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## EFFECTS OF SENSORI-MOTOR LEARNING ON MELODY PROCESSING ACROSS DEVELOPMENT

Elizabeth M. WAKEFIELD\* and Karin H. JAMES

Department of Psychological and Brain Sciences, Indiana University, Bloomington, USA

### Abstract

Actions influence perceptions, but how this occurs may change across the lifespan. Studies have investigated how object-directed actions (e.g., learning about objects through manipulation) affect subsequent perception, but how abstract actions affect perception, and how this may change across development, have not been well studied. In the present study, we address this question, teaching children (4–7 year-olds) and adults sung melodies, with or without an abstract motor component, and using functional Magnetic Resonance Imaging (fMRI) to determine how these melodies are subsequently processed. Results demonstrated developmental change in the motor cortices and Middle Temporal Gyrus. Results have implications for understanding sensori-motor integration in the developing brain, and may provide insight into motor learning use in some music education techniques.

### Keywords

fMRI; visual-motor learning; music; MTG

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Perception of the world requires interaction between our bodies and the environment. Cognition, being determined by our perceptions, can thus be considered *embodied* – not only formed by our active interactions with the world, but also augmented by our ongoing interactions. One line of evidence supporting this embodied framework is that motor systems are recruited when organisms perceive their environment: a history of our actions is stored and reactivated upon subsequent perception of learned stimuli (e.g., Arevalo, 2008; Arevalo et al., 2007; Chao & Martin, 2000; Hauk, Johnsrude, & Pulvermüller, 2004; James, 2010; James & Atwood, 2009; James, Butler, & Mueller, 2008; James & Gauthier, 2006; James & Maouene, 2009; James & Swain, 2011; Longcamp, Anton, Roth, & Velay, 2003; Nyberg et al., 2001; Pulvermüller, Harle, & Hummel, 2001; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Pulvermüller, Lutzenberger, & Preissl, 1999; Saccuman, Cappa, Bates, Arevalo, Della Rosa, Danna, & Perani, 2006). Furthermore, the same perceptual task will recruit different neural systems depending upon whether the task was initially learned with or without motor system involvement (e.g., Hauk et al., 2004; James, 2010; James & Atwood, 2009; James & Maouene, 2009; James & Swain, 2011; Lahav, Saltzman, & Schlaug, 2007; Nyberg et al., 2001).

In adults, this influence of the motor system has been demonstrated during perception of items such as tools (Chao & Martin, 2000), kitchen utensils (Chao & Martin, 2000), letters (Longcamp et al., 2003; James & Gauthier, 2006), action-related words – both verbs (e.g., Hauk et al., 2004; Pulvermüller et al., 2001; Pulvermüller et al., 2005; Pulvermüller et al., 1999) and nouns (Saccuman et al., 2006; Arevalo, 2008; Arevalo et al., 2007), during action commands (Nyberg et al., 2001) and during perception of action in some cases (e.g., Buccino et al., 2004; Decety, Chaminade, Grezes, & Meltzoff, 2002; Grezes, Armony, Rowe, & Passingham, 2003; Iaconobi & Dapretto, 2006; Iacoboni, Woods, Brass, Bekkering, & Mazziotta, 1999; Rizzolatti & Craighero, 2004). Other examples of the motor system influencing perception come from studies on gesture which show that individuals' gestures when explaining a task affect their representation of the task, and how they will perform it in the future (Beilock & Goldin-Meadow, 2010; Goldin-Meadow & Beilock, 2010), and from studies of musicians who show motor reactivation when listening to a piece they have learned on their instrument (e.g., Bangert et al., 2006; Baumann et al., 2007; Haslinger et al., 2005; Landau & D'Esposito, 2006; Margulis, MIsna, Uppunda, Parrish, & Wong, 2009). Thus, there are many examples of how adults' perceptions are shaped by motor system involvement.

Whether or not motor experience also leads to the recruitment of different systems during visual perception in children has been addressed by a handful of studies. In particular, some researchers have investigated the neural substrates of perception in children, comparing 'active' learning – learning with actual manual exploration with 'passive' learning – learning only through the perceptual system. For example, children showed increased motor system activation during visual and auditory object recognition tasks if they had explored objects actively, rather than passively, prior to a recognition task (James & Swain, 2011). In addition, children learning to recognize letters showed an increase in neural activation in visual association areas when viewing letters if they had been taught letters actively, through printing, as opposed to when they had been taught letters passively, through visual recognition alone (James, 2010). Finally, studies on gesture use have shown that learning a concept with the help of gesture results in learning that is retained across time, compared to learning without gesture (Cook, Mitchell, & Goldin-Meadow, 2008). The findings from these studies suggest that utilizing a motor system component while learning changes how the brain processes subsequent information in children, not just in adults.

In the majority of the research discussed, the actions performed by children and adults have directly changed something about their perception of the object being acted upon. When a child writes letters, she actively creates figures on a paper. When an adult hammers a nail or strikes a piano key, the movement of the hammer or finger is causal. In the case of gesturing, gestures are not performed on objects, but are often representative of actions. Gestures are thus concretely representative, although they are not directly causal. This leads to an interesting question: how are actions that are not directly causal or concretely representative, but more abstractly representative through learned associations, connected to perceptions, and does this change across development? If a history of learning through motor interaction facilitates learning and/or allows the individual to associate more abstract motor movements with perception, then we would expect to see a difference in performance and neural activation patterns between adults and children. Addressing this question will

further our understanding of how and when our actions influence cognition, and whether there is a limit to embodied cognition. In the present study, we address this question through a paradigm driven by a real world use of non-causal, abstract, but representative actions in music education.

Non-causal motor movements are often incorporated into music education techniques to increase the speed of acquisition of musical skill, and the musicality of students (Shiobara, 1994; Sidnell, 1986). Teachers employing the Dalcroze method, developed in the early twentieth century, stress movement to music as a way for children to internalize rhythm, and improve their musicality (i.e., eurhythmics) (Seitz, 2005). Educators working from the Kodály and Orff traditions, which were also developed in the early twentieth century, teach sight singing with motor signs (i.e., Curwen hand signs) to help children learn intervals and maintain good pitch memory. Previous literature indicates that the way we internalize and conceptualize music is integrally related to movement (e.g., Eitan & Granot, 2006; Keller & Koch, 2008), thus it is not surprising that educators would naturally incorporate motor components into music education techniques. Given this strong connection between music and movement, adding a movement component during music learning may be beneficial because it grounds learning in the physical world; however, there are very few empirical studies that have been conducted to evaluate the actual effects of using these techniques, as compared to traditional methods that do not stress a motor component. Of the studies that do exist, some show that motor movements aid learning (Liao & Davidson, 2007), whereas others indicate that a motor component does not appreciably improve music-learning ability (Cassidy, 1993). These inconclusive results may stem from the type of movement being used. Liao and Davidson instructed children to create movements that they felt represented the music, whereas Cassidy (1993) utilized Curwen hand signs: a system in which hand signs are paired with single steps of the musical scale. Although some hand signs are related to the scale step they represent (i.e., the leading tone is paired with an upward pointing of the finger, as if to point to the tonic), most are only meaningfully connected to the pitches they represent after being learned, and none are intuitively connected outside of the context of the scale. The movements used in Liao and Davidson's study, then, are similar to the causal movements that are known to affect perception. The abstract movements, used by Cassidy (1993) may not affect perception in the same way, although anecdotal evidence of their benefit in music education suggests that the movements are helpful in some way.

In the present study, we investigated how non-causal, but associable movements can change neural processing during the learning of sung melodies, and affect subsequent recognition of melodies by adults and children. Importantly, we compared learning with and without a visuo-motor component within both populations; then compared this difference between the groups. Based on previous literature, we hypothesized that (a) we would see reactivation of the motor system to melodies learned in the visuo-motor condition, as opposed to other conditions that did not include a motor component if associable motor movements are processed in a similar way to more causal movements, (b) if motor movements must be concretely representative of the to-be-learned stimuli, then we may not see any facilitation in this study, due to the abstract nature of our motor movements and their arbitrary (although consistent) connection with the to-be-learned melodies, but if the brain processes abstract

and more direct, causal movements similarly, we may see an improvement in learning with the motor system, as has been seen in the literature (e.g., gesture studies).

