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Reading sheet music activates the mirror neuron system of musicians: an EEG investigation.

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Reading sheet music activates the

Mirror Neuron System of musicians:

An EEG investigation

By

Lawrence Paul Behmer Jr.

Accepted in Partial Completion

Of the Requirements for the Degree

Master of Science

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Lawrence Behmer
May 17, 2010
Reading sheet music activates the

Mirror Neuron System of musicians:

An EEG investigation

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Lawrence Paul Behmer Jr.
April 2010

Abstract
Recent brain imaging studies have demonstrated that the 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. Growing evidence suggests that such mappings are learned leading to the hypothesis that the motor system may respond to any stimuli strongly associated to a specific motor response. Reading sheet music is an excellent example in which musicians rapidly and automatically translate arbitrary visual symbols into music by a well practiced series of actions. Here we test the hypothesis that when musicians read sheet music an associated motor program is automatically recruited in the same way as when we observe the actions of others. Using EEG, we measured mu desynchronization in the alpha and beta bands of the sensorimotor cortex while musicians and non-musicians observed various music stimuli. Musicians showed significantly greater mu desynchronization than non-musicians in both alpha and beta bands when observing sheet music and musical performances. Our results demonstrate that mirror neuron activity is not restricted to motor acts and their consequences, suggesting that the symbolic representation of music and its performance activate the mirror neuron system. The implication of these findings is that the learning of a broad range of arbitrary sensorimotor mappings may be represented within the motor system and facilitated by the mirror neuron activity.

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1.1 Frontal and parietal areas involved in movement

It was once believed that the cortex is organized according to anatomically and functionally discrete regions that serve specific roles in sensation, perception, and motor activity. Moreover, classical theory held that a somatotopic representation of the body surface for controlling the execution of movement was found exclusively in the primary motor cortex. This idea is reflected in most psychology, neuroscience, and anatomy textbooks as Woolsey’s simiunculus and Penfield’s homunculus. Rizzolatti points out in his book, *Mirrors in the Brain* (Rizzolatti & Sinigaglia, 2006) that, historically, this simplistic example has provided a convenient explanation for the localization of movement in the motor cortex, but also led to the belief that the motor cortex is simply a relay for executive function related to movement, with no perceptual or cognitive role in movement.

Today, however, it is accepted that a number of regions in the frontal cortex, in addition to the primary motor cortex in Brodmann’s area 4 (FI in monkeys and MI in humans), contribute to motor representation and execution. These so-called premotor areas are located within BA 6, an anterior motor area that can be divided into mesial, dorsal, and ventral regions, each of which are further subdivided into anterior and posterior sections. This region is often referred to as the agranular cortex, as its fourth layer is agranular, giving it a unique cytoarchitecture when compared to other regions of the frontal cortex (Matelli, Luppino, & Rizzolatti, 1985; 1991). In macaques, electrophysiological stimulation has shown that these motor areas contain diverse somatotopic maps (Rizzolatti, Lupino, & Matelli, 1998). The posterior mesial region contains the supplementary motor area (SMA; F3 in monkeys), which when stimulated with low electrical currents results in a complete representation of body movements. The anterior mesial regions (known in human as the pre-SMA and in monkey as F6) elicits arm movements only after the
application of high intensity currents. The posterior dorsal region (PMd or F3) contains a somatotopic representation of the leg and arm, while the anterior area (prePMd or F7) is not responsive to electrical stimulation (Schlag & Schlag-Rey, 1987). The ventral region (PMv) contains a posterior area (F4) that responds to electrical stimulation with movements of the arms, neck, and face, while the anterior area (F5) involve movements of the hand and mouth (Figure 1).

An examination of the afferent and efferent connections between these cortical areas is important for understanding how these regions contribute to motor behavior and cognition (Rizzolatti & Sinigaglia, 2006). Areas F2-F5 have direct connections to F1, and together with F1, project dorsally via the corticospinal tract. Furthermore, F1 axons terminate in the intermediate section of the spinal cord in the lamina containing the motor neurons and are responsible for the fine control of movement, while F2-F5 end almost entirely in the intermediate region of the spinal cord, determining the overall frame of movement (He, Dum, & Strick, 1993; 1995). In contrast, F6 and F7 share direct connections only with the areas F2-F5 and project to the brainstem, controlling movement indirectly via subcortical relays (Keizer & Kuypers, 1989).

Premotor and supplementary motor areas receive afferent connections from the prefrontal cortex and the cingulate cortex (Luppino & Rizzolatti, 2000). Projections from prefrontal cortex to the anterior premotor and supplementary motor areas may communicate intentions of actions. Cingulate input to these same areas is likely related to the emotional and motivational aspects of our actions. In contrast, the posterior parietal lobe and the intraparietal sulcus project to the more posterior motor areas and are likely engaged in visual motor transformations.

Based on more recent functional and anatomical information, contemporary theories of motor function propose that the agranular primary and supplementary areas are involved in the
representation and execution of behavior and work in parallel with the posterior parietal cortex to integrate sensory and motor information relative to specific stimuli. Additionally, the prefrontal and cingulate cortices provide a mechanism for intentions and motivation to influence the planning, and temporal execution of movement.

1.2 Evidence for a mirror neuron system in macaque monkeys

Early single-unit recordings in macaque monkeys found that a subset of neurons in F5 discharged when a monkey performed goal-directed motor actions, such as grasping a piece of food with either their left hand, right hand, or mouth (Rizzolatti et al., 1988). F5 activation was strongest during actions such as grasping with the hands or mouth, tearing, or manipulating an object. Subsequent research by Sakata, Taira, Murata, and Mine (1995) and Murata, Gallese, Luppino, Kaseda, and Sakata (2000) focused on neural activity in the anterior parietal area, which not only sends efferent connections to F5, but also discharges during hand movements. They identified neurons in the anterior intraparietal area (AIP) that could be divided into three categories. Motor dominant neurons discharged when the monkey grasped an object in either the light or dark, but not during visual fixation on the object. Visual and motor neurons were active in all three conditions, but showed the most activity during grasping in the light. Finally, visual dominant neurons were most active during the light and object fixation condition, but not in the dark condition. Given these findings, it was suggested that the parietal-F5 circuit may be involved in the process of visuo-motor transformation that facilitates grasping.

Taking this a step further, Rizzolatti, Fadiga, Gallese, and Fogassi (1996) observed unique visual motor neurons in the macaque F5 that discharged both when the monkey grasped or manipulated a piece of food, as well as when the monkey observed the same action being performed by a conspecific or human experimenter. These visual motor neurons were labeled
“mirror neurons.” They also observed that the type of motor oriented stimuli the mirror neurons reacted to varied, based on the specificity of the stimuli. Certain F5 neurons were considered strictly congruent, and fired only when the monkey observed or executed goal directed actions that were virtually identical to what they observed. Broadly congruent mirror neurons appeared to be more flexible, firing when the monkey observed an experimenter place a piece of food on a sheet with a precision grip or when an experimenter grasped an object with their whole hand. However, these same neurons were active only when the monkey executed the action utilizing the precision grip and not the whole hand (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996).

