the onset of each trial for each stimulus and session. Noisy epochs were rejected for final analysis using the same criteria described in the previous paragraph. ICA weights derived from the shorter epochs were imported into the larger epochs (see Grandchamp *et al.*, 2012 for using ICA weights across different sessions). Independent EEG components localized in EEGLAB were fitted to a single equivalent current dipole to the scalp potential using DIPFIT. The ICs were included in the analysis only if they were located within the brain and had <15% residual variance. This procedure resulted in the selection of an average of 13 components (±4) with a range between 6 and 19 components. A robust k-means clustering algorithm (MATLAB statistics toolbox) separated a total of 262 valid ICs into 22 clusters corresponding to the common neural sources for the participants. ICs more than 3 SD from any of the cluster centroids (19 ICs) were excluded from analysis as outliers (Onton & Makeig, 2006). When clusters contained more than one IC from an individual participant, the IC with the lowest residual variance was retained in the cluster. Three ICs were removed from the right motor cluster, and nine ICs were removed from the left motor cluster. The neural region represented by each dipole cluster was estimated by averaging the Talairach coordinates of the dipoles in the cluster.

Figure 3 shows the topographic plots and mean dipole locations for the right and left motor clusters for all three sessions identified using the k-means algorithm. Wavelet coefficients were estimated at 50 equally spaced frequencies from 3 to 128 Hz and 200 time points from a baseline of −1 s prior to the onset of each trial to 5.5 s using Gaussian tapered complex Morlet wavelets (Delorme & Makeig, 2004). Event-related spectral perturbations in power were computed in each frequency by normalizing the power spectral estimate in each frequency bin by the mean power level during the prestimulus baseline. A decrease in spectral power from baseline was interpreted as an increase in event-related cortical activity or arousal (ERD), and an increase in spectral power from baseline indicated a resting state of cortical neural activity (ERS).

Statistical analyses

Event-related power values in the left and right motor clusters were extracted in the 8–12 Hz frequency range. Analyses were limited to 13 of the 16 participants who showed an IC component over the left and right motor cortex in all three sessions (Grandchamp *et al.*, 2012). A preliminary ANOVA revealed no difference in mu-event-related power between the left and right motor clusters [$F_{1,12} = 0.41$, $MSE = 16.19$, $P = 0.55$, $\eta_p^2 = 0.08$]. Additionally, this was a bimanual task, mu-event-related power from the left and right clusters were collapsed together for analysis.

Results

EEG data

A 3 (Session: pre-learning, learning/execution, post-learning) × 3 (Stimuli: *Hands*, *Dot*, *Abstract*) × 2 (Interval: Event A, Event B) repeated-measures ANOVA was performed to assess changes in mu-event-related power as a function of learning for the different stimuli. There were main effects of Session [$F_{2,24} = 28.07$, $MSE = 5.10$, $P < 0.001$, $\eta_p^2 = 0.70$], Stimuli [$F_{2,24} = 4.32$, $MSE = 0.85$, $P = 0.04$, $\eta_p^2 = 0.26$], and Interval [$F_{1,12} = 70.49$, $MSE = 0.67$, $P < 0.001$, $\eta_p^2 = 0.85$]. There were also interactions for Session × Stimuli [$F_{4,48} = 5.11$, $MSE = 0.55$, $P < 0.008$, $\eta_p^2 = 0.30$], Session × Interval [$F_{2,24} = 57.46$, $MSE = 0.58$, $P < 0.001$, $\eta_p^2 = 0.83$], and Stimuli × Interval [$F_{2,24} = 5.88$, $MSE = 0.60$, $P = 0.02$, $\eta_p^2 = 0.33$]. The Session × Stimuli × Interval interaction was not significant [$F_{4,48} = 1.72$, $MSE = 0.25$, $P = 0.20$, $\eta_p^2 = 0.13$].

Figure 4 shows the changes in mu-power averaged across all participants. The top panel (panel A) displays the changes in mu-event-related power across sessions for the *Abstract*, *Hands*, and *Dot* stimuli, whereas the bottom panel (panel B) shows the changes for each stimuli across the pre-learning, learning/execution, and