## Experiment 1

### Method

**Participants**—Fifteen undergraduate and graduate students (7 male and 8 female), at Indiana University participated in the study. All participants were right-handed, native English speakers who reported no history of neurological or psychiatric disorders and reported normal or corrected-to-normal visual acuity. Participants were between the ages of 19–27 years ( $M = 24$  years). Informed consent was obtained from 17 university students, according to the guidelines of the Indiana University Internal Review Board. Twelve of the 15 participants had learned to read musical notation, but only 9 remembered how to read music at the time of the experiment. Adults had various amounts of instrumental training. The data from 2 participants were excluded from the analysis, based on a failure to successfully complete a required training session.

### Stimuli

**Melodies:** Twenty-eight melodies were composed for the study and 12 of the 28 melodies were taught to participants during a training session. All 28 melodies were recorded for use in an fMRI session. Melodies consisted of four short sections (i.e., measures), and were composed in the style of simple children's songs, with simple rhythmic patterns (See Figure 1a for melody example). Melodies were recorded by a female vocalist as two separate stimuli, the first two sections and the second two sections, at 96 beats per minute (bpm) using an Edirol R-09 24-bit WAVE/MP3 Recorder (Roland Corporation, Nakagawa, Japan). Each of the 56 resulting half melodies was approximately five seconds. Melodies were edited on a Macbook using Audacity 1.2.6. Typicality ratings were not acquired, however, none of the participants commented that melodies were familiar or similar to other songs, and melodies were specifically composed *not* to resemble known songs.

**Hand signs:** Eight hand signs were used during training. These hand signs were adapted from preexisting hand signs created by John Curwen. Each hand sign corresponded with a discrete pitch, and a discrete modified solfège syllable (hand signs are depicted in Figure 1c). Hand signs were created so as not to be intuitively representative of particular pitches, thus are not directly related to the melodies – the association must be learned through the training.

### Procedure

**Training session:** Participants underwent one training session in which they learned 12 melodies under three conditions from an experimenter; four melodies per condition. Conditions were presented in a randomized order across participants. In an *auditory* condition, participants heard melodies that were sung using nonsense syllables analogous to solfège syllables (e.g., Fo, Ga, Di instead of Do, Re, Mi), and repeated them. In a *visuo-motor* condition, in addition to hearing melodies, participants learned hand signs corresponding to notes in the melody with their right hand (analogous to Curwen hand signs,

see Figure 1c), and repeated both the melodies and hand signs. When the experimenter produced the melodies, vertical height of the hand signs corresponded with the pitch being sung (i.e., hand signs paired with high pitches were produced spatially higher than hand signs paired with low pitches). Participants were not specifically told to incorporate the spatial aspect of the hand signs and observation of learning demonstrated that hand signs were not consistently produced at particular heights. In a *visual* condition, in addition to hearing melodies, the syllables being sung were presented visually (see Figure 1b), and participants repeated the melodies. Therefore, for the visual and motor conditions, there was additional input to the system—in one case visual, in the other, motor.

Melodies were taught using a recall procedure adapted from Racette and Peretz (2007). For each melody, participants listened to the experimenter sing a complete melody once, after which the experimenter taught participants the melody in sections. To learn sections of the melody, participants listened to the experimenter sing a section, then sang the section with the experimenter, then sang the section by themselves. Melodies were made up of four sections (i.e., measures). Using the procedure described, participants learned the first and second sections; then sang the first and second sections together. The third and fourth sections were learned the same way. Finally, participants performed the complete melody. Training for the visual and auditory melodies was complete when participants had sung each melody accurately without help from the experimenter. For melodies learned with a visuo-motor component, participants were required to produce the hand signs correctly in addition to accurately performing the melodies.

**fMRI session:** Participants underwent a scanning session the day following training, which consisted of six functional imaging runs and a high-resolution structural scan. **Functional localization:** Participants had two block-design runs to localize functional regions of interest in the brain, including areas involved in auditory, motor, and visual processing. To localize regions for auditory processing, participants heard 3-note sung melodies. To localize motor regions, participants made hand movements of their choice with their right hand, and to localize visual processing areas, they viewed modified solfège syllables that were similar to, but not the same as, those used in the training session. Blocks were 14 seconds in duration, with a 10 second inter-block interval. There were four blocks of each stimulus type, presented randomly within a run. Runs were 5 minutes and 8 seconds, containing 12 blocks total. There were two localizer runs in total. **Experimental sessions:** Following the localizer runs, four additional runs were presented in a fast event-related design, during which participants listened to parts of melodies (the first or second half of each melody). These melody segments were either learned in the training session, or were novel (unlearned) melodies, composed using the same guidelines as the learned melodies. Participants were not presented with visual stimuli, or asked to produce motor movements during these runs; they simply listened to melodies they had learned in the training session, and the novel, unlearned melodies. Participants indicated whether they remembered learning each melody via button-presses on a left-hand paddle. The melodies were presented in a random order and no hand movements were detected during scanning, as confirmed by a camera in the bore of the magnet, except for the button press response (which was present during all melody conditions). Melody stimuli were five seconds long, with inter-stimulus intervals

(ISIs) of 8, 10, or 12 seconds. There were 32 presentations of the melodies per run, 24 learned and 8 unlearned and four runs in total. Different unlearned melodies were used in each run. The final scan was a high-resolution anatomical scan, onto which the functional data were overlaid for the purpose of analysis.

Visual stimuli were presented via a Mitsubishi XL30 projector, which projects images onto a screen that participants viewed through a mirror from the rear part of the bore of the scanner. Auditory stimuli were presented via headphones worn by the participants (Siemens). Both types of stimuli were presented via SuperLab 4.0.7b software on a Macintosh MacBook laptop.

**fMRI parameters:** Imaging occurred in a 3-Tesla Siemens Magnetom Trio whole-body MRI system and a phase-arrayed eight-channel head coil in the Imaging Research Facility located in the Indiana University Psychological and Brain Sciences department. The field of view was 220 mm, 100%, with an in-plane resolution of 64×64 pixels and 33 slices per volume (3.4 mm thick, no gap). Images were acquired using an echo-planar technique (echo time, TE = 30 ms, time of repetition, TR = 2,000 ms; flip angle = 90°) for brain oxygen level-dependent (BOLD) imaging. Although sparse sampling is often used when auditory stimuli are presented, it was determined that the possible effect of scanner noise was equated for all conditions, and thus subtracted out of any comparisons among conditions. Analysis was conducted using Brain Voyager. Images were 3D motion-corrected, linear trend was removed, and Gaussian spatial blurring (FWHM 6 mm) was applied. Individual functional volumes were aligned with anatomical volumes using an intensity-matching, rigid-body transformation algorithm. Individual anatomical volumes were normalized into Talairach space using the eight-parameter affine transformation (Talairach & Tournoux, 1988).

**fMRI data analysis procedures:** To localize regions of interest (ROIs), a whole-brain analysis of the data from the functional localizers was performed. In each individual, the contrasts of interest were performed: Motor (hand movements) versus rest, visual (perception of syllables) versus rest, and auditory (melody perception) versus rest. Based on these contrasts, five ROIs were identified: one motor region in the left somatosensory cortex (resulting from motor vs. rest; peak average Talairach coordinates x(-38), y(-26), z(53)), one visual region in the occipital cortex of each hemisphere (resulting from visual vs. rest; peak average Talairach coordinates x(-28), y(-81), z(-1) and x(34), y(-79), z(-1)), and one region involved in auditory processing in each temporal lobe (resulting from auditory vs. rest; peak average Talairach coordinates x(-50), y(-19), z(8) and x(58), y(-16), z(3)). Within these individually defined ROIs, we extracted the percent signal change of the BOLD response for the experimental runs in which the learned and novel melodies were presented. A deconvolution procedure was used to separate the BOLD signal of the melodies from the ISIs due to the short duration of the ISIs relative to the stimulus events. The deconvolution parameters in Brain Voyager were used to achieve the deconvolved data. Within each deconvolved time course for an event, the peak percent signal change relative to baseline was used as a dependent measure of BOLD response. Data from each ROI were then averaged across participants. A repeated measures analysis of variance (ANOVA) was conducted on the data from each ROI, followed by planned comparisons in each ROI



between conditions: Motor versus Auditory, Motor versus Visual, and Visual versus Auditory.