To test the extent to which knowledge of a motor act affected the processing of sensory information, Umilta and coworkers (2001) recorded F5 activity using a grasping and miming paradigm. The first portion of this experiment consisted of two conditions. In the first condition, the researcher reached out and grasped a block placed in front of the monkey. In the second condition the researcher mimed the same grasping movement in the absence of the block. During the grasping condition, F5 neurons were active in the monkey as soon as the researcher formed the full hand grip and continued to fire as he grasped the block. No significant activity occurred during the miming condition. During the second portion of the experiment the monkey observed the researcher placing the building block behind a partition, or miming the same action. F5 “mirror” neurons fired when the object was actually behind the partition. The fact that the monkey neurons could discriminate between the two hidden conditions suggests that they were able to utilize knowledge from past perceptual activity and use that knowledge understand an action directed towards the object. Mirror neurons did not show activity regarding the presence of the object, but did show activity when an action was taken upon the object. The selective
response during hidden conditions suggested that inference of the hidden object and action
directed toward the object enabled the monkey to determine the goal of the action.

Ferrari, Gallese, Rizzolatti, and Fogassi (2003) further observed that in addition to coding
for hand actions, mirror neurons in F5 code for the execution and observation of biological
actions performed with the mouth, such as ingestive acts. What was most remarkable about this
study was the finding that certain “mouth neurons” also discharged when the monkey performed
or observed communicative mouth actions, such as lip smacking or lip protrusion. This
“communication” component to the MNS caused Ferrari and others (see for example, Skipper,
Goldin-Meadow, Nussbaum, & Small, 2007) to speculate that F5 may be a homologue to
Broca’s area (the left hemisphere speech areas first reported by Paul Broca) and that biological
communicative actions may be mapped onto the MNS.

The behavior of this fronto-parietal motor circuit in macaques led to the hypothesis that
the purpose of this mirror neuron system was to facilitate action imitation and the implicit
understanding of biological actions and their sensorimotor consequences (Rizzolatti et al., 1996).
That is, observation of an action would evoke simulation of the same action in one’s own motor
system, thereby providing a reference for understanding the intentions of the action and its
performer.

1.3 Evidence for a mirror neuron system in humans

Given the important role attributed to mirror neurons in monkeys, a critical and ongoing
question is whether a similar mirror neuron system (MNS) exists in humans. Brodmann’s area
40, in the inferior parietal lobe, is the human homologue to the rostral inferior parietal lobule of
the macaque, where monkeys have been shown to exhibit mirror neuron activity. As mentioned
previously, the frontal operculum in the inferior frontal gyrus (BA 44 and functionally known as
Broca’s area in the left hemisphere) is the human homologue of the monkey F5. In addition to Broca’s area being responsible for speech production, this region contains a somatotopic representation of the hand and mouth. Given the evidence that F5 and parietal regions respond during action-observation in macaques, several recent investigations considered the possibility that similar “mirror” activity might be found in humans.

Functional magnetic resonance imaging (fMRI) experiments have shown strong evidence for the existence of a mirror neuron circuit in humans. For example, Iacoboni and colleagues (1999) used fMRI to show that both Broca’s and the parietal area were activated while participants observed and imitated basic finger movements. The activation of these areas suggested that human BA 40 and 44 constitute a comparable circuit that facilitates direct matching of an executable action with an observed action, as witnessed in the macaque studies. Buccino and colleagues (2001) had participants observe video of individuals performing biological actions towards objects (food, cups) and non-objects (miming a grasping action). fMRI revealed significant activation in different areas of the premotor cortex when participants observed object directed action with the mouth, hand, or foot. Additionally, parietal activity was strongest during the object vs. non-object conditions. Iacoboni et al. (2005) reported similar findings when participants observed videos of situations that included a context, an action, and a setting that implied intention. Overall, these findings suggest that a critical component of the MNS may be to encode intentions regarding actions that are being observed.

The summed electrical activity of large numbers of cortical neurons can be recorded from on or above the surface of the scalp using electroencephalography (EEG) and magnetoencephalography (MEG). Cortical activity is characterized by typical spectral components that fall roughly into functional bands ranging from the lower delta (up to 4 Hz) and
theta (4 to 7 Hz), to alpha (8 to 12 Hz), beta (12 to 30 Hz), and gamma ranges (30 to 100 Hz). Activity in these bands reflects dynamic changes in perception cognition and action (Chatrian, Petersen, & Lazarte, 1959; Markand, 1990). With respect to motor behavior, somatosensory processing is most strongly associated with activity in the alpha range (~10Hz). In 1952, Gestaut described the rolandic mu, a waveform in the alpha band (8-12 Hz) with a bimodal shape and localized over primary motor cortex (cited by Salmelin & Hari, 1994). The bimodal shape of the mu rhythm results in two dominant frequency components, one in the alpha band (8-12 Hz) and one in the beta band (10-30 Hz). According to Gestaut, the mu rhythm was present in the absence of movement and was suppressed on the contralateral side during movement.

Subsequent experiments have associated the 10 Hz and 20 Hz components of the mu rhythm with activity in somatosensory and motor cortex respectively (reviewed in Hari & Salmelin, 1997). Suppression of intrinsic cortical rhythms has been termed desynchronization and is related to activation of the underlying cortical areas. Thus a decrease in power within alpha and beta bands over contralateral sensorimotor cortex may be taken as an index of increased activity in the somatosensory and motor cortex respectively.

