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Reading sheet music facilitates sensorimotor mu-desynchronization in musicians

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HIGHLIGHTS

- This work demonstrates the important role of the human motor system in perception and understanding.
- The data support the general theory that experience allows for the formation of functional links between arbitrary, abstract percepts and associated acts.
- The important role of the motor system in perception and cognition should be considered in clinical evaluation and treatment of movement disorders.

ABSTRACT

Objective: Recent brain imaging studies have demonstrated that the human mirror system, in addition to becoming active while viewing the actions of others, also responds to abstract visual and auditory stimuli associated with specific actions. Here, we test the hypothesis that when musicians read sheet music an associated motor act is automatically recruited in the same way as when we observe the actions of others.

Methods: Using EEG, we measured event related desynchronization of the sensorimotor mu rhythm (mu-ERD) while musicians and non-musicians listened to music, observed movies of a musical instrument being played and observed a static image of the corresponding sheet music.

Results: Musicians showed significantly greater mu-ERD than non-musicians when observing sheet music and musical performances.

Conclusions: Our results demonstrate that the human motor system aids in the process of perception and understanding by forming functional links between arbitrary, abstract percepts and associated acts.

Significance: This research uniquely adds to the existing body of literature by demonstrating that abstract images are capable of triggering an "action understanding" system when viewed by experts who have formed the appropriate visual-motor association.

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1. Introduction

Both electrophysiological studies in monkeys (Rizzolatti et al., 1996; Umiltà et al., 2001) and neuroimaging studies in humans (Rizzolatti et al., 1996; Iacoboni et al., 1999; Nishitani and Hari, 2000; Buccino et al., 2001; Heiser et al., 2003) support the existence of a neural network comprised minimally of the posterior parietal lobe and the inferior frontal cortex, which responds when performing an action as well as when observing the same action in others. Intracranial recordings from patients support the existence of neurons with mirror properties in humans and demonstrate that a much broader cortical and subcortical network may be involved in the mirror system (Mukamel et al., 2010) and its related functions such as imitation (Babiloni et al., 2008). Activity across the human mirror system is thought to underlie an observation-action matching system that allows for a direct mapping between observed and performed behaviors (Rizzolatti and Craighero, 2004). A series of electroenchapholographic (EEG) (Cochin et al., 2001; Rossi et al., 2002; Muthukumaraswamy and Johnson, 2004a,b; Muthukumaraswamy et al., 2004; Oberman et al., 2005, 2007; Muthukumaraswamy and Singh, 2008; Marshall et al., 2009), magnetoencaphalographic (MEG) (Hari et al., 1998; Nishitani and Hari, 2000; Järveläinen et al., 2001; Caetano et al., 2007) and stimulation (Baldissera et al., 2001) studies in humans have further demonstrated that action observation modulates excitability of primary sensorimotor and spinal neurons. Empirical evidence strongly supports the role of this "human mirror system" in understanding the intention of the actions of others by mapping an observed act onto the motor program for the same or similar act (Nishitani and Hari, 2000; Umiltà et al., 2001; Rizzolatti and Craighero, 2004; Iacoboni et al., 2005).

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Recent experiments in monkeys identified a related class of auditory-visual mirror neurons in fronto-parietal regions that respond not only to action performance and observation, but also to the presentation of an associated action related sound, such as the sound of a breaking peanut or the crumpling of a piece of paper (Kohler et al., 2002; Keysers et al., 2003). In humans, similar auditory induced activity was found in expert piano players listening to a professional piano performance (Haslinger et al., 2005). Functional imaging studies have further shown that reading action words referring to arm, face and leg movements activates primary motor cortex in a somatotopic manner (Hauk et al., 2004; Pulvermüller et al., 2005; Tettamanti et al., 2005). Taken together, these data suggest that the premotor-posterior parietal network is capable of coding abstract representations of actions and their functional consequences (Kohler et al., 2002).

Further evidence leads to the hypothesis that the human mirror system facilitates direct sensorimotor mapping by coding the learned relationship between any arbitrary abstract stimulus and a motor act within an individual's behavioral repertoire. Partial support for this hypothesis comes from recent evidence that the response mapping of this system is malleable and capable of adapting with experience. For example, Catmur et al. (2007) demonstrated that sensorimotor learning quickly reconfigures the network to respond to a novel mapping between an observed and executed act. Lahav et al. (2007) similarly showed greater inferior frontal gyrus (IFG) activity in response to piano tunes that participants were trained to play compared to novel tunes.

