Short-term Motor Training, but Not Observational Training, Alters Neurocognitive Mechanisms of Action Processing in Infancy

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Abstract

■ The role of motor experience in the processing of perceived actions is hotly debated on both behavioral (e.g., action understanding) and neural (e.g., activation of the motor system) levels of interpretation. Whereas some researchers focus on the role of motor experience in the understanding of and motor activity associated with perceived actions, others emphasize the role of visual experience with the perceived actions. The question of whether prior firsthand motor experience is critical to motor system activation during perception of actions performed by others is best addressed through studies with infants who have a limited repertoire of motor actions. In this way, infants can receive motor or visual training with novel actions that are not mere recombinations of previously acquired actions.

In this study, 10-month-old infants received active training with a motorically unfamiliar action that resulted in a distinct sound effect. They received observational experience with a second, similarly unfamiliar action. Following training, we assessed infants' neural motor activity via EEG while they listened to the sounds associated with the actions relative to a novel sound. We found a greater decrease in mu power to sounds associated with the motorically learned action than to those associated with the observed action that the infants had never produced. This effect was directly related to individual differences in the degree of motor learning via motor training. These findings indicate a unique effect of active experience on neural correlates of action perception. ■

INTRODUCTION

Links between action and perception have been established across several species, throughout development, and via a variety of measures. Across these findings, the general notion is that action and perception of goal-directed actions are connected via shared neural representations and that this connection allows us to use our action experience to recognize and predict the goals of others' actions (Prinz, 1997). The identifying feature of these shared representations, the so-called mirror system, is that similar brain regions or neurons (as measured via fMRI, EEG, single cell recording, or other neuroimaging measures) are active when performing an action and perceiving the same action (or the sound or effect of that action; Kohler et al., 2002).

The Controversial Role of Expertise in Mirror System Activation

To understand the intricate relation between perception and action and differentiate the roles of motoric and visual experience, researchers are investigating the links between motor expertise, action perception, and activation of the motor system. One avenue of investigation that aims to parse out unique effects of motor experience, exemplified by Casile and Giese (2006), is to directly examine the role of motor experience on action perception, independent of any visual experience. In this experiment, participants were trained to perform a novel movement while blindfolded. Their accuracy in identifying this movement via visually presented point light displays improved after motor training despite a lack of visual information during training. Interestingly, individual differences in visual recognition performance strongly correlated with participants' accurate performance of the newly learned action during blindfolded training.

Similar effects of experience on brain activation over motor regions further corroborate the behavioral effects of motor training. For example, Calvo-Merino, Grèzes, Glaser, Passingham, and Haggard (2006) measured brain activation during the observation of dance moves professional dancers had previously performed relative to moves with which they had visual familiarity but no motor experience (i.e., moves produced by a dance partner of the opposite gender). They found increased premotor, parietal, and cerebellar activity for those actions within the dancers' own motor repertoires relative to the visually, but not motorically, familiar actions. Cross, Hamilton, and Grafton (2006) further showed that training

dancers to perform novel dance moves increased premotor activity when viewing the trained, but not untrained, actions. Similar effects of expertise on motor activation and activation of larger mentalizing brain networks have been found for chopstick use (Järveläinen, Schuermann, & Hari, 2004), handwriting (Quandt, Marshall, Bouquet, Young, & Shipley, 2011), sports (Kim et al., 2011; Aglioti, Cesari, Romani, & Urgesi, 2008), and music (Bangert et al., 2006).

In contrast to the evidenced differences between motor experts and nonexperts in motor activation across domains, other research indicates comparable or increased motor activity to motorically unfamiliar actions. For example, in a follow-up to the Cross et al. (2006) study, the researchers compared physical and observational learning of dance moves and found increased activity in premotor and parietal regions for both types of actions (relative to actions not performed/watched, Cross et al., 2006; see also Cross et al., 2012; Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009). Thus, the current state of the adult literature on experience is inconclusive. Development provides a unique window in which to look at effects of experience on neural activation of the motor system because infants have a more limited repertoire of experience on which to draw. Furthermore, intervening in early development allows one to manipulate the timing of naturally emerging motor actions and study the direct effects of this manipulation.