## Results

**fMRI Behavioral Performance**—During the scanning session, participants were asked to listen to melodies and indicate whether they learned the melodies in the training session on the previous day, or whether the melodies were new (i.e., novel). A *d* prime analysis was conducted to determine a percent correct value that accounts for response bias, correcting for hit and false alarm rates. Based on this analysis, participants correctly identified 95.4% ( $SD = 0.05$ ) of the melodies from the motor training condition, 96.4% ( $SD = 0.06$ ) from the visual training condition, and 98.2% ( $SD = 0.02$ ) from the auditory condition. To determine whether participants were making correct identifications of learned melodies based on recognition of melodies instead of random guessing, *t*-tests were conducted between the percentage of correct identifications for each condition and chance ( $p = 0.25$ ). The percentages of correct identifications made by participants were significantly above chance,  $t(14) = 14.83, p < .001$ ;  $t(14) = 15.19, p < .001$ ; and  $t(14) = 52.95, p < .001$ , for motor, visual, and auditory melodies, respectively. A repeated measures ANOVA was conducted to determine whether participants were more proficient at learning melodies in a particular condition. There was no significant difference between percentages of correct identifications between melodies in the visuo-motor, visual, and auditory conditions,  $F(2, 14) = 1.98, ns.$ , indicating the melodies in the three conditions were learned equally well.

### fMRI ROI Analyses

**Auditory ROIs:** Repeated measures ANOVAs were conducted on the percent BOLD signal change in both the right and left auditory ROIs for melodies in the three learning conditions (visuo-motor, visual, and auditory). A significant effect of learning condition was found in both the left auditory ROI,  $F(2, 14) = 15.872, p < .001$ , and right auditory ROI,  $F(2, 14) = 8.375, p < .001$ , (see Figure 2). Planned comparison within-group *t*-tests were conducted in both the left and right auditory ROIs. The main effect of learning condition shown bilaterally in the auditory ROIs was driven by significantly greater activation to the melodies learned in the auditory condition than to those learned in the visual condition, ( $t(14) = 4.73, p < .01$ , and  $t(14) = 3.53, p < .01$  in the left and right ROIs, respectively), and by greater activation to melodies learned in the auditory condition than to those learned in the visuo-motor condition, ( $t(14) = 3.92, p < .01$ , and  $t(14) = 2.92, p < .01$  in the left and right ROIs, respectively). No other significant differences were found between percent BOLD signal change to melodies learned in different conditions. These results indicate that learning melodies through auditory perception resulted in a re-activation of auditory regions. Re-activation of auditory cortex did not result after learning melodies with visual stimuli (in addition to auditory) or after learning with hand signs (in addition to auditory).

**Visual ROIs:** Two repeated measures ANOVAs were run on the left and right visual ROIs, again to determine whether the condition in which melodies were learned would affect percent BOLD signal change. No significant effect was found in either the left,  $F(2, 14) = 1.974, p = 0.16$ , or right visual ROIs,  $F(2, 14) = 1.125, p = 0.34$ .

**Motor ROI:** Finally, a repeated measures ANOVA was conducted to determine whether significant differences in activation to melodies learned in the three conditions occurred in the motor ROI. No significant difference was found between learning conditions,  $F(2, 14) = 1.39, p = 0.27$ . This lack of effect may be driven by the method by which the ROI was defined. The area of the brain involved in producing motor actions, which was found using the functional localizer, may be different than the area of the brain activated when remembering motor movement. Thus, additional direct contrasts were performed to further investigate those data.

**fMRI Direct Contrasts**—Three whole-brain contrasts were performed: one contrasting BOLD activation to melodies learned in the visuo-motor condition to those learned in the visual condition, a second comparing visuo-motor to auditory conditions, and a third comparing visual to auditory conditions. There were two areas that showed significantly greater activation to melodies learned in the visuo-motor condition, as compared to those learned in the visual condition: a region of the left precentral gyrus (PrCG) and a region of the left middle temporal gyrus (MTG) (see Figure 3). There were no regions that showed a significant difference in activation to melodies learned in the visuo-motor condition, as compared to those learned in the auditory condition, nor were there significant differences in activation to melodies learned in the visual or auditory conditions.

## Discussion

Our ROI analyses demonstrated that learning melodies by simply listening to, and repeating them, resulted in greater auditory cortex re-activation bilaterally than learning melodies with either a visuo-motor or visual component. However, there was no significant re-activation in the motor, visual, and auditory ROIs as a result of learning melodies with an auditory *and* visual component, or as a result of learning melodies with an auditory *and* motor component. In contrast with the ROI findings, our direct whole-brain contrasts of the experimental runs demonstrated that learning melodies with motoric hand signs activated a part of the cortical motor system and the MTG upon subsequent auditory presentation of the learned melodies.

Interestingly, there were no re-activations found in the visual cortex upon subsequent auditory presentation of melodies, and, there was no behavioral effect of the different learning conditions: all melodies were learned equally well. The significance of these findings is discussed below.

### 1. Reactivation of auditory cortex to auditory melodies

The auditory cortex was reactivated bilaterally upon subsequent presentation of melodies learned with the auditory system alone to a greater extent than to those learned with the auditory and motor or visual systems. This finding suggests that a trace of the learning experience is stored in the auditory system, but only when auditory information is not paired with another modality during learning. This activation seems to encompass both primary and secondary auditory processing areas.



One possible explanation for this finding is that participants were dividing their attention between listening to the melodies and looking at the visual representation of the melodies, or making motoric hand signs in the visual and visuo-motor conditions, respectively. Specifically, in the visual condition, using the visual representation of the melodies may have allowed the participants to attend less closely to what the experimenter was singing, as they did not have to listen to the experimenter to know what syllables to sing. If this is true, the use of the visual representation may have led to less effortful auditory processing. In the visuo-motor condition, as previously discussed, the hand signs were not intuitively representative of the pitches they were associated with, thus participants may have had to concentrate on learning the motor movements, perhaps attending less to auditory processing. Therefore, although multisensory processing is usually beneficial, in this case, the addition of either the visual or visuo-motor component to the melody learning may have caused less intentional processing of the auditory information, resulting in no auditory re-activation in these cases. Alternatively, the findings could have resulted from competitive inhibition of auditory processing by the motor and visual cues that were learned in the visuo-motor and visual conditions, respectively. Forming associations between the visual cues and the melodies, or between the motor hand signs and the melodies may have interfered with deeper auditory processing in these conditions, whereas auditory processing would not have been inhibited when participants learned melodies in the auditory alone condition. In support of this idea, research has shown that when individuals simultaneously attend to stimuli in more than one modality while only making responses based on one of the stimuli sets, as opposed to only attending to the set of stimuli being responded to, performance deficits are seen (Dell'acque & Lolicoeur, 2000; Fernandes & Moscovitch, 2000; Jolicoeur, 1999). For example, Dell'acque and Lolicoeur (2000) showed that when individuals were asked to pay attention to the pitch of a tone that accompanied stimuli in a visual discrimination task, participants were less accurate than when they were told they could ignore the tone. This demonstrates that auditory information can interfere with the encoding of visual information. In other words, whereas participants were being tested on the visual information, having to attend to and remember tones interfered with learning this visual information. In the present study, the opposite phenomenon may have been occurring – the main task was to learn set of auditory stimuli (i.e., the melodies), but the additional visual and visuo-motor stimuli may have been taxing attentional resources that would otherwise have been allocated to auditory processing. Moreover, in a second study, participants were asked to listen to, and encode a word while paying attention to various visual stimuli sets (Fernandes & Moscovitch, 2000). The authors found that when the visual and auditory sets were lexical in nature, encoding interference occurred. In our study, participants saw syllables visually while hearing and singing these syllables in the melodies; thus, the visual representation of the syllables may have interfered with the auditory encoding.

## 2. Reactivation of PrCG to motor melodies

Associating melodies with hand signs during learning resulted in the recruitment of the left PrCG upon hearing the learned melodies again. This result is consistent with several findings suggesting that when stimuli are learned actively, that is, with motor system involvement, the motor system is re-activated upon subsequent *perceptual* encounters with the stimuli (e.g., D'Ausilio, Altenmüller, Belardinelli, & Lotze, 2006; Lahav et al., 2007;

Margulis, et al., 2009). Note that this activation was not due to button presses, as these occurred to all test stimuli, those learned with motor signs, and with visual stimuli.