EEG is well suited to the study of such sensory motor mappings, as prior EEG and MEG investigations have demonstrated similar event related desynchronization of the sensorimotor mu rhythm, regardless of whether participants observe, imitate or execute actions (Hari et al., 1998; Nishitani and Hari, 2000; Muthukumaraswamy et al., 2004). Sensorimotor mu-desynchronization (mu-ERD) associated with action observation is thought to reflect downstream modulation by the premotor region, and thereby provide a reliable measure of observation-induced activity in human mirror circuits. In support, mu-ERD over the sensorimotor region is coupled with the observation of basic finger movements (Cochin et al., 1999), meaningful actions performed by a robotic arm (Oberman et al., 2007), and when participants are instructed to observe and imitate an experimenter drawing abstract pictures (Marshall et al., 2009). Additionally, EEG studies have demonstrated sensorimotor cortex desynchronization in response to such abstract modalities as hand clapping (Pizzamiglio et al., 2005) and tongue clicking (Hauk et al., 2006).

Here we provide a further test of the hypothesis that the motor system maps learned relationships between abstract stimulus and a motor acts by examining whether the human motor system is sensitive to the arbitrary associations musicians learn between musical notes and the physical act of producing the associated sound. To this end, we use EEG to investigate whether viewing musical notation produces sensorimotor mu-ERD in musicians compared to non-musicians. Musical notation is an abstract visual representation of a musical performance that has putative sensorimotor consequences for those who know how to read music and to translate it into a specific sequence of actions. According to the present hypothesis, the ability to read music is, in part, facilitated by a direct sensorimotor mapping between the notes on the page and the performance they represent. EEG was recorded from musicians and non-musicians who passively observed a piece of sheet music. We predicted that viewing sheet music should result in significant sensorimotor mu-ERD for musicians but not non-musicians. We further predicted that viewing another individual playing an instrument, a basic action observation condition, would result in mu-desynchronization in both musicians and non-musicians. Similarly, viewing unplayable sheet music, created using a series of musical notes that cannot be performed on the primary instrument of the musicians, should result in a lack of (or decrease in) mu-desynchronization in musicians and no desynchronization in non-musicians.

2. Methods

2.1. Participants

Twenty-four right handed (Oldfield, 1971) participants were recruited from the music department and general population at Western Washington University and divided into musician and non-musician groups. Musicians ($n = 12$, 19.6 ± 1.6 years, 6 males) reported having played music for an average of 9.29 years (±3.67 years) and had been reading sheet music for an average of 7.82 years (±4.28 years). Although attempts were made to recruit exclusively violin and trumpet players, nine of the musicians reported that they played additional instruments. The participants in the non-musician ($n = 12$, 19.85 ± 2.58 years, 8 males) could not read sheet music and had never played any musical instruments. All procedures were conducted with written consent from participants and with the approval of the Western Washington University Human Subjects Committee.

2.2. Apparatus

Auditory and visual stimuli were presented using custom Visual Basic software that controlled the timing and added event markers to the EEG record for subsequent segmentation of individual data epochs. All experimental conditions involved the presentation of a simple monophonic melody composed by one of the authors in 4/4 time. The musical piece was broken down into two 4 bar segments, each 7 s in length. Visual images were presented using a 19-inch LCD monitor located approximately 75 cm. from the participant. Audio was presented to the subject using over-ear Senhausser headphones. Trained musicians were videotaped playing the musical piece. Because the majority of participants were violin and trumpet players, both types of stimuli were created. For the trumpet stimuli the movies showed the right hand fingering the valves. For violin stimuli the movie showed the left hand fingering the notes on the violin neck.

2.3. Procedure

Four experimental conditions were explored: (1) *Audio Video* (*AV*), (2) *Audio Sheet* (*AS*), (3) *Sheet Music* (*S*) and, (4) *Unplayable Sheet* (*U*). In the *AV* condition, participants observed the audio–video performances of the solo violin (Fig. 1C) and trumpet performance (Fig. 1D). In the *AS* condition participants were presented with the same audio track as in the *AV* (violin and trumpet) condition while viewing the corresponding static image of the sheet music (Fig. 1A). The *AV* and *AS* were controls intended to elicit human mirror system activity in response to action observation (Muthukumaraswamy et al., 2004) and music presentation (Lahav et al., 2007). The key condition for testing the present hypothesis was the *S* condition (Fig. 1A) in which participants viewed the same static images of sheet music presented in the *AS* condition in the absence of the corresponding sound track. The *U* condition (Fig. 1B) presented sheet music that followed the same rhythmic arrangement as in *S* but the musical notes were placed on the staff in locations making them unplayable. That is, the both the *S* and *U* conditions presented arrays of the same number and general pattern of musical notes, however, only the notes presented in the *S* condition were physically playable to the musicians.