A Developmental Perspective on Active Experience

Both behavioral and neuroimaging studies have been conducted with infants in the first 2 years of life to examine the role of active experience on action perception. In intervention studies, infants are trained to perform novel actions, and their recognition of the goal of these actions is then assessed. For instance, 3-month-old infants who were trained to perform reaching actions (using Velcro mittens), but not untrained infants, recognized the goal of a reaching action (Sommerville, Woodward, & Needham, 2005). Importantly, several studies have now contrasted active with observational experience. When 3-month-old infants were given active versus observational training with reaching actions, only those who received active experience benefited from training (Gerson & Woodward, 2014a, 2014b). Similarly, 10-month-old infants benefited from active, but not observational, training with cane-pulling actions (similar to cloth-pulling; Sommerville, Hildebrand, & Crane, 2008). Investigating the role of motor, relative to visual, experience is crucial for understanding the role that the motor system plays in action perception.

Other researchers have focused on neural measures to assess effects of active experience on the motor regions of the infant brain. The most common assessment of motor activity in the infant brain is the measure of the so-called "mu rhythm," measured via EEG. In both infants and adults, reduced power (relative to a baseline condition) in the alpha frequency bands (approximately 8–12 Hz in adults and 6–9 Hz in infants; Marshall, Bar-Haim, & Fox, 2002) has been found over motor regions of the brain (central and frontocentral electrodes) both when individuals perform and observe goal-directed actions (Cuevas, Cannon, Yoo, & Fox, 2014; Marshall & Meltzoff, 2011, 2014; Vanderwert, Fox, & Ferrari, 2013). Using this measure, some studies reveal striking parallels to the neuroimaging research on expertise in adults and the behavioral evidence in infancy. For example, Paulus, Hunnius, van Elk, and Bekkering (2012) found motor activity in 8-month-olds during perception of sounds associated with previously learned actions but not sounds associated with objects on which infants did not act during a training phase (see also Lloyd-Fox, Wu, Richards, Elwell, & Johnson, 2013; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). This research, however, examined actions with which infants already had previous experience and did not assess whether newly acquired actions led to similar effects in the motor system.

Furthermore, as with adults, data concerning the role of experience in infancy are not all consistent. In a recent study by Southgate and Begus (2013), there was no difference between motor activation during the observation of executable and nonexecutable actions (e.g., movement of objects by a claw) in 9-month-olds. In a follow-up to the Paulus study (Paulus, Hunnius, & Bekkering, 2013), infants saw their parents shake a rattle that made a novel sound. These infants later showed motor activity to the sounds associated with the observed action. In this study, however, the observed action was one that infants were capable of producing before the training study. Thus, it is still unknown whether such mapping via observation would occur with motorically unfamiliar actions.

In summary, the question of whether active experience is crucial to processes underlying action perception is still open. In this experiment, we examine the possibility that a close link between action production and perception early in development can be built upon with greater experience. According to this proposal, given that rattle shaking in the Paulus et al. (2013) study was within the motor repertoire of these infants, the subsequent motor activation to the sound associated with the observed shaking could be a function of the infant mirroring the shaking action during training. Rather than relying on assumptions of previous action experience, we created new experiences with a novel action and assessed the effects of this experience on neural responses to action perception. To do so, we manipulated young infants' experience with unfamiliar actions and measured the effects of motor versus observational learning of novel actions on the motor system. This training manipulation closely matches those used in behavioral research with infants that have found unique effects of active, above and beyond, observational experience (Gerson & Woodward, 2014a, 2014b; Sommerville et al., 2008). Incorporating an