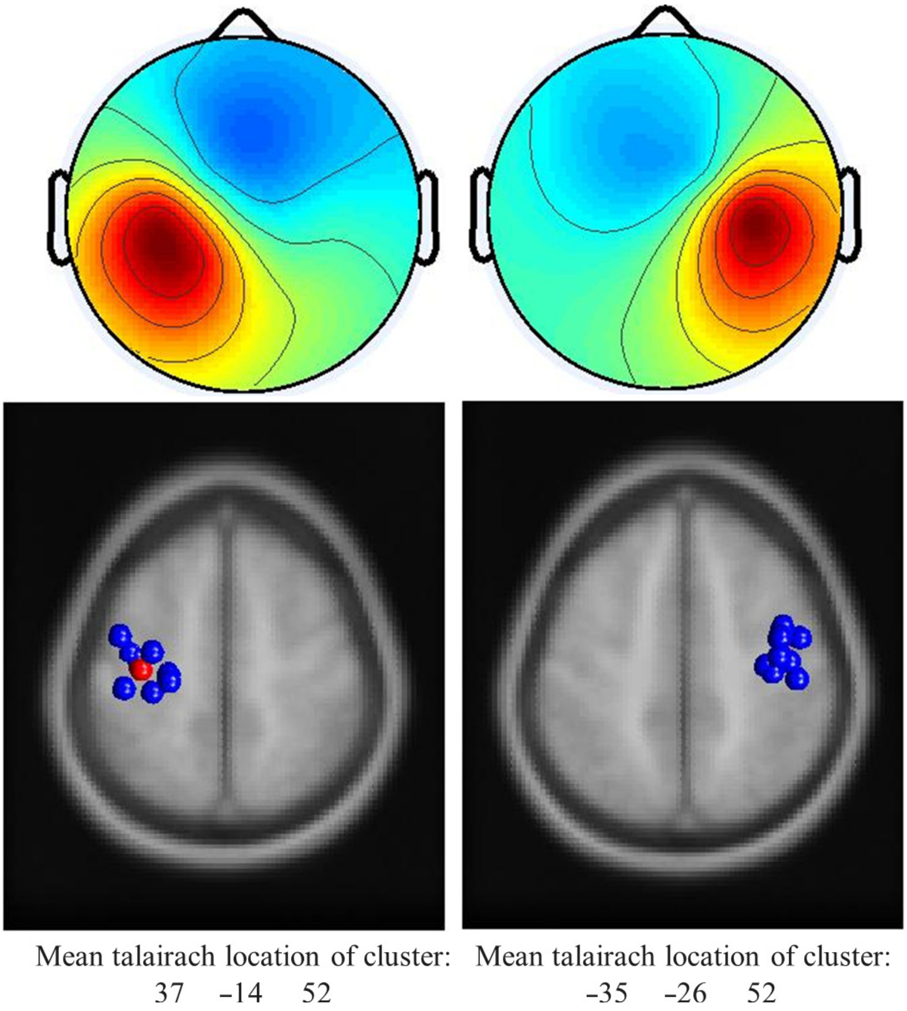

FIG. 3. Topographic plots and dipole location for the left and right motor clusters. Brain slices are from the standard BESA model. Mean talairach locations for each cluster are displayed below each dipole plot..

post-learning sessions. Planned comparisons were performed on the Session × Stimuli interaction, between and within sessions, for a total of 18 comparisons with pairwise corrected *t*-tests values of $P < 0.003$. Figure 5 shows the grand average, 95% confidence intervals, and grand averages for each participant during all sessions and stimuli. Figure 6 compares the difference waves and proportion of participants who showed an effect for all significant differences. A majority of participants showed an effect during the Event A and Event B intervals. Specifically, we observed mu-suppression for the *Abstract* stimuli during the learning/execution session ($M = -2.80$, $SE = 0.58$) which was greater than mu-power during pre-learning [$M = 0.29$, $SE = 0.33$, $t_{12} = 5.65$, $P < 0.001$] and mu-suppression during post-learning sessions [$M = -0.73$, $SE = 0.20$, $t_{12} = -4.02$, $P = 0.002$]. Most importantly, mu-suppression for the *Abstract* stimuli was greater in the post-learning session compared to baseline levels of mu-power for the pre-learning session [$t_{12} = 3.71$, $P = 0.003$]. Mu-suppression for the *Hands* stimuli during the learning/execution session [$M = -2.81$, $SE = 0.51$], was also greater than the pre-learning [$M = -0.50$, $SE = 0.25$, $t_{12} = 4.45$, $P < 0.001$] and post-learning sessions [$M = -1.10$, $SE = 0.20$, $t_{12} = -4.27$, $P < 0.001$]. However, mu-suppression for the *Hands* stimuli during the post-learning session compared to the pre-learning session was not significantly different [$t_{12} = 2.32$, $P = 0.04$]. A similar pattern was observed for the *Dot* stimuli. Mu-suppression for the *Dot* stimuli during the learning/execution session ($M = -2.99$, $SE = 0.40$) was greater than the pre-learning [$M = -0.72$, $SE = 0.32$, $t_{12} = 6.67$, $P < 0.001$] and post-learning sessions [$M = -0.62$, $SE = 0.22$, $t_{12} = -6.69$, $P < 0.001$]. However, mu-suppression for the *Dot* stimuli during the post-learning session compared to the pre-learning session was not significantly different [$t_{12} = -1.04$, $P = 0.32$].

There was no difference in mu-event related power between the *Dot* and *Abstract* stimuli [$t_{12} = -2.94$, $P = 0.01$] or between the *Dot* and *Hands* stimuli during the pre-learning session [$t_{12} = -0.11$, $P = 0.91$]; however, the difference between the *Abstract* and *Hands* stimuli was very close to significant [$t_{12} = 3.57$, $P = 0.004$]. Mu-suppression occurred only for *Dot* and *Hands*. During the learning/execution session, there was no difference in mu-event-related power between the *Dot* and *Abstract* stimuli [$t_{12} = -0.78$, $P = 0.45$] or between the *Dot* and *Hands* stimuli [$t_{12} = -0.03$, $P = 0.98$]. Additionally, there was no difference between the *Abstract* and *Hands* stimuli [$t_{12} = 0.83$, $P = 0.42$]. Mu-suppression was observed for all three stimuli. Finally, during the post-learning session, there was no difference in mu-event-related power between the *Dot* and *Abstract* stimuli [$t_{12} = 0.70$, $P = 0.50$] or between the *Dot* and *Hands* stimuli [$t_{12} = 2.38$, $P = 0.04$]. All three stimuli