There were a total of 20 trials for each condition. Half the trials presented the first 4 bars of the musical stimulus and half pre-

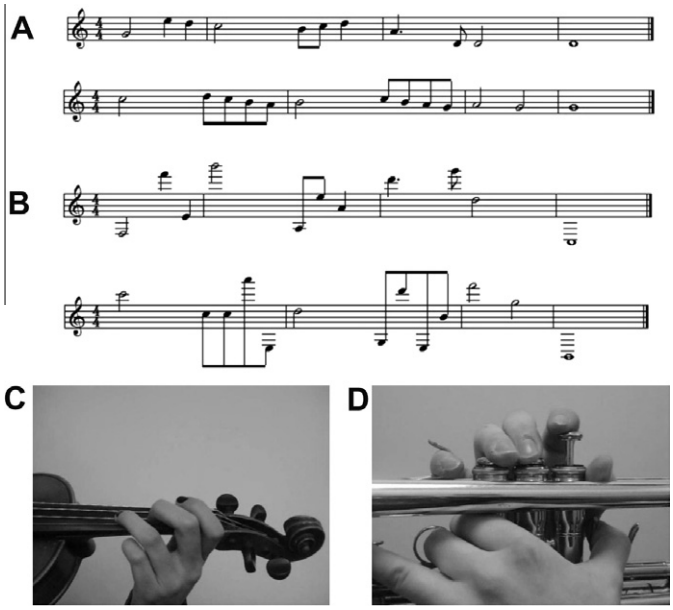

Fig. 1. Music stimuli. (A) The Sheet music condition (*S*) consisted of the static presentation of musical notation. This stimulus was also presented with audio accompaniment of violin and trumpet in the Audio Sheet condition (*AS*). (B) The unplayable condition (*U*). (C and D) Stills from the audio-video (*AV*) condition presenting audio and video of the violin and trumpet performing the musical score presented in the sheet music condition.

sented the second 4 bars. Preliminary analysis showed no significant differences in mu-ERD between musician type (trumpet/violin) or between music type (trumpet/violin). As a result all subsequent analysis was performed on the combined data from all musicians and both trumpet and violin conditions (40 trials each for *AS* and *AV*). During each trial, participants were instructed to passively observe the stimuli on the video monitor and listen to the music in the headphones. Each trial was preceded by a 4 s inter-stimulus interval. Trials were presented in a random order across two blocks of 40 trials each. The total recording time was under an hour.

In addition to the main experiment, each recording session began with a baseline experiment in which participants made simple self paced right and left hand movements. The goal of this experiment was to positively identify the topographical location of mu-ERD. EEG data was collected while participants made rhythmic alternating index and middle finger flexions/extension movements in response to visual instruction to move the fingers of their "right" or "left" hand. Participant's behavior was recorded as a digital trigger in the EEG record generated by a multi button response pad. Each movement segment lasted for 4 s and was followed by a 4 s "rest" cue. An equal number of right and left hand trials were collected.

2.4. EEG data acquisition

Electroenchapalographic signals were recorded continuously from 64 Ag/AgCl active electrodes (Biosemi, Active Two) mounted in an elastic headcap according to a 10-10 configuration. Signals were conducted using a saline-based conductive gel (Signa Gel) and all offsets were maintained below 20 μV. Unreferenced signals were amplified and digitized at 512 Hz using Biosemi Active Two amplifiers and acquisition software. Although electromyography activity was not recorded, all participants were given specific instructions to refrain from moving during the experiment and participants were monitored for evidence of unintended or unconscious movements. The experimenters did not observe any overt movement and participant's self reported that they did not move in response to any stimuli. Because we did not record EMG from the arms, hands, legs and feet, we cannot preclude the occurrence of small, sub-threshold muscle activation present in musicians and not in controls. Nonetheless, even if such activity were found for musicians, it could reflect increased corticospinal activity similar to that observed during action observation and when listening to action sounds (Fadiga et al., 2005).

2.5. Data analysis

Data processing and visualization was accomplished using the EEGLab toolbox running under Matlab 7.0. Continuous data from each participant were referenced to the average potential of all electrodes before bandpass filtering between 1 and 50 Hz. For the preliminary movement paradigm, EEG epochs were extracted from −500 to 4000 ms around the time of the first tap. For the *AV*, *AS*, *S* and *U* conditions, EEG epochs were extracted in the interval from −500 to 7000 ms around the onset of the stimulus. Excessive data loss due to the presence of various artifacts was reduced by using independent component analysis (ICA) to remove obvious artifacts including line noise, muscle artifact and eye blinks, from the data (Jung et al., 2000).