Figure 1. (A) An infant learning to perform a new action at home: hitting a toy with a stick. (B) An infant observing her dad perform a new action at home: pulling a duck with a cane.
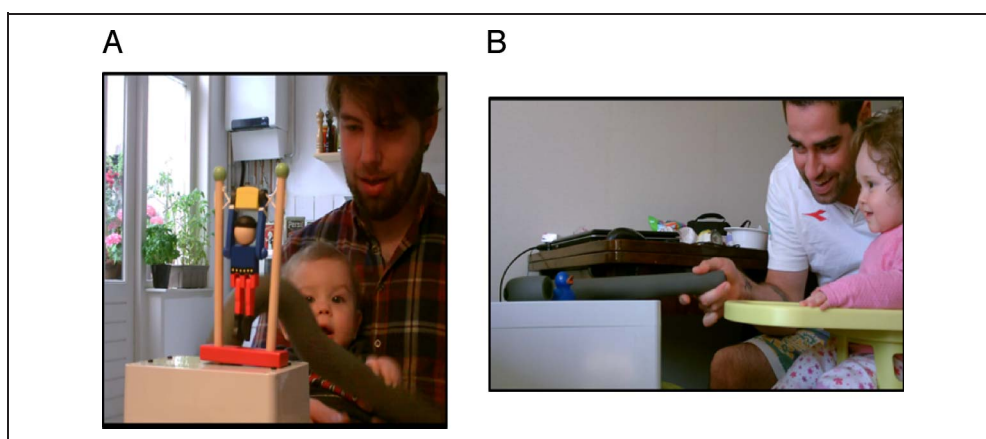
interventional training design with neural measures allows us, for the first time, to examine causal claims about the effects of active versus observational experience on action perception links on a neural level and test the assumption that active experience is critical to motor activity during action perception early in development. We expected more motor activity to sounds associated with actively learned actions than observed actions that the infants had never produced (Hunnius & Bekkering, 2014; Woodward & Gerson, 2014; Elsner & Hommel, 2001). Furthermore, we hypothesized that those infants who were better able to perform the learned action at the end of training would have a more precise motor representation of the action and thus show greater motor activity to the sound associated with the learned action.

METHODS

Participants

Twenty-six infants were scheduled based on previous research, and 17 infants were included in the final sample for this study. Nine infants began the study but were not included in final analyses because of not returning for the EEG session after training ($n = 1$) or not sitting through at least nine trials of each condition before movement and artifact rejection ($n = 8$). No infants were excluded from final analyses because of outlying data points. As suggested in recent reviews (Cuevas et al., 2014), we also examined whether data were similar when we removed outliers from analyses. After calculating the event-related desynchronization (ERD; the relative decrease in power to the event versus baseline, as described in the Results section below), any infant who had an ERD greater than three standard deviations above the mean at any site and in any condition. This excluded four infants, and we saw the same pattern of results (active ERD lower than observational ERD). The final data set of infants ranged in age from 9 months 16 days to 10 months 16 days at the pretraining session (mean age = 10 months, 0 days). Research was approved by the local ethics board.

Materials and Procedure

Infants' participation in this study consisted of three phases: a pretraining behavioral session, behavioral training sessions at home, and a posttraining EEG session. In each of these sessions, the same two toys were used during the behavioral portion (see Figure 1). Both toys afforded means-end actions that resulted in a unique sound effect (a series of tones that lasted approximately 2 sec). One toy had a wooden puppet atop a rectangular box ($10.5 \times 10.5 \times 17$ cm). When the box was hit with a staff-like tool (approximately 34 cm long), the puppet spun around and a sound was played. The second toy was a rectangular box ($31 \times 25 \times 11.5$ cm) with an indentation at the front. When a cane-like tool (approximately 40 cm) was used to pull a toy duck into the indentation, a sound was played. The particular sound associated with each toy was counterbalanced across infants. The toy on which the infant performed versus observed an action was also counterbalanced.

Pretraining Session

In the first session, infants observed the experimenter perform the appropriate means-end action on one of the two above-described toys (and heard the associated sound). After the experimenter performed the action, she asked the parent to perform the action and made sure the parent was demonstrating the action in a similar fashion (e.g., drawing the infant's attention to the toy during the action and during the playing of the sound, if necessary). The infant was then taught to perform the action on the other toy. The action was demonstrated for the infant, and the infant was encouraged to attempt the action himself or herself. If the infant did not act, the experimenter encouraged the parent to help move the child's hand toward the tool and coach them through the action in scaffolded steps. After training, the child and the parent on each of the two actions, the experimenter gave the parent a schedule for training throughout the following week. The experimenter also helped

the parent learn how to use the camera that they would take home to record home training sessions.