EEG and MEG investigations reveal that observing or imitating meaningful biological actions results in sensorimotor mu-desynchronization in the motor cortex. This desynchronization also occurs when individuals execute these same actions on their own (Hari et al., 1998; Muthukumaraswamy, Johnson, & McNair, 2004; Nishitani & Hari, 2000). The sensorimotor cortex origin of desynchronization associated with action observation is thought to reflect the downstream modulation of motor activity by fronto-parietal mirror neurons and thus provides a reliable measure of MNS activity. When measuring mirror neuron activity, BOLD detection in fMRI tends to reveal activation in the premotor areas, while EEG/MEG studies
localize MNS activity by measuring oscillations in the primary sensorimotor cortex. When comparing data between fMRI and EEG/MEG experiments, it is important to take into account that the two imaging methods record different facets of brain activity, therefore, comparison of the use of these two methods should be looked at as complementary, and not necessarily contradictory. BOLD measurements are sensitive to opened- and closed-field configurations, while EEG/MEG are sensitive to open field configurations (Muthukumaraswamy & Singh, 2008a). Spiny stellate cells, which represent roughly 15% of the neocortex have closed-field configurations (Creutzfeldt & Houchin, 1974). These cells elicit little to no activity when measured with EEG/MEG (Murakami & Okada, 2006). However, the firing rates of these cells, as well as their metabolic demands, allow for robust recording under fMRI. These same cells are virtually absent of activity when recorded using EEG/MEG. Conversely, EEG/MEG is extremely sensitive to synchronous neural activity, and has been shown to detect activity that is absent in fMRI (Muthukumaraswamy & Singh, 2008a). A recent experiment compared BOLD and MEG activity in the visual system. MEG oscillations demonstrated large changes in the gamma band, with no changes in the BOLD response (Muthukumaraswamy & Singh, 2008b). This result is consistent with previous modeling work which suggested that as little as 1% of mini-columns firing in synchronous activity can account for 75% of the EEG/MEG signal detected at the scalp (Nunez, 1981). These small changes in synchrony that are detected with EEG/MEG are not likely to produce enough activity to be detected by fMRI (Nunez & Silberstein, 2000).

In support, mu event related desynchronization (mu-ERD) over the motor region accompanies the observation of basic finger movements (Cochin, Barthelemy, Roux, & Martineau, 1999), meaningful actions performed by a robotic arm (Oberman, McCleery,
Ramachandran, & Pineda, 2007), and when participants are instructed to observe and imitate an experimenter drawing abstract pictures (Marshall, Bouquet, Shipley, & Young, 2009). In adolescents, observing meaningful biological actions resulted in desynchronization over motor areas in the theta band, the developmental equivalent to adult alpha and beta (Cochin, Barthelemy, Roux, & Martineau, 2001). Thus it appears that EEG is a valuable tool for investigating how the MNS modulates activity in the primary sensorimotor cortex.

1.4 Mirror neuron activation in response to abstract stimuli

In addition to their sensitivity to the observation of biological actions, researchers have discovered that mirror neurons in the macaque respond to abstract stimuli, such as action oriented language (Keysers, et al., 2003; Kohler, Keysers, Umilta, Fogassi, & Gallese, 2002). Single-unit recording in monkeys identified audiomotor neurons in the F5 that respond both when the monkey broke a peanut or heard the sound of a peanut being broken. The firing rate of the F5 neurons increased further when the monkey simultaneously observed and heard the peanut being broken. In this way, action understanding via the MNS was shown to arise from an auditory stimulus that indirectly signaled a meaningful action. Recent brain imaging studies have demonstrated MNS activation in humans during presentation of abstract stimuli. For example, EEG studies have shown motor cortex activity indicative of mirror system activation in response to abstract auditory stimuli such as hand clapping (Pizzamiglio et al., 2005) and tongue clicking (Hauk et al., 2006).

When examining the overall body of MNS literature, it is clear that the MNS may respond to a broad range of biological and abstract stimuli as long as an association between the stimuli and a motor response has been established. In addition to stimuli involving grasping, researchers have also observed mirror neuron activation when participants read action related
words (Hauk, Johnsrude, & Pulvermuller, 2004; Pulvermuller, Hauk, Nikulin, & Ilomoniemi, 2005; Tettamanti et al. 2005). Montgomery and Haxby (2008) reported activation of the mirror neuron system when participants viewed or imitated communicative hand gestures and facial expressions, or produced their own gesture or expression in response to a prompted word stimulus that described the action. This suggests that the MNS facilitates the processing of biological images critical for understanding of non-verbal social communication. Conversely, during neutral hand gestures (open palm) and facial expressions (non-emotive), participants showed no MNS activity. These latter studies are interesting, not only from a standpoint of presenting further evidence for a human MNS equivalent of the macaque, but also because they suggest that this action understanding mechanism may be sensitive to learned associations between actions and their functional importance.

1.5 Mirror neurons and expertise

The sensitivity of MNS to learned associations is exemplified by research demonstrating that MNS is most active for the observation of actions within the viewer’s own behavioral repertoire. In macaques, F5 neurons displayed activity when monkeys observed researchers performing ingestive or communicative (lip smacking or lip protrusion) facial gestures (Ferrari et al., 2003), suggesting that the monkey MNS encodes mouth actions that are part of the monkey’s motor repertoire. In an fMRI study, Calvo-Merino, Glaser, Grezes, Passingham, and Haggard (2005) found that when trained dancers observed dance styles that corresponded to their area of expertise, they showed significant activation of the MNS and superior temporal sulcus as opposed to a control group of naïve non-dancers who showed no significant MNS activity. In addition, Haslinger and coworkers (2005) found activity in the MNS circuit when expert piano players listened to a professional piano performance suggesting that auditory stimuli are capable
of activating the MNS in those for whom the stimuli impart specific motor information or consequences. The assumption is that the sound of a piano music was translated into the motor action of executing the piano performance.

1.6 Mirror neurons and sensorimotor learning

Considered together, the mounting evidence leads to the hypothesis that the mirror neuron system provides a 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 the MNS is malleable and capable of adapting with experience. For example, Catmur, Walsh, and Heyes (2007) demonstrated that sensorimotor learning quickly reconfigures the mirror neuron system to respond to a novel mapping between an observed and executed act. Lahav, Saltzman, and Schlaug (2007) similarly showed greater IFG activity in response to piano tunes that participants were trained to play compared to novel tunes. These studies suggest that properties of the MNS may be acquired via observation and experience. Thus, through sensorimotor training the mirror neuron system became sensitive to new representations of a learned behavior.

1.7 Hypotheses

When considered together, the foregoing data suggest that the mirror neuron system provides a flexible and adaptable mechanism for the efficient mapping of environmental events and stimuli onto their motor consequences and associations. Such research leads to the suggestion that the mirror neuron system is capable of directly representing motor related information within any abstract stimuli regardless of the modality over which they are presented or of the representational form they take. This study extends previous work by examining the
ability of the mirror neuron system to respond to novel and completely abstract stimuli that are associated, through learning and experience, with specific behaviors. To this end we use EEG to investigate the effect of iconic images in sheet music and music performance on the mirror system of musicians and non-musicians. As a musician acquires competency a sensory motor mapping is formed between the notes on the page and the performance they represent. In short, we predict that the mirror neuron system allows for “notes on a page” to be translated directly into the associated motor action by those who can both play and read music. Observing the sheet music should facilitate action-understanding by implicitly translating the music notation into a potential motor act, matching what is being observed with an already understood action within the trained musician’s motor repertoire. In contrast, viewing musical notes should have no influence on the activity in non-musicians because no mapping exists between the perception of the notes and the action of playing an instrument.