Spectral power was estimated in successive overlapping windows using Gaussian tapered Morlet wavelets as implemented in EEGLab. To achieve an adequate tradeoff between temporal and spectral resolution, the number of cycles per wavelet increased from 1 at the lowest frequency to 35 (increasing by a factor of 0.3 per frequency). Spectral amplitude was estimated at 26 equally spaced frequencies from 4 to 30 Hz and 200 times points from −360.4 to 6858.4 ms. On each trial the magnitude of event related synchrony or desynchrony (Event Related Spectral Perturbation in EEGLab) was expressed in terms of the deviation (in db) from the pre-stimulus interval by subtracting the log of the average pre-stimulus amplitude from the log of each spectral estimate in that bin. Power values were subsequently averaged across trials and collapsed across the 10–12 Hz frequency range to provide an estimate of power in the mu band.

For statistical analysis, results of the ERD analysis were averaged across the time interval from 1500 to 6000 ms after the onset of the stimulus. This temporal interval captured the central portion of the stimulus period while avoiding onset and offset transients. Activity was further collapsed across pairs of electrodes representing the left and right sensorimotor cortex. The selection of these electrode pairs was based on the existing literature and confirmed by the topographic distribution of mu-ERD (10–12 Hz) from the preliminary motor experiment (Fig. 2). Data from the preliminary motor experiment were segmented into right and left hand epochs extending from −1 to 4 s around the onset of the cue to move. Data from each channel was processed in the same manner as described above and averaged across musicians and non-musicians and across left and right hand condition. Results (Fig. 2) are in keeping with the literature (Hari et al., 1998; Nishitani and Hari, 2000; Muthukumaraswamy and Johnson, 2004a,b; Muthukumaraswamy et al., 2004; Oberman et al., 2005, 2007; Muthukumaraswamy and Singh, 2008) and clearly show that right and left hand movement resulted in mu-ERD localized to electrodes C3/CP3 and C4/CP4, respectively. Data from this preliminary experiment were not analyzed further.

Two levels of statistical analysis were performed on the mu band data. First, we sought to characterize the data across all experimental conditions by performing a 2 group non-musician/musician) × 2 hemisphere (left/right) × 4 conditions mixed-design ANOVA. Hemisphere and condition were treated as within subject variables. Post-hoc Bonferroni tests were applied to all significant

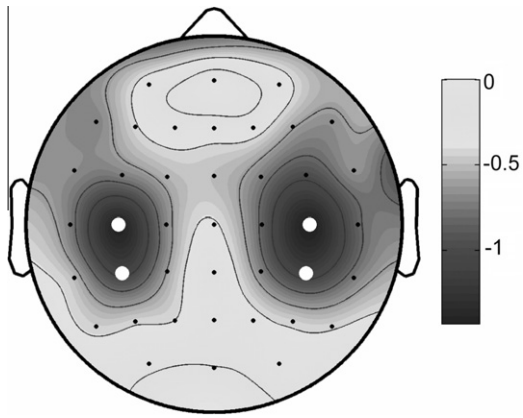

Fig. 2. EEG topographic plot showing alpha ERD during alternating index and middle finger flexion. ERD values are averaged over the interval from 100 to 4000 ms after the onset of a cue to begin moving for both left and right hand trials. The topographic plot clearly demonstrates mu-desynchronization in sensorimotor regions identified by the highlighted electrodes; C3/CP3 in the left and C4/CP4 in the right hemisphere.

main effects and interactions. Second, a series of one sample *t*-tests were employed to determine if the mu-ERD in each condition and group differed significantly from a baseline of zero. Significant deviation from zero was taken as an indication that the stimulus condition modulated activity in sensorimotor cortex for that particular group.

3. Results

A 2 group (musician/non-musician) × 2 hemisphere (left/right) × 4 condition (*S*, *U*, *AV*, *AS*) mixed ANOVA was performed on the mu (10–12 Hz) data. There was a significant main effect of group ($F(1, 22) = 4.54$, $p < 0.045$, $\eta^2 = 0.17$). There was no main effect of hemisphere ($F(1, 22) = 3.131$, $p < 0.091$, $\eta^2 = 0.13$), or condition ($F(3, 66) = 1.19$, $p < 0.320$, $\eta^2 = 0.05$). There was a significant group × condition interaction ($F(3, 66) = 3.14$, $p < 0.031$, $\eta^2 = 0.12$). Post-hoc Bonferroni comparisons revealed that the sheet music condition resulted in greater mu-ERD in musicians ($M = -0.450$, $SD = 0.254$) than non-musicians ($M = -0.162$, $SD = 0.177$), with no other comparisons reaching significance. The mean mu-ERD for musicians and non-musicians across hemisphere and condition is shown in Fig. 3 and Table 1.