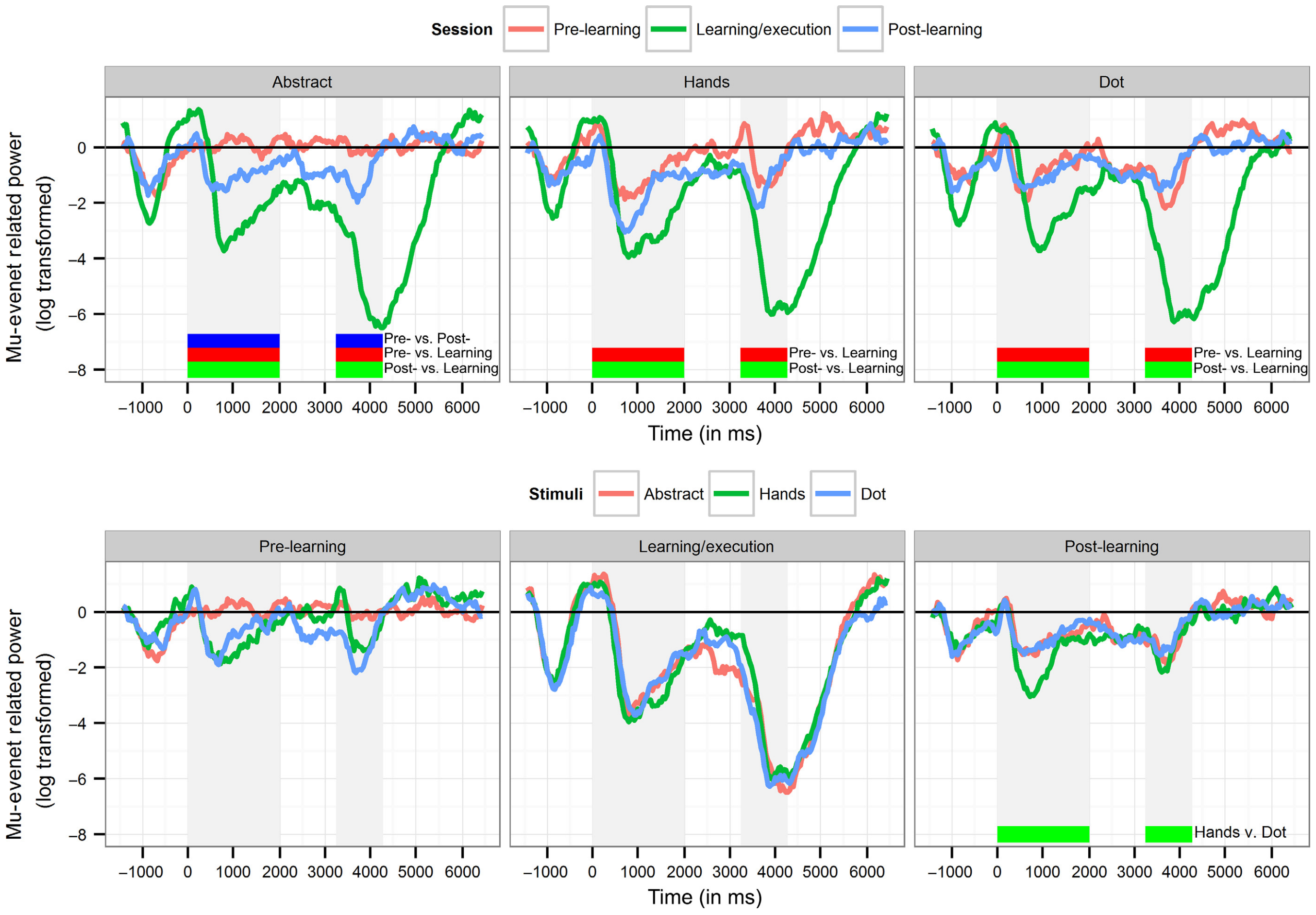

FIG. 4. Grand averaged time-frequency mu-power changes for left and right motor cortex clusters. Areas shaded in gray represent the collapsed epochs of interest for the Stimuli × Session interaction (0–2000 ms. Event A, 3250–4250 ms. Event B). The top panel displays changes in mu-power (y-axes) across time (x-axes) for each Stimulus across Sessions. For example, the “Abstract” panel shows the mu-grand average for all participants during the pre-learning (solid line), learning/execution (dashed line) and post-learning sessions (dot-dashed line). Shaded bars denote significance ($P < 0.003$). The bottom panel displays changes in mu-power (y-axes) across time (x-axes) for Sessions and Stimuli. For example, the ‘Pre-learning’ panel shows the mu-grand average for all participants for the Abstract (solid line), Hands (dashed line) and Dot stimuli (dot-dashed line). Shaded bars denote significance ($P < 0.003$).

showed mu-suppression; however, mu-suppression for the *Hands* stimuli was significantly greater than the *Abstract* stimuli [$t_{12} = 4.51$, $P < 0.001$].