Method

2.1 Participants

Nineteen 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 could play music and read sheet music, whereas non-musicians could neither play an instrument nor read sheet music. One of the non-musicians was dropped from the analysis because of excessive muscle and eye movement artifacts in the EEG. Musicians (N=12, 20.3 ±3.02 years, 5 males) reported having played music for an average of 8.33 years (+/- 4.01 years) and had been reading sheet music for an average of 8.96 years (+/- 2.74 years). Although attempts were made to recruit violin and trumpet players, nine of the musicians reported that they played multiple instruments. The participants in the non-musician
(N=6, 19.82 ±2.48 years, 4 males) group all reported that they 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 novel piece of
music composed by one of the authors. The piece of was written in 4/4 time and consisted of a
simple monophonic melody. The musical piece was broken down into two 4 bar segments, each
7 seconds 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. 2c) and trumpet performance (Fig. 2d). 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. 2a).
The AV and AS were controls intended to elicit MNS activity in response to action observation
and music presentation. The key condition for testing the present hypothesis was the S condition (Fig. 2a) 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. 2b) 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 twenty trials for each condition. Half the trials presented the first 4 bars of the musical stimulus and half presented 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 four second interstimulus interval. Trials were presented in a random order across two blocks of 40 trials each. The total recording time was under an hour.

Prior to gathering data during the music conditions, EEG data was collected from each participant to positively identify the topographical location of the sensorimotor cortex. We asked participants to perform 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 visual cue lasted for four seconds followed by a four second “rest” cue. An equal number of right and left hand trials were collected. Figure 3 shows the
topographic distribution of mu desynchronization (12-20 Hz.) grand averaged across musicians and non-musicians. Results are in keeping with the literature (Hari et al., 1998; Hari and Salmelin, 1997; Muthukumaraswamy, Johnson, & McNair, 2004; Muthukumaraswamy & Johnson, 2004a; Muthukumaraswamy & Johnson, 2004b; Salmelin & Hari, 1994) and clearly show right and left hand motor activity localized to electrodes C3/CP3 and C4/CP4 respectively. Data from this preliminary experiment were not analyzed further.

2.4 EEG data acquisition

Electroencephalographic signals were recorded continuously from 64 Ag/AgCl active electrodes (Biosemi) mounted in an elastic headcap according to a 10-20 configuration. Signals were conducted using a saline-based conductive gel (Signa Gel) and all offsets were maintained below 20 uV. Unreferenced signals were amplified and digitized at 512 Hz using Biosemi amplifiers and acquisition software.

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 ms 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 in the range 4 to 30 Hz (1 Hz bins) was computed using a series of non-overlapping sinusoidal wavelets transformations. On each trial the power values in each bin were corrected by subtracting the average pre-stimulus power level for that bin. Thus power is expressed in terms of deviation from baseline or prestimulus levels. Power values were subsequently collapsed into discrete alpha (10 – 12 Hz), and low beta (12 -20 Hz) bands.

The precise frequency for mu suppression in the sensorimotor region varies based on the experiment. Hari and colleagues have consistently examined mu rebound in the 7-14 Hz and 14-25 Hz range (Caetano, Jousmaki, & Hari, 2007; Hari et al., 1998; Hari and Salmelin, 1997; Salmelin & Hari, 1994). Muthukumaraswamy and colleagues reported mu suppression in the 10 – 12 Hz and 15 – 25 Hz range (Muthukumaraswamy, Johnson, & McNair, 2004; Muthukumaraswamy & Johnson, 2004a; Muthukumaraswamy & Johnson, 2004b). Additionally, researchers have observed mu suppression in the 8 – 13 Hz and 14 – 25 Hz range (Oberman et al., 2005; Oberman, et al., 2007; Pineda, 2005; Pineda, 2008). Most of these experiments selected ranges of interest based on the magnitude of mu suppression exhibited by their participants. In this experiment participants exhibited the most robust mu-ERD in the 10 – 12 Hz and 12 – 20 Hz bands.

For statistical analysis, results of the ERD analysis were averaged across the time interval from 1500 to 6000 milliseconds after the onset of the stimulus. The temporal interval used captured the central portion of the stimulus period in order to avoid onset and offset transients. Activity was further collapsed across pairs of electrodes representing the left and right sensorimotor cortex.

Several levels of analysis were performed on the frequency band data. First, we sought to characterize the data across all experimental conditions by performing a separate 2 group non-
musician/musician) x 2 hemisphere (left/right) x 4 conditions mixed-design ANOVA on each frequency band. Hemisphere and condition were treated as within subject variables. Post-hoc Bonferroni tests were applied to all significant main effects and interactions. Second, independent sample \( t \)-tests were employed to determine if the mu desynchronization in each condition and group differed significantly from a baseline of zero. Finally, paired \( t \)-tests were applied to pre-selected comparisons of interest to test for predicted differences between key experimental conditions. Specifically \( t \)-tests were used to tests differences between musicians and non-musicians at each condition.

**Results**

3.1 Qualitative Data

The topographic plot for the sheet music condition demonstrates the significant differences in sensorimotor mu-ERD between musicians and non-musicians in the beta band (Figure 4). The plot of the non-musician group viewing the sheet music condition shows EEG activity mostly in the visual areas (Figure 4a). No sensorimotor mu-ERD is present for the non-musician group. Figure 4b shows the topographic plot for the musician group while viewing the sheet music. These participants also show a robust level of activity in the visual areas, in addition to mu-ERD in the sensorimotor region. Subtracting the EEG activity of the non-musicians from the musicians helps to reduce the considerable visual area activity that is shared by both groups, which reveals apparent mu-ERD in the sensorimotor regions for the musicians (Figure 4c).

3.2 Alpha band

A 2 group (musician/non-musician) x 2 hemisphere (left/right) x 4 condition (\( S, U, AV, AS \)) mixed ANOVA was performed on the alpha band (10 – 12 Hz) data. There was a significant
main effect of group \((F(1, 16) = 5.06, p < 0.039, \eta^2 = 0.24)\), with musicians \((M = -0.759, SD = 0.185)\) showing significantly greater mu-ERD than the non-musicians \((M = -0.038, SE = 0.262)\). There was no main effect of hemisphere \((F(1, 16) = 0.68, p < 0.421, \eta^2 = 0.04)\), or condition \((F(3, 48) = 2.20, p < 0.101, \eta^2 = 0.12)\). There was a significant hemisphere x condition interaction \((F(3, 48) = 7.11, p < 0.001, \eta^2 = 0.31)\) because the alpha desynchronization was greater in the left hemisphere only for the sheet condition (table 1a).