Training Sessions

Parents were asked to have their child perform the trained action every alternate day for approximately 5 min each day between the pretraining and posttraining sessions. On the alternate days, the parent demonstrated the other action for the child. As during the pretraining session, parents were told to draw their infant's attention to the action when observing and to help their child if necessary when performing. Parents were asked to record all sessions so that coding of activity could be assessed offline via digital video. Coding of these videos indicated that parents typically practiced each action approximately three times between the pretraining and posttraining session (range = 3–5). The average length of each training session was longer ($p = .02$) for the active training sessions (5:21 min) than for the observational training sessions (4:15 min). Despite the difference in length, infants viewed, on average, more successful actions per session ($p < .001$) during the observational training sessions ($M = 16.18$) than the active training sessions ($M = 9.64$).

Posttraining Session

Posttraining sessions occurred between 6 and 11 days (mean intersession length was 7.41 days) following the pretraining session. Infants were first familiarized with the room and the experimenters and then fitted with a 32 active electrode infant-sized EEG cap (Brain Products, Munich, Germany). Infants then sat on their parent's lap in a shielded room in front of a monitor that displayed abstract pictures that were randomly changed every 1600 to 5000 msec (jittered timing between picture presentation). Pictures were an attempt to maintain infants' attention and were unrelated to the test stimuli. Audio stimuli were played from a central speaker every 2600 to 5000 msec (jittered presentation time and unrelated to of the presentation of the pictures). Each audio stimulus lasted 2000 msec and consisted of three different sounds: the sound associated with the performed action during training (which differed between infants because of counterbalancing), the sound associated with the observed action, and a novel sound. The order of sound presentation was pseudorandomized, with the constraint that each sound was always repeated twice (and never more than twice in a row). Each sound was presented 20 times throughout the session. Following the picture and sound presentation, infants had the opportunity to perform each of the two actions (while EEG was recorded). Infants first performed the action they had practiced at home and then the action they had only previously observed.

Coding and Analysis

Coding and Exclusion of Movement

Each video was coded offline for infant movement. No sound was played during coding so that the coder was blind to the condition of trials that were identified as consisting of movement. All movements were coded and identified as gross movement (e.g., turning toward the parent), fine movement (e.g., moving one finger), or movement that resembled grasping. For final analyses, all trials with movement were removed. On average, 37 of the 60 possible trials were removed per infant due to movement ($SD = 8.53$, range = 22–50).

Coding of Actions

At the end of the EEG session, all infants had the chance to perform each of the two actions. EEG collection was continuous throughout this portion. Five randomly selected segments of the EEG data collected during infants' action performance (for each infant) were used to identify the frequency bands used in our analyses (see below). We presented them with the object on which they had received active training first and then presented them with the object they had previously only observed. A trained coder then assessed, for each infant, his or her actions on each object. The videos were clipped and presented in random order so the coder was blind to the infant's experience with each object. The coder counted the number of times each action was successfully produced and whether the child produced the action successfully on his or her own or did so with the help of the parent or experimenter. Infants were assigned a score based on their actions on each object: Never Performed Alone (if they only ever performed the action with help or never performed the action at all) or Performed Alone (if they ever performed the action without help from the parent or experimenter). The scores were ordinal such that any infant who both performed the action with a parent and on their own was scored as Performed Alone. For actions on the actively learned object, nine infants were in the Never Performed Alone group and eight infants were in the Performed Alone group. For actions on the observed object, 11 infants were in the Never Performed Alone group and 6 were in the Performed Alone group.
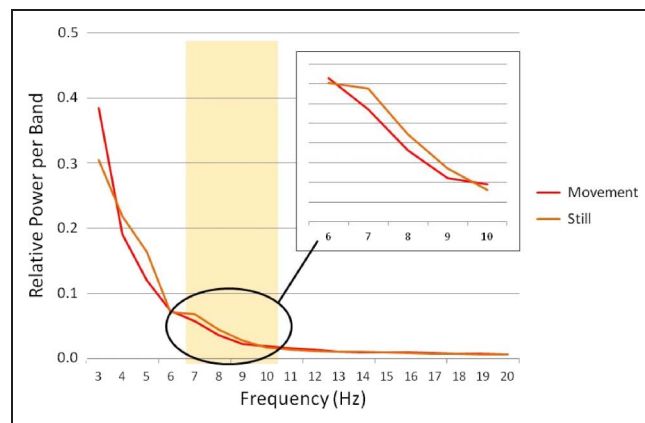
EEG Analysis

