# The Role of Auditory and Premotor Cortex in Sensorimotor Transformations

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This review first summarizes three functional magnetic resonance imaging studies conducted to elucidate the neural basis for interactions between the auditory and motor systems in the context of musical rhythm perception and production. The second part of the paper discusses these findings in the context of a proposed model for auditorymotor interactions that engage the posterior aspects of the superior temporal gyrus, and the ventral and dorsal premotor cortex. In the last section, we present outstanding issues that encompass topics, such as the role of auditory versus parietal cortex in sensorimotor integration, sensorimotor integration as an emergent property, the role of mirror neurons, and clinical applications.

*Key words:* auditory-motor interaction; sensorimotor integration; rhythm; planum temporale; premotor cortex

# Introduction

Interactions between sensory and motor systems are crucial as they allow us to navigate and engage with our environment and with others around us. We have a relatively good understanding of how the visual and motor systems coordinate, for example, during the reaching for and grasping of an object.<sup>1</sup> In contrast, the relationship between the auditory and motor systems has been less studied, although they are equally important, as both systems are necessary for speech and music performance. For example, when we learn how to speak, it is the acoustic input that shapes how we articulate each word. In the context of music, a musician must rely on auditory feedback to ensure that each note is executed at the right time and in tune. Thus, sounds can have the ability to in-

Address for correspondence: Joyce L. Chen, Department of Experimental Psychology and FMRIB Centre, University of Oxford, South Parks Road, Oxford, OX1 3UD, UK. Voice: 01865 271238; fax: 01865 310447. joyce.chen@psy.ox.ac.uk fluence our motor behaviors. One can think of an auditory-motor interaction as a process that involves communication between brain systems mediating sounds and movements. It may include for example, the transformation of auditory information into a motor representation, or the influence of motor systems on how we process sounds.

In ancient times, Plato had already raised the notion of a close link between rhythm and movement, defining rhythm as kineseos taxis, an ordering of movement. More recent empirical research has indeed demonstrated their close association. A remarkable finding is the preference that infants have in listening to rhythms whose beat they were previously bounced to, as opposed to rhythms with a novel beat structure.<sup>2</sup> Rhythmic auditory cueing has also been shown to be effective in facilitating movements, such as walking, in those with neurological disorders.<sup>3</sup> How does musical rhythm drive such coordinated actions? Evidence suggests that certain features of a rhythmic stimulus, such as the physical accentuation and temporal

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organization of events, can highlight, emphasize, and thus render these events to be more salient than others within a musical setting.<sup>4–10</sup> These types of accents may thus act as a cue to facilitate movement synchronization. Interestingly, the visual system does not seem to have as privileged a link to the motor system, at least in the context of music. Relative to auditory-motor synchronization, people are more variable in synchronizing movements with a visual cue<sup>11-13</sup> and cannot detect nor tap to the beat of a rhythmically flashing visual stimulus,<sup>14</sup> thereby demonstrating that rhythmic movement has a closer affinity with auditory than visual stimuli.<sup>15</sup> Therefore, it is precisely the intimate association of musical rhythm with movement that makes it an ideal system for the investigation of auditory-motor interactions.

Coupling between the auditory and motor systems seems to be crucial in the context of musical rhythm. Studies of patients with brain lesions that encompass various regions of the temporal lobe, including the auditory cortex, have shown that deficits associated with rhythm processing indexed by motor reproduction and/or synchronization tasks, occur despite an intact motor system.<sup>16–19</sup> This suggests that the impairment might stem at the level of auditory processing and that without precise timing or sequencing information being relayed to the motor system, the task cannot be accomplished. Neuroimaging studies have also investigated the neural basis of simple isochronous<sup>20–24</sup> and more complex $^{25-28}$  rhythm reproduction and synchronization. These studies implicate the involvement of several motor regions, such as the premotor cortex, supplementary and pre-supplementary motor areas (SMA and pre-SMA respectively), cerebellum, and basal ganglia. However, it was not the aim of these experiments to identify neural regions important for the entrainment of auditory stimuli with motor responses. For example, comparisons of experimental conditions in which subjects tap with an auditory cue versus self-paced tapping or listening are insufficient to reveal brain regions

relevant for auditory-motor coupling; one can only conclude that tapping with an auditory cue engages certain motor areas compared to tapping without a cue, and not brain regions that facilitate their coupling. On the other hand, one experimental approach that can be implemented to specifically determine the neural basis of entrainment is the use of a parametric design whereby one parameter of interest (i.e., auditory-motor coupling) is manipulated across several levels; this was the objective of experiment 1 described next.