Independent sample \(t\)-tests comparing alpha power during each condition to a baseline of zero showed that in the non-musician group (see table 3 for \(t\)-tests), the level of alpha desynchronization did not differ from significantly zero for any condition or hemisphere. In contrast, significant left hemisphere alpha desynchronization was observed in musicians (see table 2 for \(t\)-tests) during the \(S\) condition \((M = -1.199, SE = 0.257), t(11) = -4.16, p < .002, and the \(AV\) condition \((M = -0.704, SE = 0.293), t(11) = -2.33, p < .040\). Alpha desynchronization was observed in the right hemisphere during the \(S\) condition \((M = -0.849, SE = 0.240), t(11) = -3.34, p < .007\), the \(U\) condition, \((M = -0.849, SE = 0.267), t(11) = -2.81, p < .017\), and the \(AV\) condition \((M = -1.130, SE = 0.322), t(11) = -3.60, p < .004\) (table 2). Thus musicians demonstrated bilateral mu desynchronization across all but the \(AS\) condition whereas non-musicians did not demonstrate significant desynchronization across any condition. The bar graph in figure 5a demonstrates the mean mu-ERD for musicians and non-musicians across hemispheres and conditions in the alpha band.

Subsequent paired \(t\)-tests revealed that for the \(S\) condition, musicians showed significantly greater alpha desynchronization than non musicians in the right, \(t(12) = -2.74, p < .019\), and left hemisphere, \(t(15) = -2.45, p < .024\). No other paired tests were significant in this band (table 4a).
Paired t-tests were performed to compare the means of violin players and trumpet players across each condition and hemisphere. No paired t-tests were significant in the alpha band (table 5).

3.3 Beta Band

A 2 group (musician/non-musician) x 2 hemisphere (left/right) x 4 condition (S, U, AV, AS) mixed ANOVA performed in the beta band (12 – 20 Hz) revealed a main effect of group ($F(1, 16) = 8.12, p < .012, \eta^2 = 0.34$) and hemisphere ($F(3, 48) = 5.36, p < .034, \eta^2 = 0.25$). There was no significant main effect for condition ($F(1, 16) = 2.21, p < .009, \eta^2 = 0.12$) and no interactions. Desynchronization was significantly greater in the musician group ($M = -1.014, SE = 0.181$) than in the non-musician group ($M = -0.121, SE = 0.256$). Additionally, the left hemisphere ($M = -0.692, SE = 0.160$) showed significantly greater mu desynchronization than the right hemisphere ($M = -0.443, SE = 0.171$) (table 1b).

The non-musician (see table 8 for t-tests) group showed no significant desynchronization in either hemisphere during any condition. The musician group (see table 7 for t-tests) showed significant ERD power in the left hemisphere during the S condition ($M = -1.543, SE = 0.344$), $t(11) = -5.01, p < .001$, the U condition ($M = -1.543, SE = 0.344$), $t(11) = -3.90, p < .002$, the AS condition ($M = -1.543, SE = 0.344$), $t(11) = -2.75, p < .019$, and the AV condition ($M = -1.543, SE = 0.344$), $t(11) = -5.46, p < .000$. In the right hemisphere, mu desynchronization was different than zero during the S condition ($M = -1.543, SE = 0.344$), $t(11) = -3.34, p < .007$, the U condition ($M = -1.543, SE = 0.344$), $t(11) = -2.80, p < .017$, and the AV condition ($M = -1.543, SE = 0.344$), $t(11) = -4.51, p < .001$ (table 7). The bar graph in figure 5a demonstrates the mean mu-ERD for musicians and non-musicians across hemispheres and conditions in the beta band.
Paired t-tests revealed a significant difference between musicians and non musicians during the $S$ condition in the right, $t(15) = -3.18, p < .006$, and left hemisphere, $t(15) = -2.34, p < .034$, and in the $U$ condition, $t(13) = -3.45, p < .004$, and $AS$ conditions, $t(14) = -2.32, p < .038$, in the left hemisphere (table 4b).

Paired t-tests were performed to compare the means of violin players and trumpet players across each condition and hemisphere. No paired t-tests were significant in the beta band (table 6).

**Discussion**

4.1 General Findings

The current results support our hypothesis that the mirror neuron system is critical for learning and expressing 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 alpha and beta desynchronization over motor areas for most conditions. In contrast, similar motor activity was not observed in the control participants who could neither play nor read music. Importantly, musicians demonstrated greater mu desynchronization than controls in both alpha and beta bands for the key sheet and unplayable conditions. This work is compatible with a growing literature showing that the mirror neuron system can respond to a broad range of stimuli that, through experience or learning, become associated with actions in an individual’s own behavioral repertoire (Buccino, et al., 2004; Calvo-Merino et al., 2005; Haslinger et al., 2005; Keysers et al. 2003; Kohler et al. 2002; Lahav et al., 2007; Montgomery & Haxby, 2008; Tettamanti, et al., 2005).
4.2 Learning and mirror neuron system activation

Our current work closely follows recent demonstrations of the flexibility and malleability of the mirror neuron system. Lahav and colleagues (2007), provided important early evidence that the mirror neuron is malleable due to learning and experience. Functional MRI revealed that the mirror neuron system in their participants responded to the sound of practiced piano songs compared to novel pieces of music comprised of either new notes or the same notes arranged in a novel sequence. They posited that learning forged a functional neural link between the sound associated with the action and the corresponding motor representations by what they referred to as the “hearing-doing” mirror neuron system. Catmur et al., (2007) demonstrated that sensorimotor learning can quickly reconfigure the mirror neuron 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 interosseus 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 interosseus while viewing pinky movements. Thus the MNS mapped the sensorimotor relationships rather than responding strictly to homologous perceived and performed movements.

In the present study we extend previous work by showing that sensory to motor mapping by the mirror neuron 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 mirror neuron system as evidenced by alpha and beta band desynchronization. The implication of these findings is that the learning of a broad range of arbitrary sensorimotor mappings, such as green means go and red means stop may be represented within the motor system and facilitated by the mirror neuron system. Much as reading or listening to action words recruits primary motor cortex (Hauk et al., 2004; Pulvermuller 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.

Based on the results of several recent studies, some have suggested that the mirror neuron 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 MNS activation 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 MNS is sensitive to observations of behaviors within ones repertoire, Vogt and colleagues posited that left dorsolateral prefrontal activity was involved in combining visuo-spatial events into an executable motor action during learning only. More recently, Emmorey, Xu, Gannon, Goldin-Meadow, and Braun (2010) found that when compared to non-signers, hearing-impaired signers showed less activation in the MNS circuit during action-signs and action-pantomimes, and suggested that the extensive experience of hearing impaired signers with gestural communication decreased activation of the MNS. Our results, however, suggest that expertise is key for activating the mirror neuron system since observation of the sheet music did not result in mu desynchronization in the control group and resulted in strong desynchronization in the musician group. Nonetheless, it is possible that MNS
activity in our musicians reflects learning of novel sheet music and that a decrease in MNS may result if participants 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 MNS activity in non-musicians.