Thirty-two active electrodes were arranged in the 10–20 system and referenced online to FCz. The signal was amplified using a 32-channel BrainAmp DC EEG amplifier, band-pass filtered (0.1–125 Hz), and digitized at 500 Hz. We kept impedances below 60 kΩ. We analyzed the data using FieldTrip, an open source Matlab (version 7.0, TheMathWorks, Inc., Natick, MA) toolbox developed at

the Donders Institute for Brain, Cognition and Behaviour (www.ru.nl/neuroimaging/fieldtrip). Trials were identified by the onset of each sound and lasted for the length of the sound (i.e., about 2 sec). Trials during which infant movement was coded were excluded from further analyses. We then visually inspected the remaining trials to exclude EEG artifacts such as noisy channels. On average, approximately nine trials (range = 3–20) remained for each condition for each participant after movement and artifact rejection. The number of trials analyzed did not differ between conditions. When including only those infants who had six or more trials per condition (approximately 100/170 data points), results remained consistent (i.e., a significant effect of condition remained, $p = .05$). A bandpass filter was used with a frequency range of 1–30 Hz. A fast Fourier transform was then conducted using a multitaper method with a Hanning taper and a 2-Hz smoothing box to determine spectral power estimates for each condition from 1 to 30 Hz.

RESULTS

To verify that the mu rhythm was in the 6–9 Hz range for our sample (as suggested by previous research; Cuevas et al., 2014; Marshall & Meltzoff, 2011), we compared power values across the 3–30 Hz range during periods of infant movement (i.e., when infants performed the actions at the end of the EEG session) relative to periods that were free of movement (i.e., collapsing across conditions to include all trials of sound presentation that were not removed because of movement). Mu rhythm has been defined as the frequency bands that are suppressed during movement relative to nonmovement over motor regions. To account for variability in power ranges across infants, a proportional score was used to calculate relative power per band from 2 to 30 Hz: (power in each 1 Hz band) / (average power across 2–30 Hz bands). As expected, a decrease in power for the move-
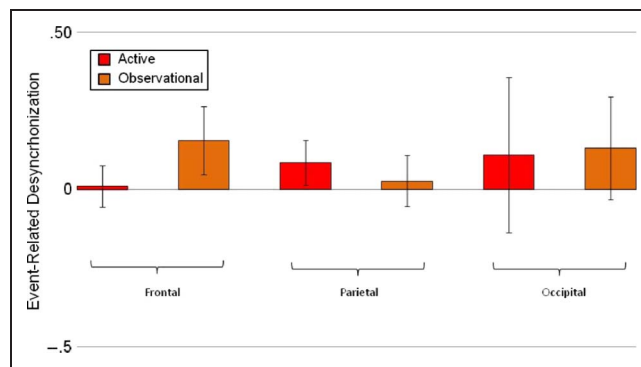
Figure 3. ERD (in frontocentral electrodes) to active and observational sounds was not significantly different in frontal, parietal, or occipital regions. ERD is defined as (event-related power − baseline power) / (baseline power) with power (6–9 Hz) during presentation of the novel sound serving as baseline (outliers excluded; error bars represent standard errors).

ment, relative to the still, phases of the experiment in the 6–9 Hz range, confirmed our choice of frequency bands for analyses (see Figure 2).