#### Experiment 1

In our first functional magnetic resonance imaging (fMRI) study,<sup>29</sup> we aimed to investigate neural regions that facilitate or drive auditorymotor interactions in those without any musical training. This was achieved by implementing an experimental design that progressively altered the metric saliency of an isochronous rhythm via the manipulation of a rhythm's physical accent structure. That is, an isochronous rhythm was manipulated across five levels by modulating the auditory input through the use of sound intensity accents: on one end of the manipulation, all events were of equal sound amplitude, and on the other, the first of every group of three tones was relatively louder or more accented than the others. Thus this pattern of accentuation progressively highlighted the triple (i.e., waltz) time metric organization of the isochronous rhythm. We hypothesized that this parametric manipulation would affect the degree of auditory-motor coupling during rhythmic synchronization. A control condition was also included whereby some tones were randomly accented so that no percept of meter could be distinctly formed. The total sound energy across all conditions was identical. Moreover, the control condition was identical to one of the conditions in the parametric manipulation with the only difference being how the pattern of accentuation was distributed, random versus metrically organized. Subjects synchronized their tapping with the tones as accurately as possible, pressing down on the mouse key when they heard the onset of a tone, and only releasing when they heard the tone offset. Thus the dependent measure was tap duration. Since all tones across all conditions were of equal duration, motor output or tapping behavior should be no different across these conditions. However, we hypothesized that the structured change in metric saliency signaled by the auditory input would result in concomitant changes in motor output during rhythmic synchronization. These behavioral changes would be an index of auditory–motor interactions and thus allow us to identify brain regions that coordinate sounds with movements.

We implemented a sparse-sampling fMRI paradigm whereby the rhythmic auditory stimuli were presented during silence so that subjects would be able to tap along synchronously with the rhythms without interference from the loud and rhythmical scanner noise. Subject responses were recorded online, and the behavioral results showed that as metric saliency of the rhythms increased, only those tones that were relatively more accented were lengthened in tap duration. In contrast, the accented tones in the random control condition did not elicit a change in motor behavior: accented and unaccented tones were executed with the same tap duration. Together, these results allow us to conclude that it is the changing auditory pattern of metric saliency that is driving the motor response across the five levels of parametric manipulation, and not accentuation. These results suggest that at the behavioral level, interactions between the auditory and motor systems are taking place. We then implemented a regression analysis on the fMRI data to look for brain regions that demonstrated increasing neural activity as a function of increasing metric saliency or, in other words, auditory-motor interactions. Only neural activity in posterior aspects of bilateral superior temporale gyrus (STG), including the planum temporale (PT) and bilateral dorsal premotor cortex (dPMC), significantly increased as metric saliency increased (Fig. 1). Of importance, neural activity in auditory and

premotor regions was temporally correlated to each other, and this functional connectivity also increased as metric saliency increased. This suggests that interactions between auditory and premotor regions are indeed taking place. In sum, this study investigated how one feature of a rhythmic stimulus, its physical accentuation, influences auditory–motor synchronization. We showed that manipulation of the auditory input modulates motor output, and this is taken to reflect interactions between the auditory and motor systems. These results provide evidence that posterior STG and the dPMC are important nodes that facilitate auditory–motor interactions in the context of rhythm.

#### **Experiment 2**

Experiment 2 manipulated another feature of a rhythmic stimulus, its temporal or metrical organization, also known to influence movement synchronization. Therefore in contrast to experiment 1, we kept auditory input and motor output parameters constant, and instead manipulated the timings of events.<sup>30</sup> We created three rhythms that differed in complexity according to the principles of metrical organization proposed by Povel and Essens<sup>31</sup>: metric simple (i.e., strongly metric), metric complex, and nonmetric (i.e., weakly metric). These three rhythms were identical in terms of the number and type of musical events (i.e., note duration), but differed in how these events were temporally arranged. In this fMRI study, we also compared performance and neural response in musicians to those without musical training, given that the former should be better at rhythmic processing due to their long-term training.