Finally, a 3 (Stimuli: pre-learning *Abstract*, post-learning *Abstract*, *Abstract Control*) × 2 (Interval: Event A, Event B) ANOVA was performed to compare mu-event-related power changes between the *Abstract Control* stimuli introduced in the post-learning session with the *Abstract* stimuli from the pre- and post-learning sessions. There was a main effect of Stimuli [($F_{2,24} = 5.55$, $MSE = 1.43$, $P = 0.01$, $\eta_p^2 = 0.32$]. There was no main effect of Interval [$F_{1,12} = 1.03$, $MSE = 0.70$, $P = 0.33$, $\eta_p^2 = 0.08$] and no Stimuli × Interval interaction [$F_{2,24} = 0.32$, $MSE = 0.31$, $P = 0.065$, $\eta_p^2 = 0.03$]. Figure 7 (top panel) shows the changes in mu-power between the three stimuli. The bottom panel shows the grand average, 95% CI, and grand average for each participant for the *Abstract Control* stimuli. The *t*-tests (corrected at $P < 0.016$) revealed no difference in mu-power between *Abstract Control* ($M = 0.18$, SE = 0.22) and pre-learning *Abstract* ($t_{12} = 0.31$, $P = 0.75$). Mu-suppression was only present for the post-learning *Abstract* stimuli and was greater than the *Abstract Control* [$t_{12} = -2.72$, $P = 0.018$] and the pre-learning *Abstract* stimuli (as noted above).

Learning/execution session (Session 2), behavioral data

A series of one-way repeated-measures ANOVAS for Stimuli (*Hands*, *Dot*, *Abstract*) was performed on the behavioral data for Event A accuracy, Event B accuracy and Event B correct RT, to assess how well participants performed during the learning/execution session. RTs for Event B were analyzed only for correct Event B responses. In general, participants were very good at the task. There was no main effect of Stimuli for Event A accuracy. Participants were equally accurate when recalling the response to *Hands* ($M = 91.0\%$, SE = 0.01), *Dot* ($M = 92.2\%$, SE = 0.01), and *Abstract* stimuli ($M = 90.6\%$, SE = 0.01). However, there was a main effect of Stimuli for Event B accuracy [$F_{2,30} = 5.85$, $MSE = 0.01$, $P = 0.006$, $\eta_p^2 = 0.22$ and correct RT [$F_{2,30} = 4.52$, $MSE = 856.12$, $P = 0.017$, $\eta_p^2 = 0.18$]. Participants were less accurate when responding to Event B *Abstract* stimuli ($M = 98.7\%$, SE = 0.004) compared to the *Hands* ($M = 99.5\%$, SE = 0.002, $P = 0.005$) and *Dot* stimuli ($M = 99.8\%$, SE = 0.001, $P = 0.05$), although these differences were very small and accuracy was near ceiling. Overall, high accuracy rates when responding to both Event A and Event B suggest that participants successfully learned the motor responses to the stimuli. Additionally, participants were slower in executing correct