4.3 Activation during the Unplayable Condition

Mu desynchronization was observed in musicians during unplayable conditions even though the sequences of notes presented could not be performed on the violin and trumpet. A possible consideration for activation during the unplayable condition may rest in the fact that nine of our twelve participants were multi-instrumentalists. Musicians who are capable of playing multiple instruments often show varying levels of proficiency and competency in some instruments over others. While everyone in our musician group played either trumpet or violin, their experience with other instruments may have altered their perception of the unplayable condition. For example, seven of the musicians also self reported that they played piano for a minimum of five years. If the ability to play piano influenced the processing of the musical stimuli then the performance, although sounding dissonant, would still be playable and result in motor activity. Given the small sample size and prevalence of piano players, there is no way to rule this possibility out.

While more stringent controls regarding future samples is prudent, it is unlikely that the ability to play multiple instruments acted as a confound during the unplayable condition, given the levels of mu-ERD in the playable sheet music condition. Although technically unplayable, the stimuli were recognizable musical notes located at interpretable locations on the staff. Thus, it is possible that the visual presentation of individual notes is associated with single actions either on the instruments identified in this study or on other instruments with which participants
may have expertise. Similar findings have been reported by Lahav and colleagues (2007), who observed unexpected premotor and right IFG activity when participants listened to a control condition that reorganized the notes from the song they were trained to play into a new, novel melody. These authors suggested that the coupling of a single note and its associated action (a press on a piano key) was able to activate a limited action-sound circuit. This limited activation was not as large as when participants heard these same auditory notes in the order that they were trained to play. Similarly, Calvo-Merino et al. (2005) found that both ballet and capoeira dancers still exhibited MNS activation when viewing each other’s dance movements. Mirror neuron activity was greatest when dancers viewed their own dance style, but was also clearly present when viewing the dance style in which they were not trained. The results of Calvo-Merino and colleagues (2005) could stem from the fact that although the two dance style may differ, much of the technique required to perform the movements is similar (spins, leg lifts, etc.). In the case of our data, the meaning of the meter and rhythm of the sheet music, regardless of the music notes position, may be sufficient to activate a limited motor representation in musicians. 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 (e.g. Stewart, Hensen, Kampe, Walsh, Turner & Frith, 2003; see Figure 6).

4.4 Mu-ERD/EEG

Mu-ERD was more pronounced in the beta band than the alpha band. Previous research has shown that mu-ERD in the alpha band (8-12 Hz.) tends to be localized in the somatosensory cortex, while mu-ERD in the beta band (12-30 Hz.) is localized in the primary motor cortex.
(reviewed in Hari & Salmelin, 1997). The greater beta activity in our data suggests that the observed mu-ERD is generated by activity predominantly within motor rather than sensory systems, and that the features of the musical stimuli provoke motor associated activity. These findings and their conclusion are in keeping with EEG and MEG investigations demonstrating that observing or imitating meaningful biological actions results in sensorimotor mu-desynchronization similar to that occurring when participants execute actions on their own (Hari et al. 1998; Muthukumaraswamy, Johnson, & McNair, 2004; Nishitani & Hari, 2000).

Recent fMRI work suggests that audio clips of music can be associated with different motor programs depending on the participant’s specific instrument of expertise, with greater activation being lateralized to the left hemisphere (Margulis, Mlsna, Uppunda, Parrish, & Wong, 2009). A recent fMRI study also found that action sounds elicited stronger left ventral premotor activation than in the right hemisphere (Gazzola, Aziz-Zadeh, & Keysers, 2005). Additionally, Aziz-Zadeh, Iacoboni, Zaidel, Wilson, and Mazziotta (2004) used TMS to observe corticospinal activation during audio stimuli which appeared to be lateralized to the left hemisphere. They suggested that action coding occurs in the right hemisphere during visual stimuli, while the left hemisphere responds to visual and auditory information. The majority of EEG studies on the mirror neuron system involve participants making/observing hand movements. This results in strong activation in the sensorimotor region of the hemisphere contralateral to the hand that is moving/being observed. While we observed greater mu-ERD in the left hemisphere in both alpha and beta bands, with levels reaching significance only in the beta band, overall activity was clearly bilateral. On the surface, our data appears to contradict findings that suggest MNS activity is left-lateralized.
One possible explanation for why the data in our study showed bilateral desynchronization may be found in the nature of our participants. While our stimuli was designed in a manner that presented violin activity being performed with the left hand, and trumpet performance with the right hand, the actual act of performing on both instruments requires bilateral recruitment of the motor areas. For example, playing violin requires the use of both hands (one hand to work the bow and the other hand to perform on the fretboard). Trumpet players press down the valves with the fingers of their right hand and steady the instrument with their left hand, however, the embouchure required to blow air into the instrument’s mouthpiece requires the use of bilateral facial muscles. It may be possible that the motor associations that activated the MNS during both viewing sheet music and performance manifested in a manner more representative of the necessary mechanics required of an actual performance, leading to bilateral motor area activation. This conclusion seems likely considering that observations of beta mu-ERD in the sensorimotor region tend to be bilateral and associated with motor activity (Hari & Salmelin, 1997).

4.5 Conclusion

In conclusion, we demonstrate that the association between abstract visual symbols and specific motor programs is mediated through the motor system and likely facilitated by the mirror neuron system. These results support the existing literature that suggests that MNS activity occurs during the presentation of a variety of motor-meaningful stimuli, and not just meaningful biological actions. Some questions exist regarding the manner in which the MNS functions during sensorimotor learning. Future studies should focus on the differences between experts and novices and how they process stimuli that they are both familiar and unfamiliar with.
References


Figure 1. Mesial and lateral view of the macaque brain. This figure shows the motor and posterior parietal cortex subdivided into a series of anatomical and functional areas. The areas of the agranular frontal cortex are designated by the letter F followed by an Arabic numeral. The areas of the posterior parietal cortex are designated by the letter P followed by one or more letters. The drawing on the right shows the region buried in the intraparietal sulcus (IP). Other abbreviations: (AI) inferior arcuate sulcus, (AS) superior arcuate sulcus, (C) central sulcus, (Ca) calcarine fissure, (Cg) cingulate sulcus, (IO) inferior occipital cortex, (L) lateral fissure, (Lu) lunate sulcus, (OT) occipital-temporal sulcus, (P) main sulcus, (POM) medial parietal-occipital fissure, (STS) superior temporal sulcus (Figure and anatomical descriptions from Rizzolatti, Luppino, & Matelli, 1998; Luppino & Rizzolatti, 2000).
Figure 2. Experimental stimuli. A) Sheet music condition (S). This stimulus was also presented with audio accompaniment of violin and trumpet and represented the AudioSheet condition (AS).