One suggestion of the mechanisms underlying reactivation is the common coding hypothesis, which posits that there is a common representation in the brain for perceived stimuli and planned actions (e.g., Prinz, 1997). In the case of the present study, the participants would therefore have coded the sung melodies and the hand signs that accompanied these melodies together, such that upon later presentation of the melodies, the stored motor movements were reactivated. This finding suggests that for adults, a motor component that is not directly causing the pitches or syllables produced was processed in a similar way, at least in the premotor system, as motor movements more directly connected to a representation. Even abstract motor representations can thus cause changes in cognitive processing.

### **3. Activation of MTG to melodies learned with a motor component**

The whole-brain contrast that was performed showed that a region of the left MTG was recruited to a greater extent when individuals listened to melodies learned with motoric hand signs as compared to those they learned with the aid of visual representations. This result can be taken as evidence that the hand signs were stored as part of the representation of the melodies: Previous literature suggests that the MTG stores semantic representations – information about stimuli in our environment that we acquire through learning (e.g., Beauchamp & Martin, 2007; Binder Desai, Graves, & Conant, 2009; Blumenfeld et al., 2006; Martin & Chao, 2001). According to the sensory-motor model of semantic representations (Martin, 1998; Martin et al., 2000), the MTG responds to the aspects of stimuli that are movement or motion related, thereby constructing part of our semantic knowledge for the stimuli. As an example, previous literature shows that MTG activation occurs when individuals see tools they have actively manipulated in use, the movement trajectories of these tools, and even the sounds the tools produce (e.g., Beauchamp & Martin 2007; Chao & Martin, 2000; Martin, Wiggs, Ungerleider, & Haxby, 1996; Doehrmann, Naumer, Volz, Kaiser, & Altmann, 2008). This suggests that the MTG was activated in conjunction with the presentation of melodies learned with a visuo-motor component in the present study because the auditory stimuli of specific notes sung on specific syllables elicited a representation of the action that had been learned with them.

### **4. No effect of different learning conditions on activation of visual cortex**

Unlike motor and auditory learning, learning visual images that corresponded to the melodies did not result in significant activation in the visual cortex upon subsequent presentation of the learned melodies. This finding suggests that either the visual images were not stored, or that the images were not associated with the auditory information strongly enough to be reactivated. Previous literature suggests that when music notation is read, musicians show excitation of the vocal cords as they covertly perform the music (Brodsky, Kessler, Rubinstein, Ginsborg, & Henik, 2008), but to our knowledge, there are no studies that show that musicians have activation of the visual system when hearing music they learned with the aid of music notation. This suggests that, indeed, visual images of a representation of music are either not stored with the auditory information, or are not

associated to the extent of being reactivated by listening to melodies learned with a notational system of any sort. Additionally, if integration is occurring, it may be that alterations in functionality occurred in a multisensory area, instead of within unisensory visual and auditory areas that were focused on in our ROI analysis. For instance, one major area of audio-visual integration is the superior temporal sulcus (STS) (e.g., Stevenson, Geoghegan, & James, 2007; Stevenson & James, 2009), which we did not include in our analyses.

### **5. No effect of different learning conditions on melody recognition**

As previously discussed, it is clear that participants were able to learn the melodies: recognition of melodies learned in each of the conditions was significantly above chance during the fMRI session, thereby indicating that training was successful. Whereas the motor system and MTG activation suggest that the hand signs are being processed and stored in a similar manner to more causal movements, this does not seem to be affecting behavior. This is puzzling, as literature on multisensory and sensori-motor learning suggests that incorporating a modality in a learning paradigm will improve an individual's ability to learn, even if this modality is not utilized during recall (e.g. Seitz, Kim, & Shams, 2006). It may be, however, that the lack of difference in the percent of recognized melodies could be due to a low sample size or a ceiling effect, as all recognition percentages were near perfect, or that differences may have arisen if we have conducted testing at a different time. This finding will be discussed more fully in our General Discussion.

The ability to process abstract motor movements in a meaningful way may be driven by previous experience using the motor system. In the embodied framework, what we do across the lifespan influences our cognitive abilities, thus, the way an adult processes abstract hand signs may be quite different from the way a child would. In Experiment 2, we address this possibility. Using the same basic experimental design with child participants, we are able to explore how children learn melodies with an abstract motor component.

## **Experiment 2**

In Experiment 1, we investigated how adults process melodies that they learned with or without a motor component. We found that adults showed reactivation in the motor cortex, as well as MTG activation, which is indicative that the hand signs were not only stored in a common representation with the melodies, but were also stored as a communicative and meaningful part of the representations. In Experiment 2, we were interested in whether we would find similar results with children, or whether there are developmental differences in how children and adults process abstract motor movements paired with melodies. Children have less experience associating abstract motor movement to sensory input. Thus, the question of the amount of everyday experience making sensori-motor associations that is required for motor system recruitment during sensory processing was addressed here. From previous literature, we can hypothesize that children will show motor cortex reactivation as a result of within-experiment experience associating sensory and motor information (e.g., James, 2010; James & Swain, 2011). It is unclear, however, whether or not children will recruit the MTG during melody perception after learning, as this may be dependent on whether they can confer meaning on abstract hand signs. If children are unable to recall

learned melodies and do not show MTG activation, this may provide evidence that the MTG is important for the retention of the melody learning. Additionally, we are interested to determine whether children will show a behavioral benefit from learning with a motor component, as literature would suggest they might, which would differ from our finding with adults.

## Method

**Participants**—Eleven children, 1 male and 10 females, between the ages of 4 years and 4 months, and 7 years and 10 months ( $M = 6$  years and 1 month;  $SD = 1$  year and 1 month) participated in the study. All participants were right-handed, native English speakers with no reported history of neurological or psychiatric disorders, and normal or corrected-to-normal visual acuity. Of the children, only 1 of the 11 could read music and had studied music for over a year. Ten of the 11 children had some experience with music in a classroom setting. Informed consent was obtained from the parent or guardian of 27 children, according to the guidelines of the Indiana University Internal Review Board. Data from 16 participants were excluded from the analysis, based on a failure to successfully complete a required training session or because of excessive movement during the imaging session.

## Stimuli

**Melodies and hand signs:** Nine melodies were composed for the study and 6 of the 9 melodies were taught to participants during a training session. All nine melodies were recorded for use in an fMRI session. Melodies were similar to those composed for Experiment 1, but consisted of 2 sections (i.e., measures), instead of 4. Each melody was approximately five seconds (see Figure 4a for example melody). Five of the 8 hand signs from Experiment 1 were utilized (see Figure 4c). The shorter melodies were used because the longer melodies were assumed to be too difficult for the children to learn.

## Procedure

**Training session:** Children learned six melodies during the training session in 2 of the 3 conditions used in Experiment 1: the *visual* condition in which children learned sung melodies while looking at a visual representation of what they were singing (see Figure 4b for example), and a *visuo-motor* condition, in which the discrete pitches of the melodies were paired with discrete hand signs (adapted Curwen hand signs), and children were required to repeat both the melodies and the hand signs. In Experiment 1, adults sang melodies on modified solfège syllables in all conditions. Because learning the nonsense syllables was deemed too difficult for children to learn (and depended on reading ability, which can be highly variable for a group of this age), each discrete pitch was paired with the name of a color for Experiment 2. The visual representation used was colored circles in the order they were sung in each melody (see Figure 4b). As in Experiment 1, melodies were taught using a recall procedure adapted from Racette and Peretz (2007). Training was complete when children had sung each melody accurately without help from the experimenter; thus, melodies were learned to the same criterion by children as by adults in Experiment 1. To assess learning, children listened to nine melodies after the training

session, 6 learned and 3 novel, and told the experimenter whether they had learned the melodies or whether the melodies were new.

After training, children were exposed to an fMRI-like environment through experience in a simulator: a model of the fMRI machine in which children can hear the sounds that will be made by the scanner and experience being inside the bore of the MRI machine. This simulation was performed because the fMRI environment is novel, and can be frightening to children. By gradually exposing children to an fMRI-like environment through experience in a simulator, children are more likely to be comfortable during the experimental session (for more on this methodology see James, 2010; James & Maouene, 2009; James & Swain, 2011).