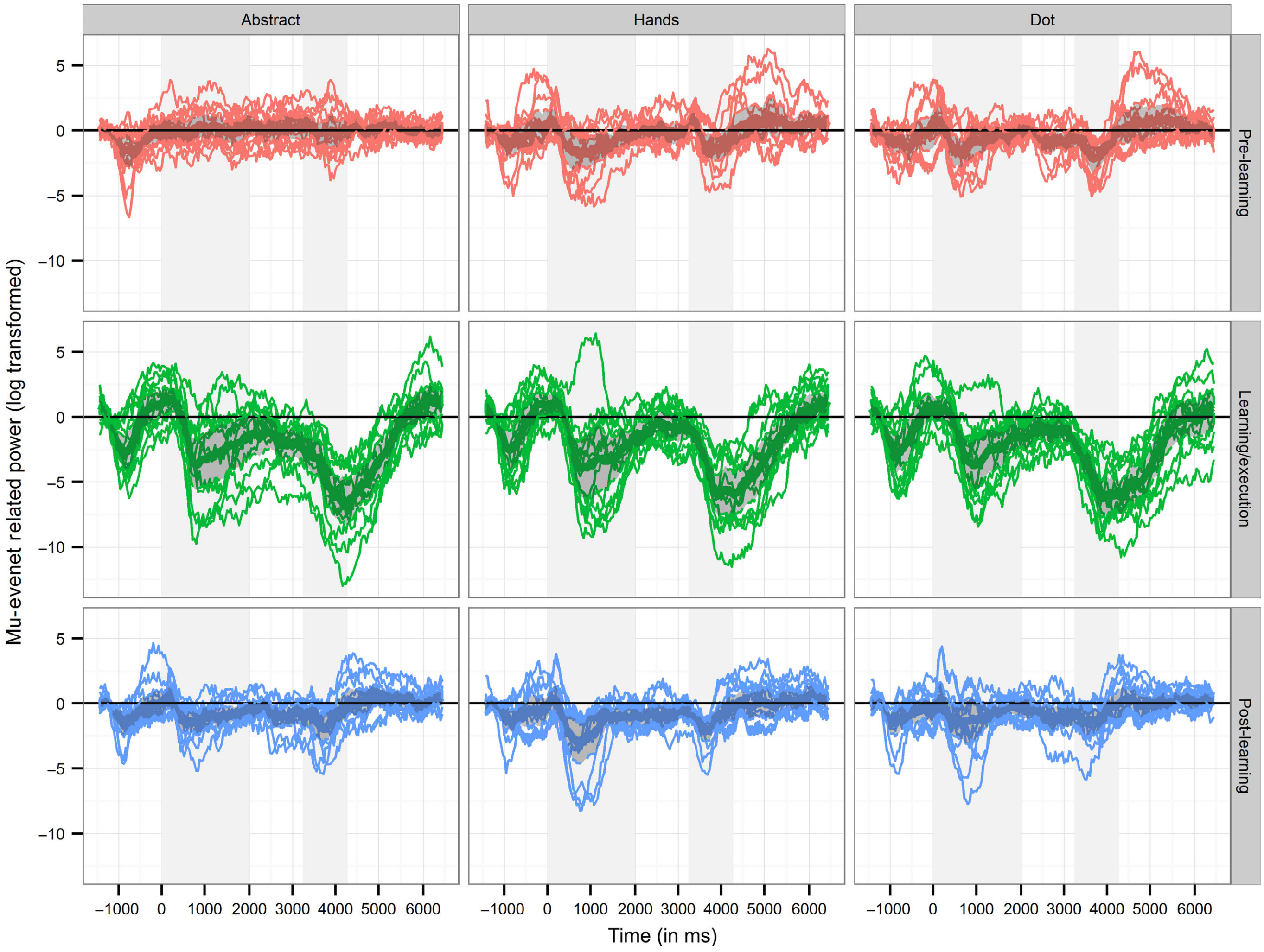

FIG. 5. mu-ERD grand average with 95% confidence intervals and grand averages for each participant superimposed. Each row shows the changes in mu-ERD for the Abstract, Hands, and Dot stimuli across the pre-learning (red), learning/execution (green) and Post-learning (blue) sessions. Areas shaded in gray represent the collapsed epochs of interest for the Stimuli × Session interaction (0–2000 ms. Event A, 3250–4250 ms. Event B). *Bold line* represents the grand average. Dark gray shaded area around the bold line represents 95% confidence intervals of the means displayed in Fig. 4. Each thin line represents the mu-ERD grand average for each participant.

responses to *Abstract* (*M* = 553 ms, SE = 23) compared to *Hands* stimuli (*M* = 526 ms, SE = 19; *P* = 0.016). However, the speed at executing correct responses were no different between *Dot* (*M* = 540 ms, SE = 18) and *Hands* (*P* = 0.10) or *Dot* and *Abstract* (*P* = 0.13) stimuli.

Discussion

The goal of this study was to determine if mirror neuron activity changes in response to ideomotor compatible, partially compatible, and non-compatible stimuli as a function of explicit learning. We found that the *Abstract* stimulus, which was ideomotor non-compatible, showed a large increase in mu-suppression after participants explicitly learned the stimulus-response associations. These findings are consistent with Associated Sequence Learning (ASL) and other theories, which predict that abstract stimuli that contain no inherent stimulus-response associations should activate the mirror system after explicit learning (Heyes, 2010). Additionally, after explicit learning, mu-suppression tended to be greater for ideomotor compatible stimuli (*Hands*) compared to partial (*Dot*) or non-compatible stimuli (*Abstract*). This is consistent with observations demonstrating a primacy in response activation for ideomotor compatible compared to non-compatible stimuli (Greenwald, 1972; Brass *et al.*, 2000; Shin *et al.*, 2010).

Changes in activation in response to the *Abstract* stimuli support one of the core theoretical principles of ASL – that the mirror system is malleable in response to sensorimotor experience. If the mirror system was only responsive to ideomotor compatible or partially compatible stimuli, then mu-suppression when viewing the *Abstract* stimuli should have occurred after the learning/execution session. A stimulus, such as a colored pound sign and asterisk, has no inherent stimulus-response associations. It was only after participants explicitly learned the motor responses during the learning/execution session that the stimuli took on any goal-directed motor response properties. The next day, when participants viewed the *Abstract* stimuli, we observed a significant change in mu-event-related power between the pre- and post-learning sessions. Additionally, we observed mu-suppression significantly greater than baseline for Abstract stimuli during the post-learning session, which we did not observe in the pre-learning session. Importantly, we introduced an