B) Unplayable condition (U). C & D) Video and audio of violin and trumpet performing the sheet music condition (AV).
Figure 3. EEG topographic plot showing alpha ERD during alternating index and middle finger flexion. ERD values are averaged over the interval from 100 ms to 4000 ms after the onset of a cue to begin moving. Data are also averaged over left and right hand movement conditions. 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.
Figure 4. Topographic plots for non-musicians and musicians while viewing sheet music in the beta band. A) shows the overall EEG power for non-musicians while viewing the sheet music condition. B) shows the overall EEG power for musicians while viewing the sheet music condition. C) shows the topographic plot when subtracting the EEG power of non-musicians from musicians. The difference eliminates the prevalence of the visual activity, revealing mu-ERD in both hemispheres in musicians while viewing sheet music. The white dots denote electrodes C3/CP3 and C4/CP4.
Figure 5. Mean mu-ERD in the alpha and beta bands during presentation of music stimuli in the alpha (A) and beta (B) bands.
Figure 6. Example of “music-like” stimuli used in Stewart et al. 2003. A) shows a standard bar of treble clef sheet music in 4/4 time, with meaningful notes and meter. B) demonstrates an example of “music-like” stimuli that could be used as a control for future experiments. Stimulus (B) appears to have characteristics that are like sheet music, they have no real meaning. This bar of sheet music lacks the necessary information to produce a performance. It is likely that it would have no salient meaning for a musician.
Table 1

ANOVA results for the alpha and beta bands

(A) Alpha band

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<th>P</th>
<th>η²</th>
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Note. *p < 0.05, **p < .010, ***p < .001

(B) Beta band

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Note. *p < 0.05, **p < .010, ***p < .001
Table 2

One-sample t-tests for musicians in the alpha band (10 – 12 Hz) across conditions and hemispheres.

(A) Left hemisphere

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<td>Unplayable</td>
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<td>0.274</td>
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<td>Instrument AudioVideo *</td>
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<td>11</td>
<td>0.040</td>
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</table>

Note. *p < 0.05, **p < .010, ***p < .001

(B) Right hemisphere

<table>
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<th>Condition</th>
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<td>Instrument AudioSheet</td>
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<tr>
<td>Instrument AudioVideo **</td>
<td>-3.596</td>
<td>11</td>
<td>0.004</td>
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</table>

Note. *p < 0.05, **p < .010, ***p < .001
Table 3

One-sample t-tests for non-musicians in the alpha band (10 – 12 Hz) across conditions and hemispheres.

(A) Left hemisphere

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Note. *p < 0.05, **p < .010, ***p < .001

(B) Right hemisphere

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<td>Instrument AudioVideo</td>
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</table>

Note. *p < 0.05, **p < .010, ***p < .001
Table 4

*Paired t-tests comparing Sheet music and Unplayable conditions across hemisphere for musicians in the alpha and beta bands.*

(A) Alpha band

<table>
<thead>
<tr>
<th>Condition</th>
<th>t-score</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left Sheet vs. Left Unplayable</td>
<td>-2.364</td>
<td>11</td>
<td>0.038</td>
</tr>
<tr>
<td>Right Sheet vs. Right Unplayable</td>
<td>-0.001</td>
<td>11</td>
<td>0.999</td>
</tr>
</tbody>
</table>

*Note. *p* < 0.05, **p < .010, ***p < .001

(B) Beta Band

<table>
<thead>
<tr>
<th>Condition</th>
<th>t-score</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left Sheet vs. Left Unplayable</td>
<td>-0.641</td>
<td>11</td>
<td>0.535</td>
</tr>
<tr>
<td>Right Sheet vs. Right Unplayable</td>
<td>-0.668</td>
<td>11</td>
<td>0.518</td>
</tr>
</tbody>
</table>

*Note. *p* < 0.05, **p < .010, ***p < .001*
Table 5

*Paired t-tests comparing trumpet vs. violin players across hemispheres and conditions in the alpha band (10 – 12 Hz).*

<table>
<thead>
<tr>
<th>Condition</th>
<th>t-score</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left Sheet</td>
<td>-1.503</td>
<td>5</td>
<td>0.193</td>
</tr>
<tr>
<td>Left Unplayable</td>
<td>-0.493</td>
<td>5</td>
<td>0.643</td>
</tr>
<tr>
<td>Left Instrument AudioSheet</td>
<td>-1.790</td>
<td>5</td>
<td>0.133</td>
</tr>
<tr>
<td>Left Instrument AudioVideo</td>
<td>1.787</td>
<td>5</td>
<td>0.134</td>
</tr>
<tr>
<td>Right Sheet</td>
<td>-0.340</td>
<td>5</td>
<td>0.748</td>
</tr>
<tr>
<td>Right Unplayable</td>
<td>0.144</td>
<td>5</td>
<td>0.914</td>
</tr>
<tr>
<td>Right Instrument AudioSheet</td>
<td>-0.673</td>
<td>5</td>
<td>0.531</td>
</tr>
<tr>
<td>Right Instrument AudioVideo</td>
<td>1.364</td>
<td>5</td>
<td>0.231</td>
</tr>
</tbody>
</table>

*Note. *p < 0.05, **p < .010, ***p < .001*
Table 6

*Paired t-tests comparing trumpet vs. violin players across hemispheres and conditions in the beta band (12 – 20 Hz).*

<table>
<thead>
<tr>
<th>Condition</th>
<th>t-score</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left Sheet</td>
<td>-1.670</td>
<td>5</td>
<td>0.156</td>
</tr>
<tr>
<td>Left Unplayable</td>
<td>0.161</td>
<td>5</td>
<td>0.878</td>
</tr>
<tr>
<td>Left Instrument AudioSheet</td>
<td>0.316</td>
<td>5</td>
<td>0.765</td>
</tr>
<tr>
<td>Left Instrument AudioVideo</td>
<td>0.327</td>
<td>5</td>
<td>0.757</td>
</tr>
<tr>
<td>Right Sheet</td>
<td>-0.890</td>
<td>5</td>
<td>0.414</td>
</tr>
<tr>
<td>Right Unplayable</td>
<td>-0.681</td>
<td>5</td>
<td>0.526</td>
</tr>
<tr>
<td>Right Instrument AudioSheet</td>
<td>-0.863</td>
<td>5</td>
<td>0.428</td>
</tr>
<tr>
<td>Right Instrument AudioVideo</td>
<td>0.992</td>
<td>5</td>
<td>0.367</td>
</tr>
</tbody>
</table>

*Note.* *p* < 0.05, **p** < .010, ***p*** < .001
Table 7

One-sample t-tests for musicians in the beta band (12 – 20 Hz) across conditions and hemispheres.