**fMRI session:** After children were comfortable in the simulator they underwent a scanning session, which consisted of three functional imaging runs and a high-resolution structural scan, similar to those in Experiment 1. **Functional localization:** Children underwent a 4-minute block-design run to localize functional regions of interest (ROIs) in the brain, including areas involved in auditory, motor, and visual processing. Auditory and motor localizers were the same as those used in Experiment 1. For the visual localizer, children were shown blocks of colored circles. Children were asked to remain still during the visual and auditory tasks, but performed hand movements during the motor task. **Experimental sessions:** Children underwent two 3 min 30 sec event-related runs, during which they listened to melodies that they had either learned in the training session, or novel (unlearned) melodies, composed using the same guidelines as the learned melodies. Children were not presented with visual stimuli, or asked to produce learned motor movements during these runs; they simply listened to melodies they had learned in the training session, and the novel, unlearned melodies. Children indicated whether they remembered learning each melody via button-presses with their index and middle fingers on a left hand paddle. The final scan was a high-resolution anatomical scan, onto which the functional data were overlaid for the purpose of analysis.

**fMRI data analysis procedures:** As in Experiment 1, we determined ROIs from our localizer. We conducted contrasts of motor versus rest, visual versus rest, and auditory versus rest in all individuals from the localizer scans. Based on these contrasts, three ROIs were identified: one motor region in the left somatosensory cortex (peak average Talairach coordinates  $x(-33)$ ,  $y(-25)$ ,  $z(55)$ ), and one region involved in auditory processing in each temporal lobe (peak average Talairach coordinates  $x(-49)$ ,  $y(-22)$ ,  $z(9)$  and  $x(51)$ ,  $y(-22)$ ,  $z(12)$ ). The visual localizer was not usable because the fixation image used to hold the attention of the children turned out to be just as visually complex as the stimuli used for the visual localizer, so visual ROI analysis was based on the adult ROIs from Experiment 1 (Talairach coordinates  $x(-28)$ ,  $y(-81)$ ,  $z(-1)$  and  $x(33)$ ,  $y(-84)$ ,  $z(-2)$ ). T-tests were conducted on the data from each ROI, comparing neural activation to melodies learned in the motor and visual conditions. Imaging parameters for the fMRI session were the same as those used in Experiment 1.

## Results

**Behavioral Data**—Children varied in their ability to follow the instructions during the fMRI session, and therefore we did not analyze responses to children's differentiation between learned and novel melodies while in the scanner. That is, it appeared that children confused the button responses: sometimes not responding at all for a period of time, sometimes using incorrect fingers, and sometimes pressing two buttons at once. In the past, we have used passive viewing/hearing during fMRI with children this young, as responses tend to be too difficult (e.g., James, 2010; James & Maouene, 2009; James & Swain, 2011), here we attempted to collect behavioral data, but as before, to no avail. Therefore, to assess learning, we used the answers given at the end of the training session, when children listened to nine melodies and identified melodies they learned, to determine whether children could correctly differentiate between learned and novel melodies. Based on a *d* prime analysis, correcting for response bias, on average, children correctly identified 50.6% ( $SD = 0.43$ ) of the melodies from the motor training condition, and 41.2% ( $SD = 0.38$ ) from the visual training condition. The percentage of correct identifications made by participants was not above chance either for motor melodies,  $t(10) = 0.05$ , *ns*, or for the melodies learned in the visual condition,  $t(10) = -0.76$ , *ns*. This indicates that although children learned the melody to the same level of performance as adults, they either could not recognize the melodies they learned, or did not understand the question they were being asked. Alternatively, the time frame of testing affected their accuracy: many children were preoccupied, knowing they were about to undergo an fMRI session. Despite their poor performance subsequent to the fMRI session, the imaging results suggest that indeed, they did differentiate the melodies (see below).

### fMRI ROI Analyses

**Auditory ROIs:** A paired-samples *t*-test was conducted to determine whether a significant difference in BOLD activation existed between melodies learned in the motor and visual conditions within the bilateral auditory ROI. No significant effect was found either in the left,  $t(10) = 0.83$ ,  $p = 0.43$ , or the right  $t(10) = 0.46$ ,  $p = 0.65$  ROI. This result is similar to that of the adults in Experiment 1, as the significant difference found in the auditory ROIs in the adults was due to a greater neural activation to melodies learned in the *auditory* condition (which was not included as a condition in Experiment 2), whereas no differences were found between activation to presentations of visuo-motor or visual melodies in the adults.

**Visual ROIs:** Paired-samples *t*-tests were run to determine if there were significant differences in BOLD activation in the bilateral visual ROI to melodies learned in the visuo-motor and visual conditions. No significant differences were found in either the left,  $t(10) = 0.08$ ,  $p = 0.93$ , or right  $t(10) = 0.91$ ,  $p = 0.38$  ROIs. These findings are similar to those in Experiment 1, in which no significant differences were found in activation patterns in the visual ROIs of adult participants.

**Motor ROI:** Finally, a paired-samples *t*-test was conducted to determine whether significant differences in activation to melodies learned in the visual and visuo-motor conditions occurred in the motor ROI. A difference was found in the motor ROI, in which greater



neural activation occurred when children heard melodies learned with a motor component, than without a motor component,  $t(10) = 2.16, p = 0.05$  (see Figure 5). This finding was particularly interesting, as the auditory and visual ROI analyses revealed the same patterns as were found in Experiment 1, but in the present experiment, children showed increased activation to melodies learned with a motor component in the Motor ROI, whereas no difference was found in the Motor ROI for adults.

**fMRI Direct Contrasts**—As with the adult participants in Experiment 1, a whole-brain contrast was performed contrasting BOLD activation to melodies learned in the visuo-motor condition, to those learned in the visual condition. This contrast revealed an area in the right postcentral gyrus (PoCG) (Talairach coordinates  $x(47), y(-27), z(40)$ ), that showed significantly greater activation to melodies learned with a motor component than to those learned without a motor component (see Figure 6). There were no regions that showed more activation when children were presented with visual melodies, as compared to visuo-motor melodies.

## Discussion

Our direct contrast and ROI analysis indicated that learning melodies with motoric hand signs activated parts of the cortical motor system upon subsequent presentation of the learned melodies. Our ROI analysis also revealed that activation patterns in the visual and auditory cortices were not affected by learning condition differences, as was found with adult participants in Experiment 1. Interestingly, unlike our adult participants, children were unable to recognize melodies learned with either a motor or visual component, despite differences in activation patterns to these melodies. Neural activation patterns are more sensitive than behavioral measures: if the children did not code the different learning sessions, then the neural activation would be the same for all conditions—but it was not. Therefore, although behavioral performance in recognition was below chance, the brain was coding and registering the different learning sessions. These findings are discussed in turn below.

### 1. Reactivation of motor cortex to motor melodies

Results from the fMRI session revealed that upon subsequent presentation of melodies learned with a motor component, children show reactivation of the left PrCG (based on the ROI analysis) and the right PoCG (based on the direct contrasts). These results complement previous research suggesting that learning with action will result in motor system recruitment upon later presentations of learned stimuli (e.g., Hauk et al., 2004; James, 2010; James & Atwood, 2009; James & Maouene, 2009; James & Swain, 2011; Lahav et al., 2007; Nyberg et al., 2001), but just as with the adults, our results show something new: The motor components used in previous research are intuitively connected with the stimuli being presented, or in some cases, cause the stimuli (i.e., depressing a key on a piano is a motor movement that causes a note to sound). Our result is novel – our motor component was more abstract than motor components used previously, in that it was not intuitively connected with the melodies that were learned, and it did not cause the melodies. Additionally, we showed activation not only in the left PrCG, an area implicated in the performance of action,

but also in the right PoCG, an area implicated in body awareness. This indicates that although hand signs were performed with the right hand, leading to reactivation in the left hemisphere, crosstalk between the hemispheres also occurred, leading to activation in the contralateral PoCG upon subsequent presentations of motor melodies. This finding complements previous findings that children show a change from more inclusive, non-differentiated processing within the brain when first performing a task, to more differentiated, or compartmentalized processing as adults (e.g., Johnson, 2000; Smith & Gasser, 2005). For example, when learning to read, children initially engage a much more diffuse network of brain areas than that of mature readers (Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003), similarly, children initially process words (e.g., Mills, Coffey-Corina, & Neville, 1997) and faces (e.g., de Haan, Pascalis, & Johnson, 2002) with large networks as infants, but as they gain more experience with these stimuli sets, more specialized regions of the brain are recruited.