All subjects were first trained to learn these three rhythms on a separate day in order to minimize effects of motor learning. On the day of fMRI scanning, subjects were first scanned while listening to a rhythm, and then in the subsequent trial, they were scanned while the same rhythm presented itself again, but this time, subjects tapped along with it, synchronizing with the onsets of each event.



**Figure 1.** fMRI covariation results. Conditions 1 through 5 on the x-axis of graphs represent stimuli conditions 0 dB through 10 dB, respectively. The percent blood-oxygenation-level dependent (BOLD) signal changes (plotted relative to condition 1) in posterior superior temporal gyrus (STG) and dorsal premotor cortex (dPMC) demonstrate a positive linear modulation of activity across the parametric variation in metric saliency. Color bar represents *t*-values. Data are reported as mean  $\pm$  standard error. Brain images taken in sagittal (x), coronal (y), and horizontal (z) planes. (In color in *Annals* online.)

Therefore rhythms were always presented in pairs, in a pseudo-randomized order. The dependent measure of global accuracy showed that all subjects were able to perform the task: there were no significant differences in percent correct scores between subject groups, nor across the three different rhythms. However, more-sensitive dependent measures used to assess sensorimotor synchronization ability revealed significant group differences (main effect of group) as well as significant differences in performance across the rhythms (main effect of rhythm type). Musicians were better able to synchronize, or time their taps, with the onsets of each rhythmic event than were nonmusicians, and for both groups, performance on this measure decreased as rhythm complexity increased. Similarly, musicians were better than nonmusicians at maintaining the inter-onset interval, that is, the interval of time between the onset of one event to the next event. Again, for both groups, performance decreased as rhythm complexity increased. Therefore at the global level, all subjects are able to perform this task equally well across all rhythm types, which allows us to suggest that the behavioral differences seen with the more sensitive measures of synchronization ability are not due to task difficulty, but to the ability to coordinate precisely timed motor responses with auditory cues.

To establish a brain-behavior relationship, we then used each subject's behavioral score as a regressor in the fMRI analysis to determine regions in the brain that increase in neural activity as performance decreases (or, in other words, as rhythm complexity increases). This analysis was performed separately for each subject group, and the results show that both musicians and nonmusicians engage the same neural regions: pre-SMA, SMA, dPMC, dorsolateral prefrontal cortex, inferior parietal lobule, and cerebellum lobule VI (Fig. 2). These regions are also functionally connected, that is, neural activity in the dPMC is temporally correlated with the other regions, and with the PT in auditory cortex. A conjunction analysis confirmed that both groups recruited these same brain regions, and a subtraction analysis similarly verified that neural activity in each of these regions was no different between musicians and nonmusicians. As a final confirmation of this finding, we extracted the percent bloodoxygenation-level dependent (% BOLD) signal changes in voxels of interest in each of these regions and showed that there were no statistically significant differences in the amount of neural activity across subject groups for these brain areas. What is different between musicians and nonmusicians, though, is that the former additionally engage more prefrontal cortex, namely a peak in the dorsolateral prefrontal cortex that is located more inferiorly than one that is common to both subject groups, and a region in the inferior frontal gyrus bordering the pars opercularis and pars triangularis (Fig. 3).

First, these results demonstrate that contrary to findings in prior studies, <sup>32–36</sup> musicians and

nonmusicians engage the same motor brain regions (pre-SMA, SMA, dPMC, cerebellum) to the same extent during a motor sequencing task. In both subject groups, the motor system is sensitive to the temporal organization of the rhythms: the number of movements and their timings is identical across the three rhythm types; what changes is how events are temporally structured, information that is conveyed by the auditory stimulus. However, our results further suggest that the superior behavioral ability of musicians to perform sensorimotor synchronization may be related to additional engagement of the prefrontal cortex in the mediation of working memory<sup>37</sup> and the selection of hierarchically organized action plans.<sup>38,39</sup> Musicians have an explicit understanding of how musical rhythm is structured, and therefore can use a top-down strategy where they retrieve, monitor, and manipulate the timings of each event, organizing temporal information into a metrical framework. In contrast, to perform the task successfully, nonmusicians likely use a bottom-up approach, such as one based on the Gestalt theory of grouping whereby elements close in time are grouped together. Last, results of this experiment corroborate those from experiment 1 in which neural activity in the dPMC and PT is temporally coupled. This is further evidence for a possible substrate that mediates auditory-motor interactions during rhythmic synchronization.

