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Musical training increases functional connectivity, but does not enhance mu suppression

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ABSTRACT

Musical training provides an ideal platform for investigating action representation for sound. Learning to play an instrument requires integration of sensory and motor perception-action processes. Functional neuroimaging studies have indicated that listening to trained music can result in the activity in premotor areas, even after a short period of training. These studies suggest that action representation systems are heavily dependent on specific sensorimotor experience. However, others suggest that because humans naturally move to music, sensorimotor training is not necessary and there is a more general action representation for music. We previously demonstrated that EEG mu suppression, commonly implemented to demonstrate mirror-neuron-like action representation while observing movements, can also index action representations for sounds in pianists. The current study extends these findings to a group of non-musicians who learned to play randomised sequences on a piano, in order to acquire specific sound-action mappings for the five fingers of their right hand. We investigated training-related changes in neural dynamics as indexed by mu suppression and task-related coherence measures. To test the specificity of training effects, we included sounds similar to those encountered in the training and additionally rhythm sequences. We found no effect of training on mu suppression between pre- and post-training EEG recordings. However, task-related coherence indexing functional connectivity between electrodes over audiomotor areas increased after training. These results suggest that long-term training in musicians and short-term training in novices may be associated with different stages of audiomotor integration that can be reflected in different EEG measures. Furthermore, the changes in functional connectivity were specifically found for piano tones, and were not apparent when participants listened to rhythms, indicating some degree of specificity related to training.

1. Introduction

Highly skilled musicians acquire strong multimodal associations from musical training. Such learned associations have been useful for investigating sensorimotor integration and action representation for sounds. MEG, TMS, and fMRI studies have established that musical training creates and/or strengthens links between auditory and motor areas, to an extent that only one of the modalities is required to activate the sensorimotor network (Bangert et al., 2006; D'Ausilio et al., 2006; Haslinger et al., 2005; Haueisen and Knösche, 2001). Importantly, musical training contexts have also provided evidence for short-term training-induced plasticity, and demonstrate that integration of auditory and motor perception-action processes after even a brief period of time may be crucial for successful training (Bangert and Altenmüller, 2003; Lappe et al., 2008). These studies provide examples for the tight sensorimotor coupling that can also be acquired after a brief amount of training.

In the visuomotor domain, investigation of neural dynamics demonstrated that different types of observation-action tasks result in modification of the action representation to varying degrees. For example, goal-directed actions are associated with greater mu rhythm desynchronisation than non-goal-directed actions (Muthukumaraswamy et al., 2004). Mu rhythm desynchronisation, or mu suppression, is described as a reduction in power for frequencies within approximately 8–12 Hz, recorded over sensorimotor cortex when an action is being performed (Pineda, 2005). Interestingly, this mu rhythm suppression also occurs when participants passively observe an action. Previous findings suggest that there is some degree of specificity in the system, as observation of goal-directed movements such as gripping an object, produced more mu suppression than observing a hand merely forming a grip (Muthukumaraswamy et al., 2004).

The sensitivity of the mu suppression effect could therefore be

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useful for gaining further insight into properties of audiomotor systems. Music perception requires complex processing of separate elements such as pitch and rhythm, and if the mu suppression effect is adequately sensitive, the differing effects that specific elements of the action-listening stimuli have on the audiomotor response may be elucidated.

Mu suppression has been examined in a musical notation observation-action paradigm (Behmer and Jantzen, 2011). We extended these findings, by establishing that mu suppression can also be measured for (non-visual) action-listening tasks in highly skilled musicians (Wu et al., 2016). The aim of the current study is to further extend these cross-sectional type of studies and investigate neural dynamics within individuals who are not musicians but are then trained over a short period of time on a musical task until they reach a specified level of performance.

An advantage of using sounds from a musical instrument with non-musicians is that training can be restricted to specific sound-action mappings. In other words, if motor coactivation is detected after training, one can determine if the action representation occurs only for the specific sounds that were learned during the sound-action mapping and not for other sounds. In one study that investigated this type of distinction, participants learned to play one musical piece over the course of five days and brain activation was compared during passive listening of trained and new melodies (Lahav et al., 2007). Interestingly, a left posterior premotor area of interest (the IFG) appeared to have a differing pattern to the right across the melodies that participants heard during an fMRI session after training. The right IFG appeared active across all presented melodies, whereas the left IFG was clearly active only when participants heard the trained melody compared to either untrained notes or a melody that was comprised of the same notes in a different order than the trained melody. This hemispheric difference could be seen as consistent with motor learning studies that suggest that during initial phases of learning, some regions of the network are activated to a greater extent relative to when proficiency is attained; i.e. some premotor areas are differentially recruited during different phases of learning. Indeed, in a review of motor acquisition studies, the right hemisphere was reported to be involved during early stages of learning, whereas a shift to the left hemisphere was revealed later in the time-course of learning – regardless of which hand was trained (Halsband and Lange, 2006).