Similar to the motor cortex reactivation to melodies learned with a motor component by adults in Experiment 1, one suggestion of the reason reactivation occurred is the common coding hypothesis, proposed by Prinz (1997). Based on this hypothesis, children in the present study coded the hand signs and sung melodies together, leading to the reactivation of the motor movements when the melodies were presented.

## **2. No effect of different learning conditions on activation of visual or auditory cortices**

Whereas differences were seen in activation of motor areas to melodies learned with a motor component as compared to melodies learned with a visual component, no significant differences in neural activation were found in visual and auditory areas. This finding is similar to that of Experiment 1, in which no differences were found in activation patterns to different melody types in the visual cortex, and the differences found in activation patterns in the auditory cortex were due to an increased activation to melodies learned in the auditory alone condition; a condition not used in Experiment 2. Although adult and children were taught with different visual components (syllables vs. colors), it can be argued that data obtained from the children could be compared to the adults as neither syllables nor colors are traditionally associated with notes or hand signs. As in our discussion of the results from adults, the lack of difference in activation either suggests that visual images were not stored with the melodies, or that they were not associated strongly enough to be reactivated during subsequent presentations of melodies learned in the visual condition. An additional interpretation is that representations were stored in audio-visual integration areas such as the STS (e.g., Stevenson et al., 2007; Stevenson & James, 2009), but that this area was not included in our ROI analysis. The lack of difference in the auditory cortex indicates that neither motor, nor visual components can strengthen an auditory representation of a melody. Thus, the use of a motor component during learning with children only seems to affect subsequent melody processing in motor areas.

## **3. Recall at chance for both visual and motor melodies**

Results indicated that children were unable to recognize melodies after learning them with a motor or visual component. This finding is unanticipated: like adults, we would have expected the motor component to be beneficial to learning based on multisensory and

sensory-motor learning research (e.g., Seitz et al., 2006), and gesture literature (e.g., Cook et al. 2008; Goldin-Meadow et al., 2009). This result will be discussed in relation to the behavioral findings of Experiment 1, the difference in procedure for Experiments 1 and 2, and the neuroimaging results from both experiments.

## General Discussion

In the present study, we investigated how adults (Experiment 1) and children (Experiment 2) process melodies learned with (visuo-motor condition) or without (auditory and visual conditions) a motor component. Our results showed that just as actions that are directly influencing something being perceived (i.e., using a tool, playing the violin, writing letters), lead to reactivation of the motor system upon subsequent perceptual encounters, actions that are only abstractly connected to a perceptual experience (i.e., hand signs learned with pitch-syllable combinations), also lead to subsequent motor system recruitment: Both adults and children showed reactivation of the motor cortex upon subsequent auditory presentation of melodies learned with a visuo-motor component. We also revealed that there were no changes in processing in the visual cortices, based on different types of training, and that there were no differences in the auditory cortices when melodies learned with a visuo-motor or visual component were processed (although we did show that adults, who received training in an auditory only condition, showed greater activation in the auditory cortex bilaterally to melodies learned in this auditory alone condition).

The similar results from Experiments 1 and 2 reveal that some of the effects of learning melodies with a visuo-motor component are consistent across development. We found, however, three differences between children and adults, indicating that the way we learn with an associable, but non-causal motor component, such as Curwen hand signs, changes with development. First, although the motor cortex was reactivated in both age groups when participants were presented with visuo-motor melodies, different areas were reactivated in adults and children. Specifically, children showed more regions of reactivation than adults. Second, adults showed activation of the MTG when presented with melodies learned with a motor component, whereas children did not show MTG activation. Third, whereas adults recognized melodies learned in all conditions equally well, children were unable to recognize the melodies they had been able to produce correctly from memory after the training session, regardless of melody learning condition.

Whereas adults and children both showed left premotor activation when listening to melodies learned with a visuo-motor component, children also showed right somatosensory activation. As previously discussed, this finding complements research demonstrating that across development and with acquisition of experience, individuals shift from a diffuse processing network to a more specialized network (e.g., Johnson, 2000; Smith & Gasser, 2005). What is interesting about the results of the present study is that part of this diffuse motor network in children is the somatosensory cortex, which is involved in body placement, not motor planning. Diffuse networks are often recruited because children need extra areas when learning to process new stimuli – for example, the recruitment of right extrastriate cortex during reading decreases as reading skill increases because as children gain experience with letters, they are less reliant on a non-lexical form recognition system

(Tukeltaub et al., 2003). The present study may indicate that children initially rely on their body placement in the world for learning to a much greater extent than adults. Perhaps for children who learn more experientially than adults, a sense of body placement is an important part of the representation of movement, and that children learn in a more 'embodied' fashion than adults who have built up other ways of representing the world. The somatosensory activation in children may also be related to the more important difference: their lack of MTG activation.

The most critical difference in our neuroimaging data is the finding that adults showed activation of the MTG when listening to melodies learned with a motor component, but children did not. The MTG has been implicated as an area that stores the motoric aspect of object or concept representations, and is reactivated when an individual perceives a stimulus with which he or she has associated a motor movement (e.g., Chao & Martin, 2000; Beauchamp & Martin, 2007; Martin et al., 1996). The MTG also shows activation when individuals process gesture (e.g., Kircher et al., 2009; Villarreal et al., 2008; Wakefield & James, in preparation). The finding that adults show this activation for non-causal motor hand signs suggests that they are able to build motoric representations related to something perceived, in this case, a melody, even when the motor movement is only abstractly related to the melody. It seems that children, however, are unable to build this type of connection, even though research indicates that this area is activated when children perceive gesture (Wakefield & James, in preparation). This may mean that it is only with enough experience connecting action and perception that abstract motor movements can become meaningful representations like concretely related actions or gestures. If this is the case, it may be that only meaningful movements can facilitate learning, and this is why adults could recognize melodies and children could not. A second possibility is that children simply lacked the motivation to retain knowledge about the hand signs. It may be that the act of producing the movements was enough to cause the motor cortex to store a motor representation connected to the melodies, but that the MTG would only be activated if children encoded the melodies and hand signs more fully. Related to the MTG activation, it may be that the somatosensory activation occurred in children but not adults because children lacked the ability to connect the movements to the melodies in a deeper way, via representation storage in the MTG. Together, these results demonstrate a developmental difference in how children and adults process action in the context of perception.

It could be argued that because there were no behavioral differences in how well adults recognized melodies learned in the visual, auditory, and visuo-motor conditions, there is no evidence that the MTG activation is facilitative. We argue that low sample size or a ceiling effect (recognition in all conditions was near perfect), led to the lack of difference in the percent of recognized melodies. A related finding of interest was that adults correctly identified learned melodies whereas children did not. This finding may be due to the difference in experimental procedure: adults completed the recognition task the day following learning, whereas children completed the entire experiment in one session. Research has demonstrated that sleep may be important for auditory learning (Gottselig et al., 2004). After learning a set of melodies, in a study conducted by Gottselig and colleagues, participants slept, relaxed in a dark room, or were asked to watch a movie and pay attention to it. This manipulation was followed by a second test of melody learning.

Participants who slept or relaxed performed better on the second learning task than those who watched a movie. The authors concluded that sleep may be a key component for solidifying auditory learning, although they did not conclusively show that sleep was better than simply relaxing without added sensory input. In our study, then, it could be that children would have recognized the melodies if they had been tested the day following. This highlights an interesting finding: both children and adults associated motor learning with the melodies, as evident from the neuroimaging data, whereas it was only adults who recognized melodies. This may indicate that motor learning happens immediately, but for auditory learning to be solidified, sleep, or a restful consolidation period, is necessary.