#### **Experiment 3**

Findings from the prior two experiments demonstrated the involvement of the dPMC and posterior STG, including the PT, during auditory-motor interactions. In these experiments, movements were always explicitly linked to sounds since subjects tapped along to the rhythms. The question posed in experiment 3 was whether the motor system would still be responsive to sounds, if sounds were not linked to movements.<sup>40</sup> That is, if we control for motor imagery and/or the anticipation to tap, would the passive perception of musical rhythms still



**Figure 2.** Brain regions modulated by temporal complexity. Results are shown for the covariation analysis for nonmusicians (column 1), musicians (column 2), and their conjunction (column 3). Regions where neural activity correlates with that of the dorsal premotor cortex (seed voxel) are shown in column 4 (functional connectivity). Graphs in column 5 represent voxel of interest analyses where the % blood-oxygenation-level dependent (BOLD) signal change is plotted across rhythm type for nonmusicians and musicians. Data are reported as mean  $\pm$  standard error. Color bar represents *t*-values: range 10.0–5.0 (range 10.0–3.0 for cerebellum) for functional connectivity images; range 5.0–2.0 for all other analyses. Pre-SMA/SMA = presupplementary motor area/supplementary motor area (row 1, sagittal view); dPMC = dorsal premotor cortex (row 2, horizontal view); IPL = inferior parietal lobule (row 3, coronal view); DLPFC = dorsolateral prefrontal cortex (row 4, coronal view); cerebellum (row 5, coronal view); MS = metric simple; MC = metric complex; NM = nonmetric. (In color in *Annals* online.)

recruit the motor system? One might hypothesize that only auditory regions should be engaged; however, the evidence briefly reviewed in the introduction suggests a tight coupling between the auditory and motor systems, which may lead one to hypothesize the recruitment of both systems during perception. We set out to explicitly test this hypothesis in



**Figure 3.** Differences between musicians and nonmusicians. Results are shown for the covariation analysis for nonmusicians (column 1), musicians (column 2), and the group contrast musicians > nonmusicians (column 3). Note that musicians recruit two peaks in the dorsolateral prefrontal cortex (DLPFC; dashed lines). Rows 1 and 3 in coronal view, row 2 in horizontal view. Graphs in column 4 represent voxel of interest analyses where the % blood-oxygenation-level dependent (BOLD) signal change is plotted across rhythm type for nonmusicians and musicians. Data are reported as mean  $\pm$  standard error. Color bar represents *t*-values; range 5.0–2.0 for all analyses. BA = Brodmann's area; MS = metric simple; MC = metric complex; NM = nonmetric. (In color in *Annals* online.)

experiment 3 by either associating or dissociating action processes from a perceptual event in the context of musical rhythm perception and synchronization. We also investigated how different parts of the premotor system would be engaged during action-perception coupling. For instance, findings from experiments 1 and 2 show the important role of the dPMC in temporally organized movements. Other studies have demonstrated engagement of the ventral premotor cortex (vPMC) in the processing of action-related sounds, that is, sounds that have an associated motor program.<sup>41,42</sup> This suggests that subregions of the premotor cortex may be sensitive to different aspects of auditoryguided actions.