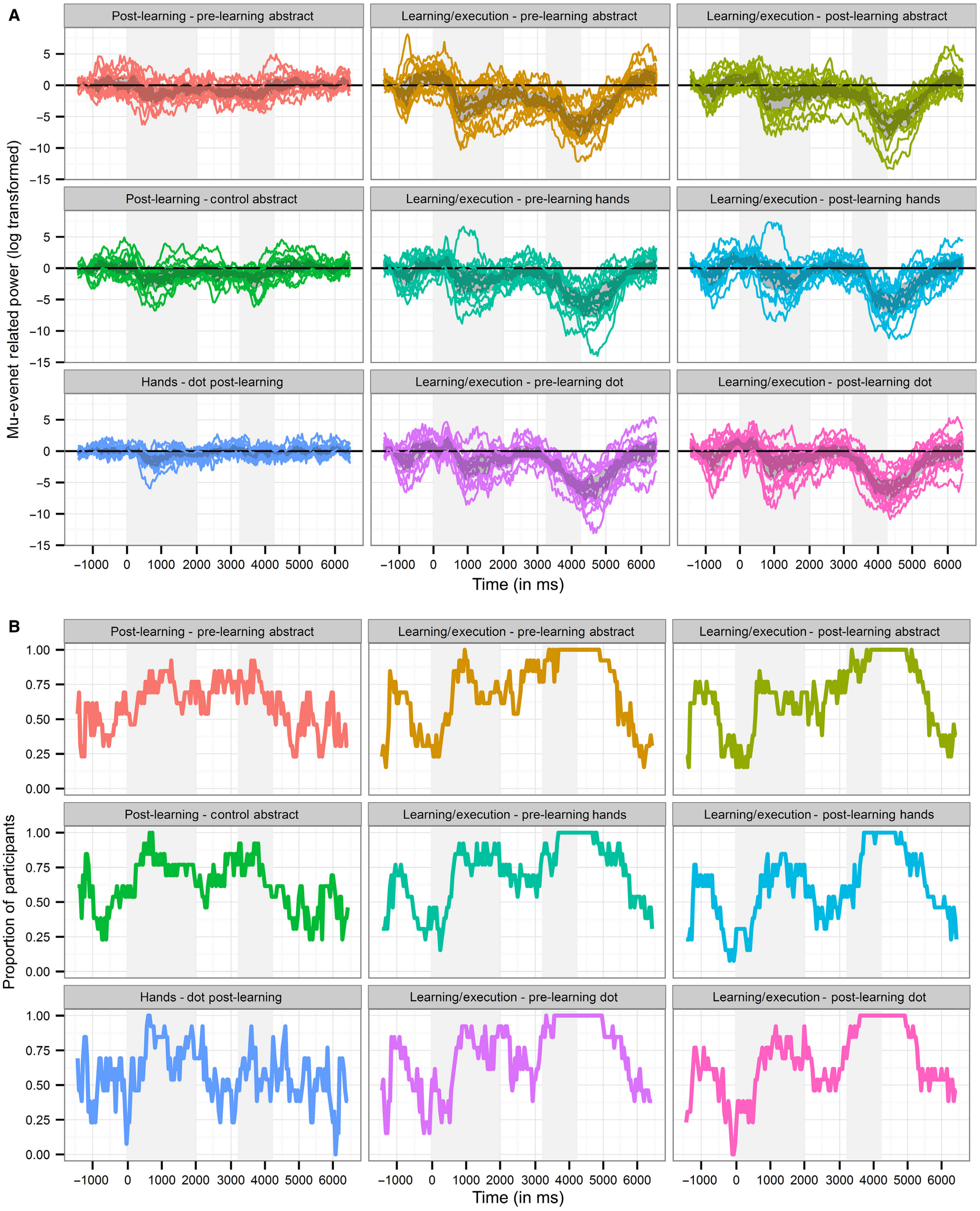

FIG. 6. Difference waves exploring the effect for significant comparisons and corresponding proportion of participants who showed an effect. Areas shaded in gray represent the collapsed epochs of interest for the Stimuli × Session interaction (0–2000 ms. Event A, 3250–4250 ms. Event B). *Bold line* is the grand average effect. Dark gray shaded area around the bold line represents 95% confidence intervals of the average difference for conditions showing a significant difference from Fig. 4. Each thin line represents the effect for each participant. Plots below each difference plot show the proportion of participants who showed an effect.

additional non-compatible abstract stimulus that our participants had no previous experience with during the post-learning session. Mu-event-related power for this new stimulus was no different than the baseline levels observed for *Abstract* during the pre-learning session. Our findings suggest that the mu-suppression observed for post-learning *Abstract* stimuli was a direct result of having learned goal-