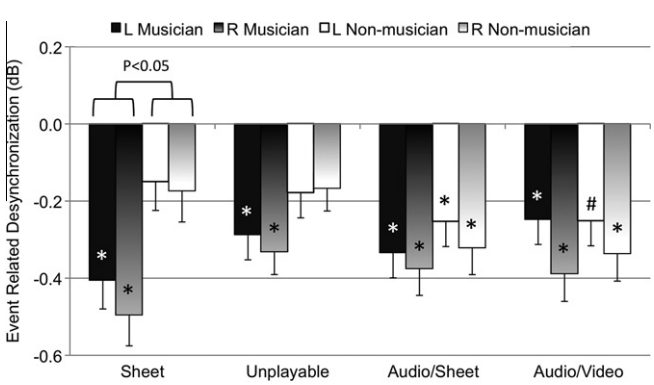

Fig. 3. Mean mu-ERD in the alpha band for all conditions and both experimental groups. Error bars represent the standard error of the mean. The dark bars show data from musicians and the light bars show data from non-musicians. The significant group by condition interaction resulted from the greater mu-ERD in musicians than controls for the sheet condition. Conditions in which mu-ERD was significantly different from zero after correction for multiple comparisons are marked with an (∗) ($p < 0.003$) and a (#) ($p < 0.007$).

Table 1
Mean and standard deviation of mu-desynchronization for each condition and group.

Group	Hemisphere	Condition	*M*	*SD*
Musician	Left	Sheet Music	−0.406	0.29
		Unplayable	−0.287	0.25
		Audio/Sheet	−0.334	0.28
		Audio/Video	−0.248	0.18
	Right	Sheet Music	−0.495	0.33
		Unplayable	−0.332	0.23
		Audio/Sheet	−0.375	0.20
		Audio/Video	−0.389	0.26
Non-musician	Left	Sheet Music	−0.150	0.21
		Unplayable	−0.179	0.19
		Audio/Sheet	−0.253	0.15
		Audio/Video	−0.251	0.26
	Right	Sheet Music	−0.174	0.22
		Unplayable	−0.167	0.16
		Audio/Sheet	−0.321	0.27
		Audio/Video	−0.116	0.23

The alpha level for the *t*-tests comparing mu power during each condition to a baseline of zero was Bonferroni corrected 0.003 to account for multiple comparisons. Musicians showed significant mu-ERD in all conditions and both hemispheres. In contrast, non-musicians showed significant left and right hemisphere mu-ERD during the *AS* condition and significant right hemisphere desynchronization during the *AV* condition. Marginal mu-ERD was observed in the left hemisphere of non-musicians for the audio/video condition ($p = 0.007$). Importantly, non-musicians showed no significant mu-ERD in response to the sheet music condition or the unplayable condition. Conditions and hemispheres demonstrating significant ($p < 0.003$) desynchronization are indicated by an asterisk in Fig. 3.

4. Discussion

The current results support our hypothesis that the human motor system participates in formation of arbitrary sensory-motor associations by demonstrating that musicians show activity in motor areas in response to viewing musical performance as well as in response to viewing the musical notes corresponding to the same performance. Musicians demonstrated significant mu-ERD over motor areas during all the sheet music and audio/video conditions. In contrast, similar motor activity was observed in the control participants during the audio/video condition, but not during the sheet music condition. Importantly, musician's demonstrated greater mu-ERD than controls during the key sheet music condition. This work is compatible with a growing segment in the literature showing that the human motor system can respond to a broad range of stimuli that, through experience or learning, become associated with actions in an individual's behavioral repertoire (Kohler et al., 2002; Keysers et al., 2003; Buccino et al., 2004; Calvo-Merino et al., 2005; Haslinger et al., 2005; Tettamanti et al., 2005; Lahav et al., 2007; Montgomery and Haxby, 2008).

Our current work closely follows recent demonstrations of the flexibility and malleability of the human mirror system. Lahav et al. (2007) provided important early evidence that the human mirror system is malleable in response to learning and experience. Functional MRI revealed that premotor-parietal regions increase activity in response to the sound of practiced piano pieces compared to novel pieces of music comprised of either new notes or the same notes arranged in a novel sequence. Lahav and colleagues posited that learning forged a functional neural link between the sound associated with the action and the corresponding motor representations via a "hearing-doing" mirror system. Catmur et al. (2007) demonstrated that sensorimotor learning quickly reconfig-

ures the motor system. In a baseline condition, TMS was used to stimulate the motor cortex while participants viewed either index finger or pinky finger movements. As expected, TMS resulted in stronger MEPs in the first dorsal interosseous abductor digiti minimi for the index and pinky finger conditions respectively. Half of the participants were then placed into an experimental condition that retrained them to move their index finger when they observed pinky movements and their pinky when they observed index finger movements. Training successfully reversed the visuomotor mapping such that the experimental group showed stronger MEPs in the abductor digiti minimi while viewing index finger movements and in the first dorsal interosseous while viewing pinky movements. Thus, training resulted in the expression of new sensorimotor relationships.