To dissociate action processes from perception, nonmusicians were recruited to participate in the experiment under the pretense that

they would be merely listening to rhythms while undergoing fMRI. We did not test musicians since their extensive training would presumably be associated with an already tightly coupled auditory and motor system. During the first part of the experiment, subjects "naively" listened to three rhythms of varying complexity, which were described and used in experiment 2 (although in this study we labeled them as simple [metric simple], complex [metric complex], and ambiguous [nonmetric]). In this condition, sounds should have no reason to be linked to movements. In the next part of the experiment, subjects were then informed that they would listen and then tap along to these rhythms: this being identical to the paradigm in experiment 2. In this perceptual condition, actions are linked to the heard rhythms since subjects are listening with the anticipation to tap in the ensuing trial. Thus, they are performing motor imagery and/or rehearsal, which recruits motor neural activity. During the tap trials, actions are also, of course, intimately linked to the heard sounds since subjects are now synchronizing their taps with the auditory stimulus.

To answer the first experimental question, we implemented subtraction analyses to contrast each of the different action-perception conditions (passive listening, listening with anticipation to tap, tapping) to a silence baseline, for all rhythm complexity levels (simple, complex, ambiguous). We then performed a conjunction analysis to show brain regions that were commonly engaged for each actionperception condition, irrespective of rhythm complexity. This analysis identified involvement of the PT and various motor regions, including the cerebellum, premotor cortex, and SMA, during each of the conditions: passive listening, listening with anticipation, and tapping (Fig. 4). We then implemented another conjunction analysis to confirm that the motor brain regions identified in the passive listening condition were identical to those in the conditions where actions were explicitly coupled to perception.

To answer the second experimental question, we first sought to replicate our prior findings whereby the dPMC is sensitive to the selection of temporally organized actions guided by an auditory cue. Thus, we implemented a regression analysis to elucidate brain regions that increase in neural activity as performance decreases while subjects tapped along with increasingly complex rhythms; this analysis is similar to the one previously described in experiment 2. This finding was replicated, and furthermore, the analysis confirmed that the vPMC is not sensitive to the higher-order manipulation of temporal complexity since neural activity in this region did not show any correlation as a function of the stimulus manipulation, and the % BOLD signal change in this region was no different across the three different rhythm complexity levels. However, our findings do confirm those in the prior literature in showing that the vPMC is sensitive to processing action-related sounds. This region was only significantly engaged during listening with anticipation and tapping, and not during passive listening. Last, neither the dPMC nor vPMC were engaged during passive listening. However, a most intriguing finding is that a third premotor region, which we have called the mid-premotor cortex (midPMC), was significantly recruited when subjects naively listened to musical rhythms. In sum, these findings show a dissociation of function for various sectors of the premotor cortex (Fig. 5), and that there may be an inherent link or coupling between the auditory and motor systems.

## Summary of Findings

Based on evidence that musical rhythm and movement are closely related, these three experiments exploited their relationship to investigate coupling between the auditory and motor systems. These findings show that auditory-motor coupling during music performance involves the posterior STG and premotor cortex. Findings in experiments 1 and 2 demonstrate that the dPMC is only engaged during rhythmic tapping, as opposed to naïve passive listening to rhythms or listening with anticipation to tap, and is furthermore sensitive to higher-order information, such as a rhythm's metric structure. Such temporal information may be conveyed via the posterior STG to enable the implementation of timely and organized movements mediated by the dPMC. In contrast, experiment 3 showed that the vPMC is insensitive to a rhythm's metrical organization; however, it is generally engaged whenever sounds are linked to the motor system. It is also interesting to note that this premotor dissociation is reminiscent of, and may be related to, behavioral findings showing that disrupted feedback in terms of period shifts in a sequence results in errors of pitch selection, whereas a disruption in timing caused increase timing variability in



**Figure 4.** Brain regions involved in action-perception coupling and decoupling. All brain images are all taken in the same Talairach coronal plane. Color bar represents *t*-values. (**A**) Left panel shows subtraction results for experiment 1 in this study: brain regions engaged while subjects listen with anticipation and tap along with rhythms relative to silence. Right panel shows subtraction results for experiment 2 in this study: brain regions engaged while subjects for experiment 2 in this study: brain regions engaged while subjects passively listen, listen with anticipation, and tap along with rhythms, relative to silence. (**B**) % Blood-oxygenation-level dependent (BOLD) signal change is plotted for voxels of interest in each condition (passive listening, listening with anticipation, tapping), averaged across rhythm type, for experiments 1 and 2 in this study. Data are reported as means  $\pm$  standard error. (In color in *Annals* online.)

movement execution.<sup>43</sup> Last, when sounds do not communicate any intention for action, such as during the naïve passive perception of musical rhythms, the midPMC along with other motor regions, such as the SMA and cerebellum, are still recruited. However, findings from experiment 2 also revealed that the expert ability

of musicians in executing rhythmic sequences does not further implicate the motor system. Interestingly, this skill may be related to working memory processes mediated by the prefrontal cortex whereby each sensory event is actively retrieved and monitored during rhythmic sequencing.