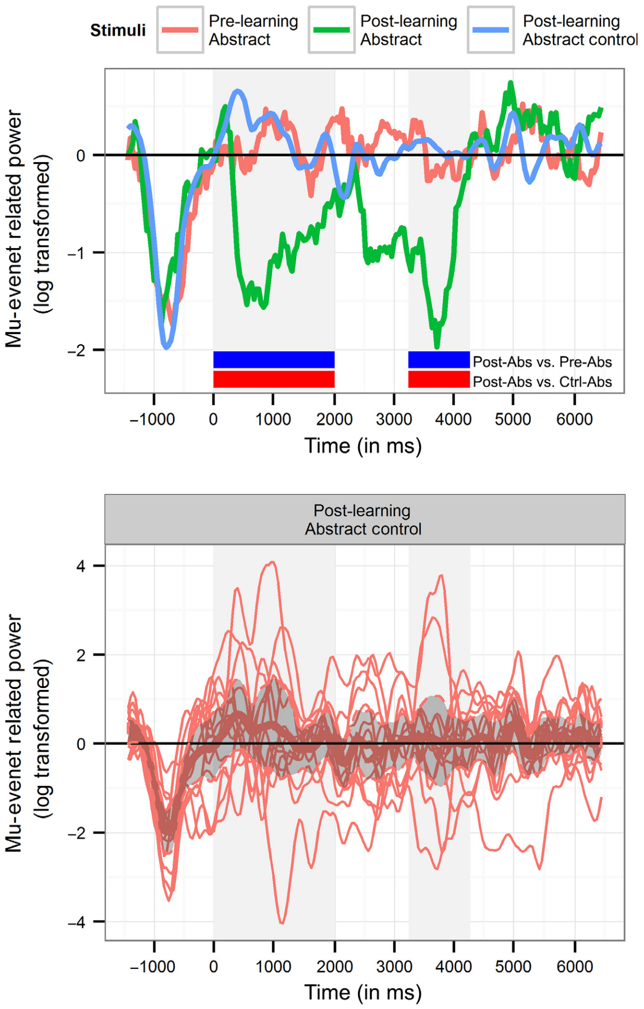

FIG. 7. Grand averages comparing Abstract Control with pre and post-learning Abstract mu-power. The top panel displays changes in mu-power (y-axes) across time (x-axes). The solid line shows changes for the Abstract stimuli during the pre-learning interval, the dashed lines shows changes for the Abstract stimuli during the post-learning interval, and the dot-dashed line shows changes for the Abstract Control stimuli during the post-learning interval. Shaded bars denote significance ($P < 0.003$). Areas shaded in gray represent the collapsed epochs of interest for the Stimuli × Session interaction (0–2000 ms. Event A, 3250–4250 ms. Event B). The bottom panel displays the grand average changes for Abstract Control with 95% confidence interval with grand averages for each participant superimposed. Bold line represents the grand average. Dark gray shaded area around the bold line represents 95% confidence intervals. Each thin line represents the mu-ERD grand average for each participant. See Fig. 5, for grand average, CI's, and individual results for per- and post-learning Abstract.

directed motor responses for those stimuli. Behavioral data from the learning/execution session clearly showed that participants performed well on the task. In addition, the robust levels of mu-suppression during the learning/execution session indicate that participants were engaged in the task. Taken together, these findings support the ASL model (Heyes, 2010) which assumes that the mirror system is not only malleable (Catmur *et al.*, 2007), but can also automatically respond to diverse stimuli once a stimulus-response association is learned and practiced.

Mu-suppression while viewing the *Hands* stimuli during the pre- and post-learning sessions is consistent with observations in the mirror neuron literature. Mu-suppression was robust during Event A and Event B when viewing the *Hands* stimuli. Several studies using mu-suppression as an indicator of mirror neuron activity have shown robust activity when participants observe others engaging in biological goal-directed behaviors such as grasping a cup or squeezing a manipulandum (Muthukumaraswamy *et al.*, 2004; Muthukumaraswamy & Singh, 2008).

When we compared differences in mu-event related power between the stimuli within sessions, mu-power between *Hands*, *Dot*, and *Abstract* were in some ways inconsistent with what was reported by Iacoboni *et al.* (1999) and Heiser *et al.* (2003). For example, Iacoboni and colleagues observed that mirror neuron activity was greater for biological (finger flexions) compared to abstract stimuli (static biological and abstract images) during imitation. Furthermore, they did not report any differences between biological and abstract stimuli during the condition when participants engaged only in passive viewing. We did not observe mu-suppression differences between the stimuli during the learning/execution session; however, we did observe that mu-suppression for *Hands* was greater than *Abstract*, but not *Dot*, during the pre- and post-learning sessions. One possible explanation for our inability to replicate Iacoboni *et al.* (1999) could be driven by the differences between their stimuli and ours. In the observation session for Iacoboni *et al.*, participants viewed a hand making a finger flexion, an image of a hand with an 'x' imposed over one of the fingers, and a gray box with an 'x' in the location where a finger should be. It is plausible that participants were able to reasonably infer a goal-directed outcome, even when they were not required to respond, between all three stimuli, which in turn led to the equal levels of activation that they observed during passive viewing. Prior to learning, our abstract stimuli of a color pound sign and asterisk (which always appeared in the same location) did not have any motor salience to convey any sort of response associations (even though it appeared in the same block as the *Hands* and *Dot* stimuli) in the way that Iacoboni and colleagues stimuli may have done (see also Jansson *et al.*, 2007). When participants were asked to respond to stimuli, Iacoboni and colleagues found increased mirror neuron activity for the biological compared to abstract conditions. Heiser *et al.* (2003) observed that rTMS lesions to the motor cortex while participants imitated the keypress responses led to significant performance deficits for the biological compared to the dot animation condition. In both cases, participants were asked to execute a sequence of fairly simple responses simultaneous with the stimulus presentation. Conversely, during the learning/execution session in our study, participants were instructed to execute sequences of complex responses, some of which had to be maintained in memory. It may be the case that these increased task demands modulated the mu-suppression that we observed in the learning/execution session. This is consistent with previous studies that observed changes in mu-suppression as a function of working memory ability. For example, in a novel motor learning task, Behmer & Fournier (2014) showed that mu-suppression was greater for low- compared to high-span individuals when they were forced to maintain a newly learned motor plan in working memory. Additionally, Derambure *et al.* (1993) reported that older adults showed increased mu-suppression compared to younger adults while planning a voluntary movement, presumably because the effort required greater cognitive resources in older compared to younger adults.

We found no difference between the pre- and post-learning sessions between *Hands* and *Dot*; however, mu-suppression was greater for *Hands* compared to *Abstract*. These findings are consistent with reports from the ideomotor literature (Greenwald, 1972; Brass *et al.*, 2000; Shin *et al.*, 2010). Ideomotor Theory suggests that the more compatible a stimulus is with the goal, the more activated the potential response should be. It is possible that since the *Hands* and *Dot* stimuli shared a compatible dimension (movement), participants were easily able to infer the action-goal associations between both stimuli. This further explains why Iacoboni *et al.* (1999) showed no differences between biological and abstract stimuli during passive observation, since all three of their stimuli were compatible for movement. Additionally, other labs have reported mirror neuron activation when participants observed point-light animations of goal-directed behavior (Saygin *et al.*, 2004, 2010; Ulloa & Pineda, 2007). In both cases, partially compatible stimuli were salient enough to trigger mirror neuron activation. Our findings provide further corroborative evidence that the mirror system may facilitate the ability to infer associations between compatible and partially compatible stimuli when those stimuli can be interpreted as a goal-directed biological behavior.