ERD was defined as (event-related power − baseline power) / (baseline power) with power during presentation of the novel sound serving as baseline (Vanderwert et al., 2013; Pfurtscheller, 2003). On the basis of previous research (Marshall & Meltzoff, 2011), mu power was calculated as power in the 6–9 Hz frequency range over frontocentral sites (C3, C4, Cz, FC1, and FC2). ERD was calculated separately for time-locked to sounds associated with performed actions and sounds associated with observed actions. A generalized linear model (GLM) with ERD as the dependent variable and Condition (performed or observed), Region (C or FC), and Site (1/3 [i.e., FC1 or C3], 2/4 [i.e., FC2 or C4], z [i.e., Cz]) as within-subject factors revealed a main effect of condition, $F(1, 152) = 6.20, p = .014, \eta_p^2 = .039$, and no other main effects or interactions. The difference between conditions was a function of a lower ERD in the performed than the observed condition.

Identical GLM analyses that replaced frontal, parietal, and occipital regions with the central and frontocentral regions in the above-described GLM (e.g., ERD as the dependent variable, Condition [performed or observed] and Site [3, 4, z] as within-subject factors for frontal sites) revealed no significant differences between conditions, $ps > .30$; $\eta_p^2 \leq .01$, indicating that the effect was localized to frontocentral sites (see Figure 3; note: when outliers were excluded for these other regions, the results remained the same).

In an additional GLM (with Site and Region as within-subject factors), raw power data (i.e., not ERD corrected for baseline, so that activation to the novel sound, previously baseline, could be compared directly with activation to the other sounds) was compared between the sound associated with the performed and observed action versus the novel sound. A significant decrease in

Figure 2. Relative power values as a function of frequency (Hz) depicted for still periods (collapsed across conditions) and execution of actions. The yellow shaded area illustrates the alpha-frequency range.

Figure 4. Raw power to active and observational sounds collapsed across all participants (A) and split by infants' ability to perform the actively learned actions (B) (error bars represent standard errors, *p < .05).
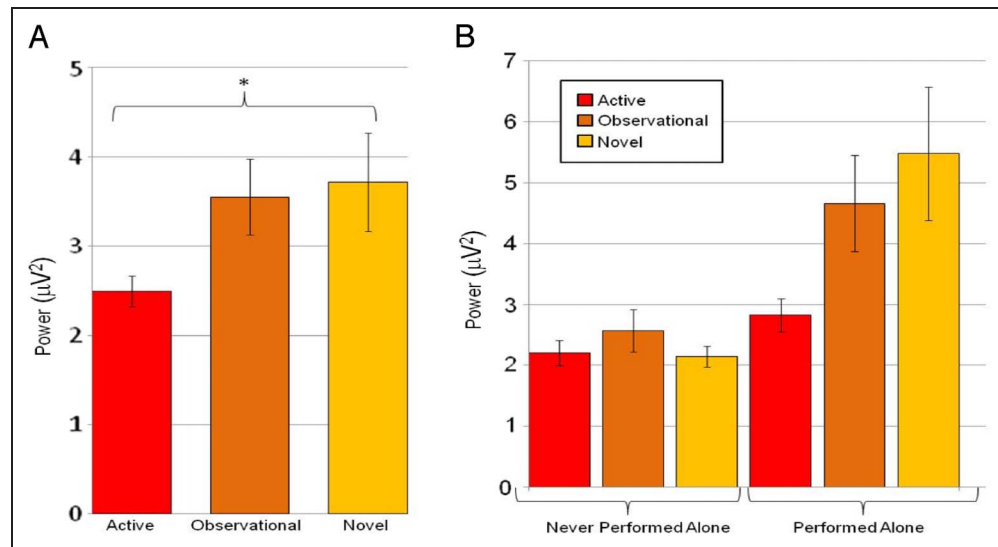
power was found in response to the sound associated with the actively trained action, $F(1, 152) = 4.29$, $p = .04$, $\eta_p^2 = .027$ (see Figure 4). There was no difference in power between the observed versus novel sound, $p = .84$, $\eta_p^2 < .001$.