**Figure 5.** Neural activity in three distinct premotor regions: dorsal premotor cortex (dPMC), mid-premotor cortex (midPMC), and ventral premotor cortex/pars opercularis (vPMC/BA 44). (**A**) Illustration of the premotor functional dissociation with data from experiment 2 in this study projected onto a three-dimensional anatomic rendering from one subject. Brain regions that increase in neural activity as rhythm complexity increases are shown in hot metal (dPMC); brain regions engaged during passive listening are shown in green (midPMC); brain regions engaged during tapping are shown in blue (vPMC/BA 44). The midPMC is engaged during both passive listening and tapping (listening with anticipation is not depicted in this image); this region is color coded with a mix of blue and green. (**B**) Illustration of dPMC sensitivity to metric organization; brain image taken in the Talairach horizontal plane of the covariation contrast from experiment 2 in this study with graph showing corresponding % blood-oxygenation-level dependent (BOLD) signal change plotted across rhythm type for each condition (passive listening, listening with anticipation, tapping). (**C** and **D**) Illustration of midPMC sensitivity across all conditions and vPMC/BA 44 sensitivity during action and action-related sounds; brain images taken in the Talairach sagittal plane of the conjunction contrast "tap minus silence" from experiment 2 in this study (graphs in same format as in A). Color bar represents *t*-values. Data are reported as means ± standard error. (In color in *Annals* online.)

# A Model for Auditory–Motor Interactions

The findings from these three experiments along with the current literature have led us to put forth a hypothesis concerning how auditory information is transformed into a motor representation in the context of music perception and production.<sup>44</sup> The following section will recapitulate this proposal and integrate discussion about how auditory and premotor systems might be engaged.

## **Auditory Cortex**

Literature in this field<sup>45,46</sup> has focused on the role of auditory regions in mediating auditory-motor transformations. The evidence, corroborated with findings from these three experiments, points to the involvement of posterior auditory regions in the STG, including the the PT. Griffiths and Warren<sup>47</sup> have suggested that the PT may serve as a general computational hub whereby complex sounds are disambiguated. That is, the PT analyzes and decomposes spectrotemporal patterns so that they can be segregated according to the type of information embedded in the acoustic cue, for example, by patterns associated with specific auditory objects versus those with sound position. This segregation can also take place across successive time points as, for example, when musical rhythms are processed. Once spectrotemporal patterns are analyzed, the information is then relayed to other higher-order cortical regions for further processing. In particular, it is proposed that information relevant for the motor system is relayed via the dorsal auditory processing stream,<sup>46</sup> similar to the way that visual information is relayed via the dorsal visual stream. A strength of this model is that it parsimoniously accounts for involvement of the PT in processing a wide variety of acoustic inputs, such as speech, music, and spatial and cross-modal processes.

## Premotor Cortex

While these prior models discuss the role of posterior auditory regions in auditory–motor transformations, we have proposed that the premotor cortex is also an important area. One piece of evidence for this proposal comes from anatomy: the premotor cortex is the only cortical motor brain area that directly connects with the posterior STG and with the primary motor cortex (M1), thus giving auditory information relatively direct access to M1.<sup>44</sup> While this evidence derives mainly from data in nonhuman primates, a recent

diffusion tractography imaging study in humans shows the presence of white matter fiber tracts between posterior STG and rostral dPMC.<sup>48</sup>

One model of premotor function suggests that this region is organized in a somatotopic manner, and it is this somatotopy that dictates the types of stimuli that will engage it.<sup>49</sup> For example, the model suggests that since inferior parts of the vPMC are related to the mouth representation, rhythmic stimuli will preferentially engage this region. In contrast, stimuli dealing with object and space will favor the recruitment of the superior part of the vPMC and dPMC, respectively, where corresponding hand and arm representations are located. Our findings suggest that this model may not explain all cognitive processes, as we have shown that the same rhythmic stimulus engages different regions of the premotor cortex, depending on the nature of the sensorimotor interaction.