While Lahav et al. (2007) stress the importance of having acquired specific sound-mappings in one's motor repertoire, others argue that a rhythmic stimulus alone is sufficient to produce these motor coactivation patterns during passive listening because it is human nature to 'move to' the beat in music (Chen et al., 2009).

Humans move to music from an early age (Phillips-Silver and Trainor, 2005). Does this seemingly automatic response suggest that our sensorimotor networks already have the necessary integration required for action representation during listening to music? This viewpoint would suggest that we have an association of sound to movement without having to acquire expertise in music performance or having to understand what action is required to produce the sound. The sensorimotor system could be more generalised; i.e. hearing any musical or rhythmic stimulus will involve an involuntary motor response regardless of how proficient you are in playing a musical instrument, and specific sound-action mappings are not required.

Evidence for a more generalised action representation system has arisen from rhythmic tapping studies to investigate synchronisation and reproducibility of rhythms. In a study that focussed on coupling of striatal to cortical sensorimotor regions, both musicians and non-musicians demonstrated activation of a distributed network of sensorimotor regions while listening to rhythms (Grahn and Rowe, 2009). Furthermore, activation appears to be dependent on task demands. Both perception of rhythms with and without the anticipation of having to reproduce them resulted in an activation of premotor regions indicative of action representation; however, listening with anticipation resulted in additional regions of activation (Chen et al., 2008). Effects could also be influenced by experience. Both musicians and non-musicians showed action representation network activation during passive listening to rhythms, although musicians showed greater activation compared to non-musicians in SMA, right PMC, and bilateral cerebellum despite both groups attaining similar accuracy for the discrimination task (Grahn and Brett, 2007). These studies suggest that the rhythmic element of music may activate the sensorimotor network irrespective of musical training experience or listening task differences.

Even if the experience of mapping sounds to specific actions is not required for action representation to occur when rhythms are heard, audiomotor training could still strengthen sensorimotor integration for rhythmic perception so that post-training effects still occur. Support for this view comes from a study that showed that the MMN reflected how multimodal, but not unimodal, training sessions enhance musical expectations for learned rhythmic patterns (Lappe et al., 2011).

The aforementioned studies show that musical training leads to associations between certain sounds and specific actions. The development of these associations requires the strengthening of connections between auditory and motor regions of the brain (Zatorre et al., 2007). One method of investigating the formation of putative audiomotor associations is to compare regional coherence of oscillatory activity before and after training. Coherence, in this context, measures the linear dependency between two signals, and oscillatory signals from EEG have been used extensively to study cortico-cortical functional connectivity (Gerloff, 2002; Weiss and Mueller, 2003). High cooperation or functional coupling between brain regions is argued to be reflected in high coherence values between EEG signals recorded over those regions (Andrew and Pfurtscheller, 1996).

For the study of sensorimotor coupling, particular emphasis is placed on alpha and beta band coherence (Andres and Gerloff, 1999). Most commonly, coherence measures for rest or baseline tasks are subtracted from coherence measured during the tasks of interest; this is termed task-related coherence (TRCoh). Increased coherence during a task relative to rest is taken as evidence for sensorimotor integration. Early studies of TRCoh during finger movement tasks demonstrated that functional connectivity in alpha (8–12 Hz) and beta (13–20 Hz) frequency bands increased for complex motor tasks (Classen et al., 1998; Manganotti et al., 1998).

Learning a musical task requires more than the skill to play a complex sequential movement. Integration between auditory and motor processes is also crucial. Thus, musical tasks may demonstrate different changes of coherence to the motor and sensorimotor studies mentioned above. Few studies on audiomotor integration use electrophysiological methods to investigate changes in functional connectivity after music training. Musical training effects on TRCoh have been studied in stroke patients, where a form of therapy is being developed that involves patients undergoing a training regime on either a piano keyboard or drum pad that produces piano sounds (Altenmüller et al., 2009). This study demonstrated increased functional coupling in the beta (18–22 Hz) band but not alpha (8–12 Hz) band after audiomotor integration was established by music-supported therapy (MST). Here, a broader exploratory approach incorporating coverage of the whole head was carried out to capture any post-therapy modulations (Altenmüller et al., 2009), whereas other studies of training-related plasticity have targeted specific sensorimotor areas that have been highlighted by previous literature, such as fronto-parietal networks (Blum et al., 2007).

Furthermore, in many of the aforementioned EEG coherence studies, participants perform the actual movements that they have learned during the training phase of the experiment. It would be interesting to determine if action representation in the absence of movement can also be investigated using coherence measures.

To further investigate the specificity effects of audiomotor training we recruited participants who had no (or minimal) musical training experience in order to examine short-term training effects on audiomotor coactivation that may relate to the human mirror neuron system.