To examine individual differences in training effectiveness, a final set of GLMs were conducted with condition as a fixed factor and region and site as within-subject factors, ERD to the active sound as dependent variable, and ability to perform the learned action in the last session (Performed Alone or Never Performed Alone) as a between-subject factor. This revealed a significant interaction between condition and performance ability, $F(1, 142) = 3.24$, $p = .034$, $\eta_p^2 = .031$ (see Figure 5), such that infants who had performed the action alone showed a significant difference in ERD to the sounds associated with the actively learned versus observed actions (mean difference = .64 [*SEM* = .19], $p = .001$), whereas infants

who never performed the action alone did not (mean difference = .08 [*SEM* = .18], $p = .68$). Because, at the end of the final session, infants also had the chance to perform the action they had previously only observed, we also measured differences in infants' ability to perform this action at the end of training (though they only received observational training with this action). When the ability to perform the observed action was added as a covariate to the above GLM, no such interaction emerged, $p = .06$, $\eta_p^2 = .02$. This suggests that variability in learning the actively experienced action, but not variability in learning a similarly difficult (but only previously observed) action, drove these effects.

DISCUSSION

The results of the current study can be summarized in two points: First, motor experience with novel actions

Figure 5. ERD (in frontocentral electrodes) plotted per participant, split as a function of infants' ability to produce the actively learned action at the end of training. Means across participants within each group are plotted as lines, and the shaded area represents the standard error. ERD is defined as (event-related power − baseline power) / (baseline power) with power (6–9 Hz) during presentation of the novel sound serving as baseline.
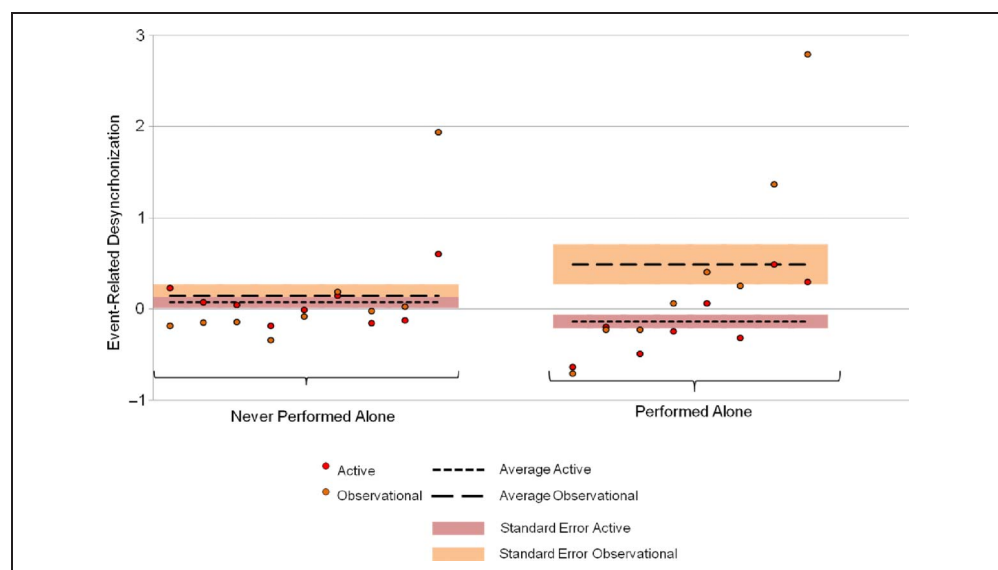
uniquely activates the neural motor system in response to perceiving the effect of this action, whereas observational experience does not. Second, this effect is directly related to individual differences in the degree of motor learning during active training. These findings suggest that active experience is critical to modulating motor activity during action perception early in development. These findings provide crucial information for the theoretical debates concerning the role of experience in action perception and motor activation. The effects of short-term training of novel motor actions on neural responses to the sensory consequences of those actions have never before been studied in infants. The training paradigm demonstrates a direct, causal effect of active experience on the neural correlates of action perception. Furthermore, the fact that neural responses were related to infants' ability to produce the actively learned, but not observationally learned, action demonstrates specific effects on neural functioning of learning particular actions. This is the first study to teach infants novel motor actions and find a relation between each infant's ability to produce that action at the end of training and activation of their neural motor system when presented with the sensory consequence of that particular action. Finally, the measure of motor activation to audio presentation of action effects ruled out any possible effects of visual processing of the action, thus ensuring that the activation was not a function of visual processing.