In this study we extend this previous work by showing that sensory to motor mapping within the motor system is not restricted specifically to motor acts and their consequences – but can include arbitrary symbolic relationships. In this case musical notes that provide a symbolic representation of music and its performance activates the motor cortex as evidenced by mu band desynchronization. The implication of these findings is that the learning of a broad range of arbitrary sensorimotor mappings may be represented within the motor system. Although imaging work implicates a parietal-prefrontal network in implicit visuomotor mappings, other brain regions including medial premotor and subcortical regions may also be involved (Babiloni et al., 2004, 2008; Mukamel et al., 2010). Much as reading or listening to action words recruits primary motor cortex (Hauk et al., 2004; Pulvermüller et al., 2005; Tettamanti et al., 2005), expert reading of musical notes may directly activate a motor program associated with the execution of the performance represented by the sheet music. In fact, recent fMRI work suggests that the same sheet music can be associated with different motor programs depending on the specific instrument of expertise (Margulis et al., 2009). Comparison between violin and trumpet players in our current study did not reveal differences in the magnitude of ERD or in the hemisphere where greatest ERD was observed. Nonetheless, the overall small sample and the ability of most participants to play multiple instruments may have precluded the ability to detect differences between groups of musicians.

Desynchronization in the mu band was observed in musicians during the unplayable condition, even though the sequences of notes presented could not be performed on the violin or trumpet. There are at least two possible explanations for this activity. First, 9 of the 12 musicians in our study played multiple instruments including piano and guitar. While the unplayable sheet music could not be performed on a violin or trumpet, it is physically possible to perform the music on a piano or guitar. Thus the notes we displayed may have been within the repertoire of our participants. Second, although technically unplayable, the stimuli were recognizable musical notes located at interpretable locations on the staff. It is possible that the visual presentation of the unplayable sheet music could still result in the motor representation of single actions associated with specific individual notes. Lahav et al. (2007) demonstrated that the coupling of a single note and its associated action (a press on a piano key) activates a limited action-sound circuit, although activity was not as large as when participants heard these same auditory notes in an order they had practiced. The finding that mu-ERD was marginally greater during the playable sheet music condition than the unplayable condition provides at least some support for this notion. Based on the present findings, future similar studies may use control images created with symbols that have similar visual properties to musical notes, but no semantic meaning (Stewart et al., 2003).

The expected mu-ERD was observed for both musicians and non-musicians in response to the visual presentation of movements in the *AV* condition (Hari et al., 1998; Nishitani and Hari, 2000; Muthukumaraswamy et al., 2004). We also predicted that musicians might show greater mu-ERD than non-musicians for the audio/sheet (*AS*) condition because of their ability to map both the sound of the music and the notes onto discrete motor acts. Interestingly, however, non-musicians demonstrated equal mu-ERD as musicians in the *AS* condition. Several studies suggest that simply listening to music activates motor and premotor areas in individuals, yet this activation tends to be significantly stronger in musicians vs. non-musicians (Haueisen and Knösche, 2001; Bangert and Altenmüller, 2003; Bangert et al., 2006; Haslinger et al., 2005). The addition of the sheet music in our study may have led all participants to learn the mapping between the sounds and their corresponding musical notes. Moreover, given that some aspects of beat perception and representation are rooted in the motor system (Zatorre et al., 2007), it is possible that the motor system plays a key role in this process. To date there are few if any multimodal investigations of the human mirror system. Our curious finding, however, encourages new studies in this direction.

Based on the results of several recent studies, some have suggested that the motor system is critical for learning sensorimotor relationships, but may no longer be recruited once expertise has been established. For example Vogt et al. (2007) found that the observation of practiced guitar chords produced less activation in human mirror system than the observation of non-practiced chords, regardless of whether or not participants were experienced or novice guitar players. That is, contrary to the more common notion that the human mirror system is sensitive to observations of behaviors within ones repertoire, Vogt and colleagues posited that left dorsolateral prefrontal activity was involved in combining viso-spatial events into an executable motor action during learning only. More recently, Emmorey et al. (2010) found that when compared to non-signers, hearing-impaired signers showed less activation in the visual-motor circuit during action-signs and action-pantomimes, and suggested that the extensive experience of hearing impaired signers with gestural communication decreased activation. Similarly, Handy et al. (2006) showed that implicit visual motor responding in parietal, premotor and motor cortex decreased with an increase in experience with the visual object.