It was important that the abstract stimulus used in this study contained no inherent features that would allow participants to infer an association between the stimulus and an action. This allowed us to establish an initial baseline of activation during the pre-learning session, when participants were naïve to the motor goals for the *Abstract* stimuli, from which we could compare changes in activity across sessions after participants had explicitly learned the stimulus-response associations. Because mu-suppression for the *Abstract* stimuli was greater during the post-learning session compared to the pre-learning session, we can argue that these changes were a direct result of sensorimotor learning, and not a result of general motor activity related to the saliency of the stimuli. If we had instead used abstract stimuli that contained spatial cues allowing participants to infer motor goals, then we likely would have found an increase in mu-suppression for the *Abstract* stimuli in the pre-learning session similar to that reported by Iacoboni *et al.* (1999) when they placed an ‘x’ in a gray box where a finger should be. Our goal was not to test the capacity for participants to infer motor associations with different stimuli, but to measure how mu-suppression changes as a function of learning explicit responses during a novel motor-learning paradigm via experience. This allowed us to corroborate one of the critical predictions of ASL, which is that even abstract stimuli can take on mirror-like properties after explicitly learning the stimulus-response associations.

It is possible that task differences among the three sessions contributed to our results. In the pre- and post-learning sessions, participants passively observed the stimuli while responding to occasional catch trials. In the learning/execution session, participants were forced to explicitly learn and respond to the stimuli. The learning/execution session had significant task demands compared to the pre- and post-learning sessions. Our choice to use such a difficult paradigm was a conscious one. Previous research investigating mirror neuron activation in response to spatially abstract stimuli has yielded mixed results, with some studies showing increases in response to simple shapes and colored boxes (Landmann *et al.*, 2011; Press *et al.*, 2012) and others showing a primacy for biological goal-directed behavior (Iacoboni *et al.*, 1999; Heiser *et al.*, 2003). All of these studies required simple responses. It may be that tasks requiring less cognitive oversight are too simple to show any significant changes to mirror neuron activity. Regardless, it is important to remember that the most important comparison in this study is between the pre- and post-learning sessions. The inclusion of the learning/execution session was to simply demonstrate that our participants explicitly learned the stimulus-response associations in response to the different stimuli. We expected that prior to executing responses during the learning/execution session, mu-suppression would be high since participants were required to maintain a motor response in memory. Importantly, the fact that mu-event-related power is weaker in the pre- and post-learning sessions compared to the learning/execution session allowed us to rule out the possibility that the changes in the mu-band during those sessions were simply the result of motor planning.

In order to further investigate the hypothesis that a stimulus must have an association with a goal-directed motor response in order to active the MNS, we introduced a novel abstract stimulus in the post-learning session as an additional control. One possible explanation for the increase in mu-suppression for all three stimuli in the post-learning session could be explained by general motor expectations associated with the stimuli. If our findings in the post-learning session were simply driven by a general increase in motor activation in response to the stimuli, then we might have expected to see increased mu-suppression for all stimuli, including the new, *Abstract Control* stimulus. Instead, we observed that mu-event-related power for the *Abstract Control* stimuli was no different than that for the *Abstract* stimuli from the pre-learning session. Furthermore, we observed mu-suppression for the Abstract stimuli during the post-learning session which was greater than mu-power for the pre-learning session and *Abstract Control*. This suggests that sensorimotor learning, and not general motor activation, was responsible for the mu-changes for the *Abstract* stimuli between the pre- and post-learning sessions.

In summary, our data support the hypothesis that the mirror neuron system is not necessarily a circuit that is exclusively or even uniquely activated when simply observing goal-directed biological behavior that is part of one’s motor repertoire. Instead, we suggest that this same circuit may be active during sensorimotor learning, and that afterwards, simply observing the learned stimuli is enough to activate the mirror system. In support of ASL theory, we have demonstrated that an ideomotor non-compatible, abstract stimulus can activate the mirror neuron system once stimulus-response associations are learned, which further demonstrated that changes to mirror neuron activity can be modulated over time, through learning and experience (Catmur *et al.*, 2007; Heyes, 2010; Catmur, 2013). Additionally, we have demonstrated that both prior to and after learning, mirror neuron activity is greater for ideomotor compatible compared to non-compatible stimuli. This is consistent with previous findings which suggest that at least two separate mechanisms underlie ideomotor compatibility effects; one that involves movement type (e.g., index finger press), and one that involves movement direction (e.g., movement sequence across a set of keys; Brass *et al.*, 2000). As such, dot movement could be ideomotor compatible if an observer was required to move his finger in the movement sequence (direction) indicated by the dot. However, ideomotor compatibility would not be as strong as that for a biological stimulus. This is because a biological stimulus can represent both the movement type (index finger press) and direction of a response (movement sequence) – and hence provides a more complete representation of the response and its effects (i.e., means and end goal).

Acknowledgements

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