The other basis for our proposal comes from models of visuomotor interactions, and we suggest that there may be parallels to the auditory domain. The premotor cortex has traditionally been divided into dorsal (i.e., dPMC) and ventral (i.e., vPMC) sectors. On the basis of considerable evidence from electrophysiological research, Hoshi and Tanji<sup>50,51</sup> propose that the vPMC and dPMC are involved in direct and indirect visuomotor transformations, respectively. Direct transformations involve a one-to-one matching of sensory features with motor acts.<sup>50,52–54</sup> In the classic reach-andgrasp example, neurons in the vPMC represent sensory properties of the target: they match properties of the visual object (e.g., shape of an apple) with an appropriate motor gesture (e.g., shape of hand). Inactivation of these neurons causes impaired hand shaping such that objects cannot be grasped, despite the absence of motor paralysis or a sensory deficit.<sup>52</sup> Neurons in the vPMC also transform targets from visual into motor frames of reference such that a seen object can be reached from the appropriate direction.53

Direct auditory-motor transformations are highly relevant during music performance. Playing music requires precise auditory-motor mapping between the sound of a note and the effector used to produce that note, and in particular, has been shown to engage the vPMC and BA 44.41,42,55 Findings from experiment 3 also support this idea, as an area at the border of vPMC and BA 44 was recruited when sounds were meaningful to the motor system, that is, during the listening with anticipation to tap, and tapping conditions. The vPMC was not engaged during the naïve passive listening condition, when sounds were of no relevance for the motor system. This finding is consistent with those<sup>42</sup> who demonstrated engagement of the vPMC and BA 44 when subjects listened to simple melodies that they had been trained to play, but not to novel melodies that were motorically unfamiliar. Furthermore, neural activity in the vPMC was no different across the three levels of rhythmic complexity, thus demonstrating its insensitivity to the higher-order features embedded in an auditory stimulus. Therefore, the vPMC is active upon hearing music for which one has an associated motor program and is thus proposed to mediate the direct transformation of sounds to movements.

On the other hand, the dPMC is thought to have a more indirect role in sensorimotor transformations: it represents motor information instructed by the sensory cues rather than their sensory properties.<sup>50,56,57</sup> In the reachand-grasp example, dPMC neurons are involved in motor planning, preparing and selecting movement parameters (e.g., direction and amplitude) in response to what the sensory cues signal. They combine and convey information about where to reach, what hand to reach with, and how to reach. Thus, neurons in the dPMC retrieve and integrate sensory information with motor instructions in order to carry out an action plan.<sup>50,51</sup> The rostral dPMC is of particular interest because it participates in more abstract or higher-order aspects of movement,<sup>50,58-60</sup> such as the selection of movements that are conditionally linked by a sensory stimulus.<sup>61–64</sup> In this case, the sensory signal does not directly indicate an action per se, but rather a conditional rule about what movement to select among competing alternatives, a function that would be highly useful for musical execution, which depends on learned actions and a hierarchical organization. Inactivation of the dPMC, not vPMC, impairs these conditional motor behaviors,<sup>56</sup> and also the ability to coordinate and time movements,<sup>65</sup> another critical feature for musical performance.

The view that the dPMC is involved in higher-order aspects of movement organization is supported by our findings that this region is sensitive to the abstract metrical structure of a musical rhythm. It is important to note that we do not suggest that the dPMC codes for how metrically structured a rhythm is. If so, then results from experiments 1 and 2 would be in conflict with each other. Instead, the dPMC is sensitive to the metrical structure of a rhythm insofar as it is implicated in action selection processes depending on the nature of the stimuli. In experiment 1, the dPMC is engaged in extracting the relevant auditory features of an isochronous rhythm in order for subjects to implement or select an appropriately timed motor response. It becomes more engaged as auditory features processed in the PT progressively convey information of a higher-order nature. In experiment 2, neural activity in the dPMC was greatest for the nonmetric rhythm that required greater motor control and reliance on auditory feedback for the selection of precisely timed movements. In other words, there was a need for greater interactions between the auditory and motor systems during performance of the nonmetric relative to the other simpler rhythms. Therefore, in experiments 1 and 2, dPMC activity is not modulated by the direct mapping of sounds to movements per se, which remain constant. Instead, the dPMC is involved in the selection of temporally organized movements based on higherorder information, such as a rhythm's metric structure, which is derived from the auditory stimulus.