Our results, however, suggest that expertise is key for inducing implicit visuomotor responses since observation of the sheet music did not result in mu-ERD in the control group and resulted in strong desynchronization in the musician group. Nonetheless, it is possible that mu-ERD in our musicians reflects learning of the novel sheet music and that a decrease in neural responding may result if participants were allowed to practice the music or were presented with sheet music representing a musical score on which they are considered an expert. However, such an explanation does not easily account for why we observed no mu-ERD in non-musicians.

In conclusion, we demonstrate that the association between abstract visual symbols and specific motor programs is mediated through the motor system. These results support the existing literature suggesting that motor system activity responds to the presentation of a variety of motor-meaningful stimuli, and not just meaningful biological actions. Future studies should focus on the differences between experts and novices and how the motor system is involved during the learning process.

References

Babiloni C, Bares M, Vecchio F, Brázdil M, Jurák P, Moretti DV, et al. Synchronization of gamma oscillations increases functional connectivity of human hippocampus and inferior middle temporal cortex during repetitive visuomotor events. Eur J Neurosci 2004;19:3088–98.

Babiloni C, Vecchio F, Bares M, Brázdil M, Nestrasil I, Eusebi F, et al. Functional coupling between anterior prefrontal cortex (BA10) and hand muscle

contraction during intentional and imitative motor acts. Neuroimage 2008;39:1314–23.
Baldissera F, Cavallari P, Craighero L, Fadiga L. Modulation of spinal excitability during observation of hand actions in humans. Eur J Neurosci 2001;13:190–4.
Bangert M, Altenmüller E. Mapping perception to action in piano practice. A longitudinal DC-EEG study. BMC Neurosci 2003;4:26.
Bangert M, Peschel T, Schlaug G, Rotte M, Drescher D, Hinrichs H, et al. Shared networks for auditory and motor processing in professional pianists: evidence from fMRI conjunction. Neuroimage 2006;30:917–26.
Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, et al. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur J Neurosci 2001;13:400–4.
Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund H, et al. Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. Neuron 2004;42:323–34.
Caetano G, Jousmäki V, Hari R. Actor's and observer's primary motor cortices stabilize similarly after seen or heard motor actions. Proc Natl Acad Sci USA 2007;104(21):9058–62.
Calvo-Merino B, Glaser DE, Grèzes J, Passingham RE, Haggard P. Action observation and acquired motor skills: an fMRI study with expert dancers. Cereb Cortex 2005;15(8):1243–9.
Catmur C, Walsh V, Heyes C. Sensorimotor learning configures the human mirror system. Curr Biol 2007;17:1527–31.
Cochin S, Barthelemy C, Roux S, Martineau J. Observation and execution of movement: Similarities demonstrated by quantified electroencephalography. Eur J Neurosci 1999;13:1839–42.
Cochin S, Barthelemy C, Roux S, Martineau J. Electroencephalographic activity during perception of motion in childhood. Eur J Neurosci 2001;13:1791–6.
Emmorey K, Xu J, Gannon P, Goldin-Meadow S, Braun A. CNS activation and regional connectivity during pantomime observation: no engagement of the mirror neuron system for deaf signers. Neuroimage 2010;49:994–1005.
Fadiga L, Craighero L, Olivier E. Human motor cortex excitability during the perception of others' action. Curr Opin Neurobiol 2005;15:213–8.
Handy TC, Tipper CM, Borg JS, Grafton ST. Gazzaniga MS Motor experience with graspable objects reduces their implicit analysis in visual- and motor-related cortex. Brain Res 2006;1097:156–66.
Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G. Activation of human primary motor cortex during action observation: a neruomagnetic study. Proc Natl Acad Sci USA 1998;95:15061–5.
Haslinger B, Erhard P, Altenmüller E, Schroeder U, Boecker H, Ceballos-Baumann AO. Transmodal sensorimotor networks during action observation in professional pianists. J Cogn Neurosci 2005;17:282–93.
Haueisen J, Knösche T. Involuntary motor activity in pianists evoked by music perception. J Cog Neurosci 2001;13:786–92.
Hauk O, Johnsrude I, Pulvermüller F. Somatotopic representation of action words in human motor and premotor cortex. Neuron 2004;41:301–7.
Hauk O, Shtyrov Y, Pulvermüller F. The sound of actions as reflected by mismatch negativity: rapid activation of cortical sensory-motor networks by sounds associated with finger and tongue movements. Eur J Neurosci 2006;23:811–21.