The discrepancy between our findings and those that suggest benefits from observational experience raise an important question: How can we move beyond initial motor experience to learn more broadly about actions and their effects in the environment? Infancy provides a unique window through which to look at the differential roles of motor and observational experience because of infants' limited repertoire of motor actions. Behaviorally, we saw no difference in the number of infants who could perform the actively versus observationally learned actions at the end of training. Importantly, there were no demonstrable benefits of learning from observation either on a group level or when infants were split based on whether they could perform the observationally learned action. Because action performance was measured at the end of the EEG session, it is an open question whether infants who could perform the observationally learned action would have shown a similar response to the sounds associated with that action (as those associated with the actively learned action) if they had had the chance to perform the action before the post-training EEG session. The precise nature of the motor representation created for each of these actions through training and how this relates to motor activity in the brain should be examined further in future research.

In this study, infants had a week's worth of active and observational training with new, two-step actions. In natural contexts, longer-term learning of motor actions likely serves as a base for and contributes to infants' sub-sequent observational learning (Gerson, 2014; Woodward & Gerson, 2014). In this way, later in development, similar motor activity is likely to be seen for observed actions within and outside one's motor repertoire, as long as the person can achieve the goal of the action (in some way) using movements already within his or her motor system (see Woodward & Gerson, 2014; Aziz-Zadeh, Sheng, Liew, & Damsio, 2012).

Southgate has presented a similar hypothesis to reconcile controversial evidence of motor activation for actions within and outside infants' motor repertoire (Southgate, 2013). In the Southgate and Begus (2013) experiment, the authors found no indication of a difference in infants' motor activation in response to observing claw actions and hand actions on an object. Similar activation for claw and hand actions would be expected if infants were able to recognize the path of the claw and relate this to an action they could use to achieve this goal (reaching with a hand). Reaching with the hand is an action that is repeatedly practiced by 9-month-olds in their everyday life and would thus easily be brought forward as an alternative action. It is possible that increased experience with a variety of simple actions leads to motor activation to the observation of a broader range of actions that can achieve similar goals through the combination or substitution of the simple actions (Buccino & Riggio, 2006). After having gained motor experience with a particular action (e.g., shaking), an infant can potentially map this motor representation, as in Paulus et al., to novel effects and goals (e.g., a new sound) that become associated with the motor action through observational, rather than active, experience (Paulus et al., 2013; cf. de Klerk, Johnson, Heyes, & Southgate, 2014).

Whether the observed effect was a function of a causal link between the motor action and the sound is an open question. That is, it is unknown whether the motor action necessarily needed to result in the sound in order for the association between the sound and the motor system to be formed. For example, if infants were to activate their own motor systems via play with another object while they viewed their parents perform the (motorically unfamiliar) action that resulted in the sound, their motor system might then later respond to the sound via association with the action the infant had produced (that was unrelated to the sound except in "coincidental" timing). This possibility would be consistent with the theoretical proposal put forth by Paulus et al. (2013) and is a question for future research. The current findings are consistent with the unique behavioral effects of active relative to observational experience early in development (Gerson & Woodward, 2014a; Hunnius & Bekkering, 2014; Sommerville et al., 2008). Whether and how this change in motor activity is related to the change in perception of the goal of the observed action is an open question. To date, as far as we are aware, no studies have simultaneously measured individual differences in motor activation and perception of the effect

of an action. Instead, similar relations between expertise and behavioral measures and expertise and motor activation have been hypothesized to support links between the behavioral and neural measures (e.g., Marshall & Meltzoff, 2014; Woodward & Gerson, 2014). Examining this relation more directly is important for uncovering the true nature of the link between motor activity and action understanding.

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