In practice, Curwen hand signs are taught and used over an extended period of time in the context of music education. With time, it is likely that these hand signs become communicative for the individuals who use them, and may be a useful tool in learning. Results from the present study may indicate that it is not only the presence of a visuo-motor component that will influence its interaction or contribution to an individual's ability to learn, but also the communicative power of the action. To further investigate this idea, it would be beneficial to conduct a study in which participants trained with motoric hand signs over a longer period of time, during which the hand signs would theoretically become analogous to gestures, or to conduct a study with individuals who are already familiar with the Curwen hand sign system, to the point of understanding them in a way that was meaningful and communicative.

In summary, developmental change occurs during melody processing in that children do not encode motor signs as part of semantic representations, but both children and adults form associations among sensori-motor systems, and children actually form a wider network of motor associations. This association leads to motor system recruitment during purely perceptual tasks only when movement is incorporated into the learning episode. Later, in adulthood, sensori-motor associations are made, and motor movement is coded as meaningful to the learning episode. Therefore, as we mature, motor movements that are not causal, but instead, are simply associated with a learned event become more meaningfully connected to the event.

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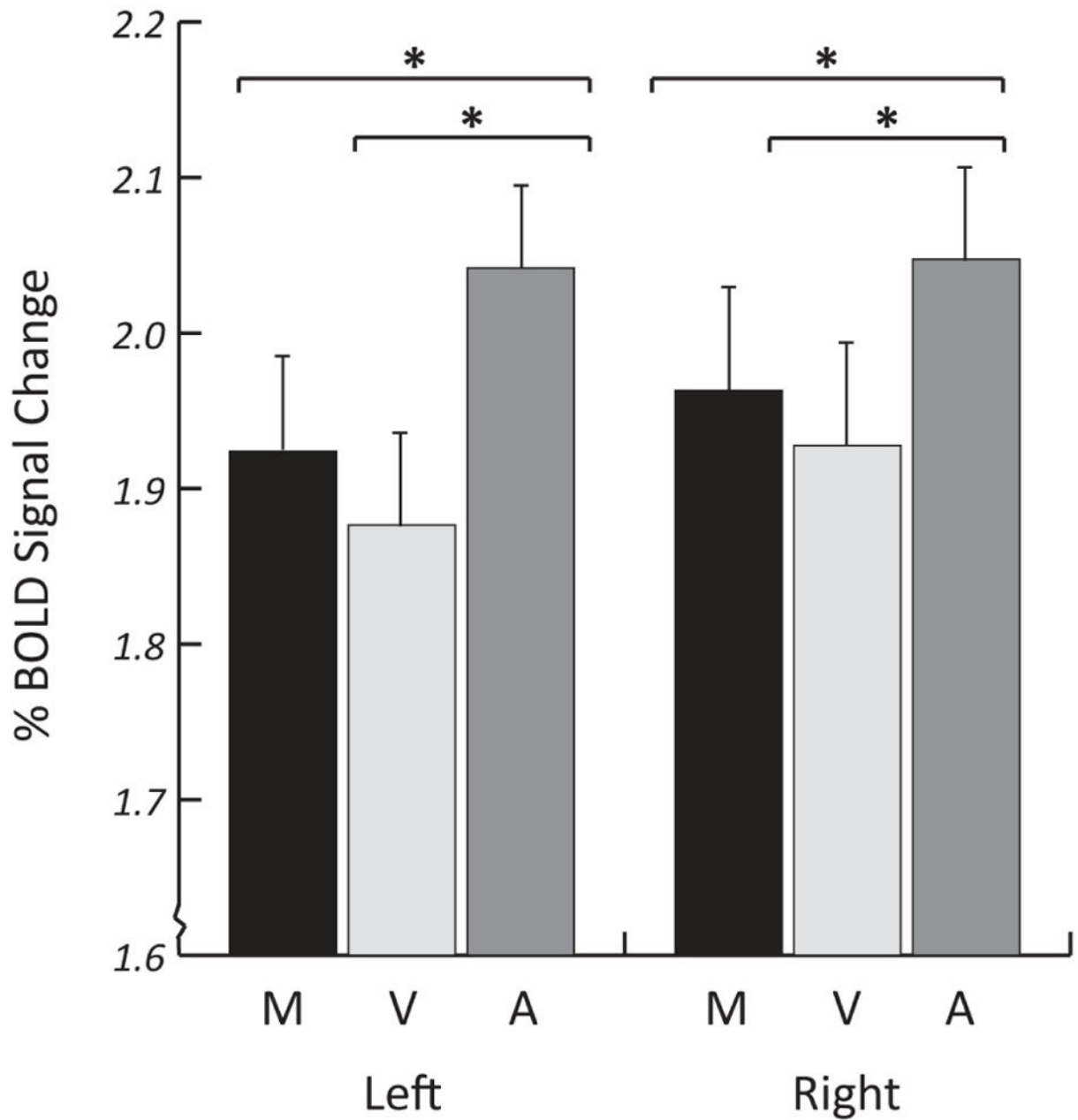
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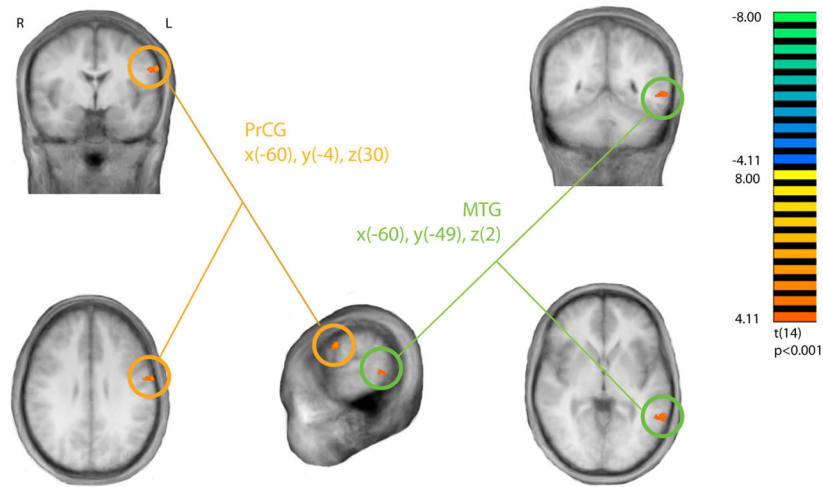
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**Figure 1.**  
 (a) An example of a melody learned by adult participants (b) An example of a visual representation of a melody learned by adults (c) Hand signs taught to adults during the motor learning condition.



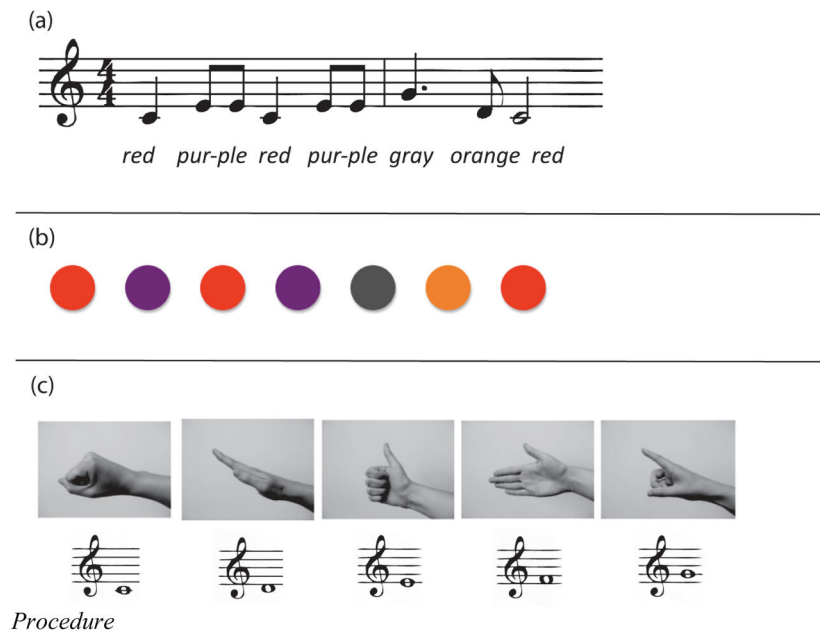
**Figure 2.**

The bar graph displays the average of the peak BOLD activation for each individual to each melody type (visual, motor, and auditory) taken from the left and right auditory ROIs. The specific talairach coordinate from which the peak BOLD activation to the melody types was extracted varied among individuals. Individual talairach coordinates were determined by performing a contrast between the auditory localizer and rest, and using the peak activation to extract data from the combined runs in which participants listened to melodies from the learning conditions.