(A) Left hemisphere

<table>
<thead>
<tr>
<th>Condition</th>
<th>t-score</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheet ***</td>
<td>-5.009</td>
<td>11</td>
<td>0.001</td>
</tr>
<tr>
<td>Unplayable **</td>
<td>-3.902</td>
<td>11</td>
<td>0.002</td>
</tr>
<tr>
<td>Instrument AudioSheet *</td>
<td>-2.748</td>
<td>11</td>
<td>0.019</td>
</tr>
<tr>
<td>Instrument AudioVideo ***</td>
<td>-5.455</td>
<td>11</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Note. *p < 0.05, **p < .010, ***p < .001

(B) Right hemisphere

<table>
<thead>
<tr>
<th>Condition</th>
<th>t-score</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheet **</td>
<td>-3.342</td>
<td>11</td>
<td>0.007</td>
</tr>
<tr>
<td>Unplayable *</td>
<td>-2.797</td>
<td>11</td>
<td>0.017</td>
</tr>
<tr>
<td>Instrument AudioSheet</td>
<td>-1.627</td>
<td>11</td>
<td>0.132</td>
</tr>
<tr>
<td>Instrument AudioVideo ***</td>
<td>-4.508</td>
<td>11</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Note. *p < 0.05, **p < .010, ***p < .001
Table 8

One-sample t-tests for non-musicians in the beta band (12 – 20 Hz) across conditions and hemispheres.

(A) Left hemisphere

<table>
<thead>
<tr>
<th>Condition</th>
<th>t-score</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheet</td>
<td>-2.212</td>
<td>5</td>
<td>0.078</td>
</tr>
<tr>
<td>Unplayable</td>
<td>0.140</td>
<td>5</td>
<td>0.894</td>
</tr>
<tr>
<td>Instrument AudioSheet</td>
<td>0.458</td>
<td>5</td>
<td>0.666</td>
</tr>
<tr>
<td>Instrument AudioVideo</td>
<td>-1.734</td>
<td>5</td>
<td>0.144</td>
</tr>
</tbody>
</table>

Note. *p < 0.05, **p < .010, ***p < .001

(B) Right hemisphere

<table>
<thead>
<tr>
<th>Condition</th>
<th>t-score</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheet</td>
<td>0.683</td>
<td>5</td>
<td>0.525</td>
</tr>
<tr>
<td>Unplayable</td>
<td>-0.936</td>
<td>5</td>
<td>0.392</td>
</tr>
<tr>
<td>Instrument AudioSheet</td>
<td>0.798</td>
<td>5</td>
<td>0.461</td>
</tr>
<tr>
<td>Instrument AudioVideo</td>
<td>-0.468</td>
<td>5</td>
<td>0.660</td>
</tr>
</tbody>
</table>

Note. *p < 0.05, **p < .010, ***p < .001
Appendix A

CONSENT FORM – PARTICIPANT’S COPY

Purpose and Benefit:
Experiments on the brains of humans and monkeys have found evidence of a mirror neuron system that discharges when someone performs goal-directed actions, such as grasping, holding, or manipulating objects, as well as when they observe the same, or similar, actions performed by someone else. It has been proposed that the mirror neuron system facilitates action-understanding through mapping onto the mirror neuron system an already learned motor repertoire, allowing one to understand or execute an observed action on an implicit level. The purpose of this experiment is to see if the iconic representations of musical notes activate the mirror neuron system in trained musicians in the same manner as language, gestures, and abstract sounds.

I UNDERSTAND THAT:
1) This experiment will involve the filling out of a questionnaire (to determine hand preference) and passively observing a series of audio and visual stimuli involving music. My participation in the experimental procedure will involve approximately 40 minutes.

2) The electrical activity of my brain will be recorded during the experiment through a set of electrodes placed in a cap and fitted onto my head. A water-soluble conductive gel will be placed on my scalp under each electrode. At the end of the experiment the position of each electrode on my head will be measured. My participation in the setup and clean up of the electrodes will involve approximately 30 minutes.

3) Although recording of the electrical activity of my brain is a non-invasive procedure, there is a small risk that I may feel discomfort from the cap or the conductive gel. There is also a small risk of experiencing fatigue during the experiment. In either event I can stop the experiment whenever necessary. I may benefit from the experience of participating in a cognitive neuroscience experiment.

4) My participation is voluntary; I may choose to withdraw from participation at any time without penalty.

5) All information is confidential. My signed consent form will be kept in a locked cabinet separate from the brain recordings and movement data. My name will not be associated with any of my data at any time.

6) My signature on this form does not waive my legal rights of protection.

7) This experiment is conducted under the supervision of Dr. Jantzen. Any questions that I have about the experiment or my participation may be directed to him at 650-4046.

If you have any questions about your participation or your rights as a research participant, you can contact Geri Walker, WWU Human Protections Administrator (HPA), (360) 650-3220, geri.walker@wwu.edu. If during or after participation in this study you suffer from any adverse effects as a result of participation, please notify the researcher directing the study or the WWU Human Protections Administrator.

I have read the above description, am at least 18 years of age, and agree to participate in this study.

________________________________________  ________________________
Participant Signature      Date

________________________________________
Participant's PRINTED NAME

NOTE: Please sign both copies of the form and retain the “Participant” copy.
### Handedness Questionnaire

<table>
<thead>
<tr>
<th>When performing the following activities...</th>
<th>Which hand do you prefer</th>
<th>Do you ever use the other hand?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Writing:</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Drawing:</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Throwing:</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Using Scissors:</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Using a Toothbrush:</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Using a Knife (without fork):</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Using a Spoon:</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Using a Broom (upper hand):</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Striking a Match:</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
<tr>
<td>Opening a Box (lid):</td>
<td>NONE  LEFT  RIGHT</td>
<td>YES  NO</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Totals</th>
<th></th>
<th></th>
</tr>
</thead>
</table>

| Handedness Score                           |                          |
|---------------------------------------------|--------------------------|-------------------------------|
Appendix C

Musical Ability Survey

1. Do you play: Violin / Trumpet / Both/ Neither

2. How many years have you been playing the violin/trumpet?: ________

3. Please list any additional instruments that you play and the number of years you have been playing them:

<table>
<thead>
<tr>
<th>Instrument</th>
<th>Years Played</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
</tbody>
</table>

4. Can you read sheet music?: Yes/No

5. How many years have you been reading sheet music?: ________