Heiser M, Iacoboni M, Maeda F, Marcus J, Mazziotta JC. The essential role of Broca's area in imitation. Eur J Neurosci 2003;17:1123–8.
Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. Grasping the intentions of others with one's own mirror neuron system. PLoS Biol 2005;3:529–35.
Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G. Cortical mechanisms of human intention. Science 1999;286:2526–8.
Järveläinen J, Schürmann M, Avikainen S, Hari R. Stronger reactivity of the human primary motor cortex during observation of live rather than video motor acts. Neuroreport 2001;12:3493–5.
Jung T, Makeig S, Humphries C, Lee T, McKeown MJ, Iragui V, et al. Removing the electroencephalographic artifacts by blind source separation. Psychophysiology 2000;37:163–78.
Keysers C, Kohler E, Umiltà MA, Fogassi L, Rizzolatti G, Gallese V. Audio-visual mirror neurons and action recognition. Exp Brain Res 2003;153:628–36.
Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, Rizzolatti G. Hearing sounds, understanding actions: action representation in mirror neurons. Science 2002;297:846–8.
Lahav A, Saltzman E, Schlaug G. Action representation of sound: audiomotor recognition network while listening to newly acquired actions. J Neurosci 2007;27:308–14.
Margulis EH, Mlsna LM, Uppunda AK, Parrish TB, Wong PCM. Selective neurophysiologic responses to music in instrumentalists with different listening biographies. Hum Brain Mapp 2009;30:267–75.
Marshall PJ, Bouquet CA, Shipley TF, Young T. Effects of brief imitative experience on EEG desynchronization during action observation. Neuropsychologia 2009;47:2100–6.
Montgomery KJ, Haxby JV. Mirror neuron system differentially activated by facial expressions and social hand gestures: A functional magnetic resonance imaging study. J Cogn Neurosci 2008;20:1866–77.
Mukamel R, Ekstrom AD, Kaplan J, Iacoboni M, Fried I. Single-neuron responses in humans during execution and observation of actions. Curr Biol 2010;20:750–6.
Muthukumaraswamy SD, Johnson BW. Primary motor cortex activation during action observation revealed by wavelet analysis of the EEG. Clin Neurophysiol 2004a;115:1760–6.
Muthukumaraswamy SD, Johnson BW. Changes in rolandic mu rhythm during observation of a precision grip. Psychophysiology 2004b;41:152–6.
Muthukumaraswamy SD, Johnson BW, McNair NA. Mu rhythm modulation during observation of an object-directed grasp. Cogn Brain Res 2004;19:195–201.
Muthukumaraswamy SD, Singh KD. Modulation of the human mirror neuron system during cognitive activity. Psychophysiology 2008;45:896–905.
Nishitani N, Hari R. Temporal dynamics of cortical representation for action. Proc Natl Acad Sci USA 2000;97:913–8.
Oberman LM, Hubbard EM, McCleery JP, Altschuler EL, Ramachandran VS, Pineda JA. EEG evidence for mirror neuron dysfunction in autism spectrum disorders. Cogn Brain Res 2005;24:190–8.
Oberman LM, McCleery JP, Ramachandran VS, Pineda JA. EEG evidence for mirror neuron activity during the observation of human and robot actions: toward an analysis of the human qualities of interactive robots. Neurocomputing 2007;70:2194–203.
Oldfield RC. The assessment and analysis of handedness: the edinburgh inventory. Neuropsychologia 1971;9:97–113.
Pizzamiglio L, Aprile T, Spitoni G, Pitzalis S, Bates E, D'Amico S, et al. Separate neural systems for processing action- or non-action-related sounds. Neuroimage 2005;24:852–61.
Pulvermüller F, Hauk O, Nikulin VV, Ilmoniemi RJ. Functional links between motor and language systems. Eur J Neurosci 2005;21:793–7.
Rizzolatti G, Craighero L. The mirror-neuron system. Annu Rev Neurosci 2004;27:169–92.
Rizzolatti G, Fadiga L, Gallese V, Fogassi K. Premotor cortex and recognition of motor actions. Cogn Brain Res 1996;3:131–41.
Rossi S, Tecchio F, Pasqualetti P, Ulivelli M, Pizzella V, Romani GL, et al. Somatosensory processing during movement observation in humans. Clin Neurophysiol 2002;113:16–24.
Stewart L, Hensen R, Kampe K, Walsh V, Turner R, Frith U. Brain changes after learning to read and play music. Neuroimage 2003;20:71–83.
Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, et al. Listening to action-related sentences activates fronto-parietal motor circuits. J Cogn Neurosci 2005;17:273–81.
Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, et al. I know what you are doing: a neurophysiological study. Neuron 2001;32:91–101.
Vogt S, Buccino G, Wohlschläger AM, Canessa N, Shah NJ, Zilles K, et al. Prefrontal involvement in imitation learning of hand actions: effects of practice and expertise. Neuroimage 2007;37:1371–83.
Zatorre RJ, Chen JL, Penhune VB. When the brain plays music: auditory-motor interactions in music perception and production. Nat Rev Neurosci 2007;8:547–58.