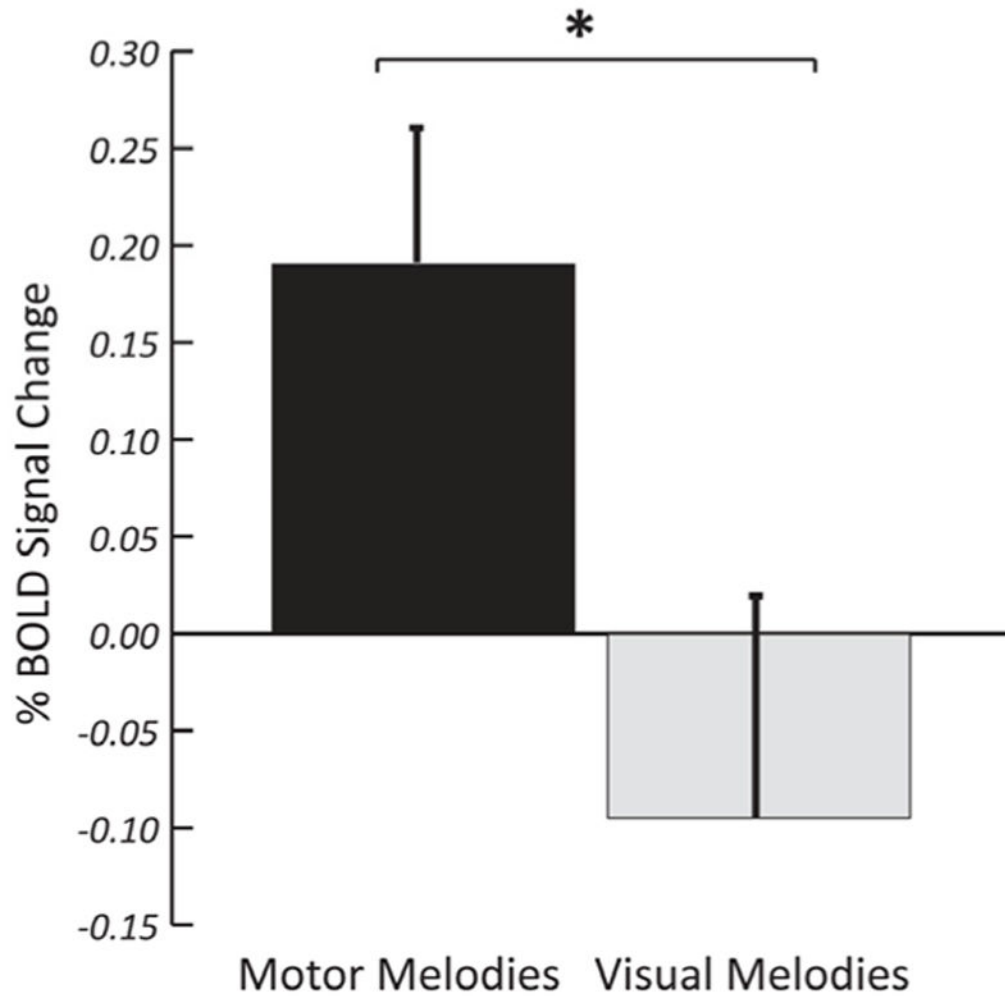
**Figure 3.**

Whole-brain contrasts between melodies learned in the visuo-motor condition and melodies learned in the visual condition. When participants were auditorally presented with melodies learned in the visuo-motor condition, a region of the lPrCG showed greater activation than when participants were presented with melodies learned in the visual condition (Talairach coordinates  $x(-60), y(-4), z(30)$ ). When participants were auditorally presented with melodies learned in the motor condition, a region of the lMTG showed greater activation than when participants were presented with melodies learned in the visual condition (Talairach coordinates  $x(-60), y(-49), z(2)$ ).

**Figure 4.**

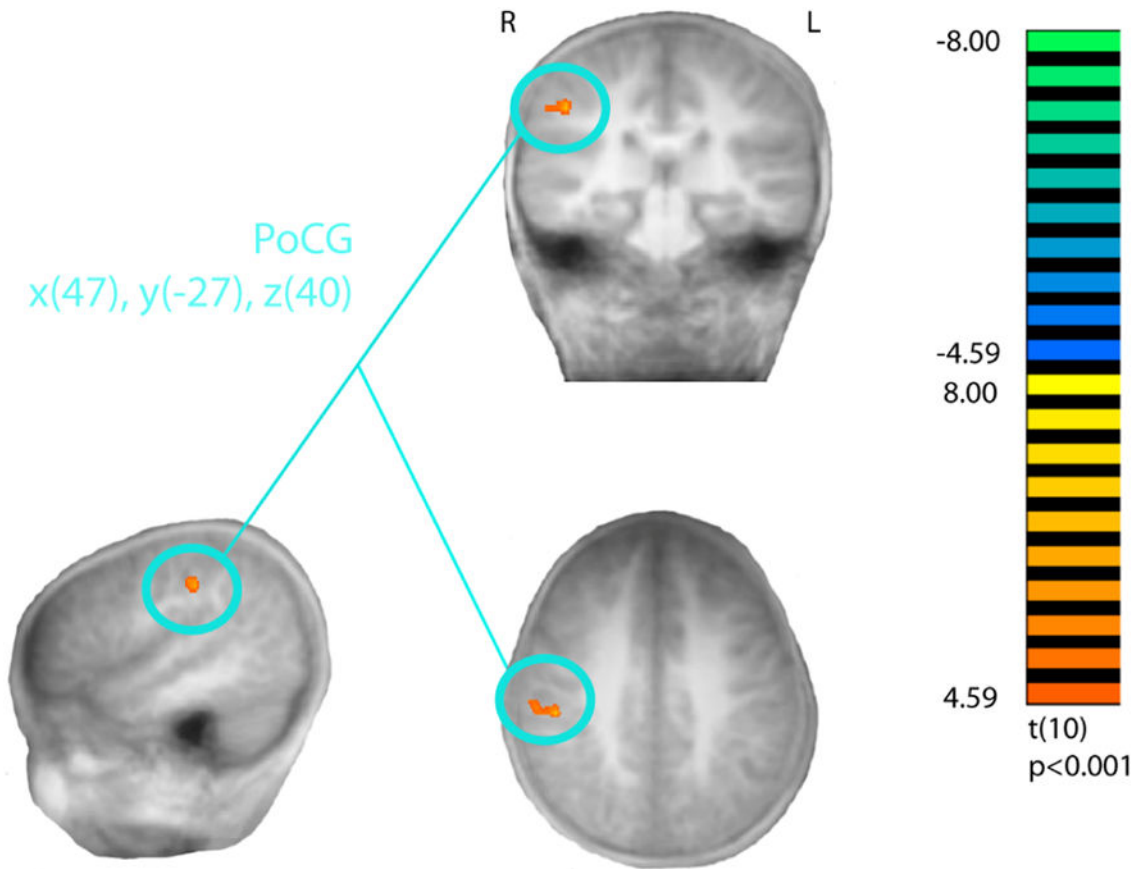
(a) An example of a melody learned by child participants (b) An example of a visual representation of a melody learned by children (note: original visual stimuli were presented in color) (c) Hand signs taught to children during the motor learning condition.





**Figure 5.**

The bar graph displays the average of the peak BOLD activation for each individual to melodies learned in the motor and visual conditions, taken from the motor ROI (peak average Talairach coordinate  $x(-33)$ ,  $y(-25)$ ,  $z(55)$ ). The specific talairach coordinate from which the peak BOLD activation to the melody types was extracted varied among individuals. Individual talairach coordinates were determined by performing a contrast between the auditory localizer and rest, and using the peak activation to extract data from the combined runs in which participants listened to melodies from the learning conditions.



**Figure 6.**

Whole-brain contrasts between melodies learned in the motor condition and melodies learned in the visual condition. When participants were auditorally presented with melodies learned in the motor condition, a region of the rPoCG showed greater activation than when participants were presented with melodies learned in the visual condition (Talairach coordinates  $x(47)$ ,  $y(-27)$ ,  $z(40)$ ).