## **Outstanding Issues in the Field**

We have put forth ideas for how auditory and premotor regions are engaged in auditory– motor transformations, and in particular our contribution has been to elucidate the role of the premotor cortex. It is now, we feel, an exciting moment in the field where one can begin to ask more specific and detailed questions about sensorimotor integration in the auditory domain. In this last section, we communicate some of the issues that are of relevance.

## Auditory–Motor Interactions: Auditory versus Parietal Cortex

We have presented evidence that posterior auditory regions encompassing the PT are important for auditory-motor transformations; however, it remains to be verified whether there are specific populations of neurons in this computational hub region that are specialized for mediating sensorimotor integration, and where or how they are precisely distributed. Another influential account suggests that a specific region within the left PT, at the border of the sylvian fissure with the temporal lobe (area SPT), mediates sensorimotor integration during speech and music for the vocal tract effector.<sup>45</sup> In particular, this proposal suggests that area SPT is not "auditory" per se, but is part of the parietal system for sensorimotor integration,<sup>66</sup> a system suggested to be organized in an effector-dependent manner.<sup>67</sup> For example, the anterior intraparietal (AIP) area is considered a subregion within the parietal system that performs sensorimotor integration for grasping, and the lateral intraparietal area is a sensorimotor integration region for eye movements. Thus the view of Hickok and Poeppel<sup>45</sup> is that area SPT is a sensorimotor integration region for the vocal tract. Cytoarchitectonic<sup>68</sup> and tracer<sup>69</sup> studies in humans and macaques, respectively, also suggest that regions in the posterior superior temporal plane are more multisensory in nature than they are auditory. Furthermore, if we assume that area SPT functions like the posterior parietal cortex as Hickok and Poeppel<sup>45</sup> suggest, then there is plenty of evidence from the visual domain that demonstrates the role of the parietal cortex in performing coordinate transformations to map visual representations with motor output.<sup>70</sup> A salient example of this can be found in patients with optic ataxia, in which lesions in the posterior parietal cortex cause impairment in reaching under visual guidance despite the absence of any sensory or motor deficit.<sup>71</sup> In contrast, patients with visual-form agnosia caused by lesions in the occipitotemporal cortex are able to accurately guide hand and finger movements to grasp an object, but demonstrate a profound inability for object recognition.<sup>72</sup> Taken together, the literature shows convincingly that the parietal system is important for visuomotor transformations; one key question, though, is whether and how neurons in these regions can also perform similar computations for audition, especially since music and speech do not necessarily involve any spatial processes. For example, several studies, including our own, that have engaged subjects in one-finger auditory-motor rhythmic tapping show involvement of posterior STG including the PT, but not parietal regions: How can these findings be reconciled with a parietal account for integration?

# Auditory–Motor Interactions: An Emergent Property of Sensory and Motor Systems?

We have proposed how the different sectors of the premotor cortex may differentially process sound information, and prior models have also implicated auditory regions for integration. One view may be that the process of sensorimotor integration is emergent from computations in both of these areas, such that the integrity of both sensory and motor systems is required for integration. Repetitive

transcranial magnetic stimulation (TMS) to either the posterior superior temporale plane or the vPMC has been shown to disrupt synchronization ability during rhythmic auditorymotor tapping: Subjects were less able to tap in phase with the auditory cue.<sup>73</sup> Neurophysiological evidence from macaques in the visual domain also show that neurons in both ventral premotor (area F5 in monkeys) and parietal (AIP) cortex are extensively connected with each other,<sup>1</sup> and have visual and motor properties.<sup>54,74</sup> Even more interesting is that functional inactivation of either area F5 or AIP in monkeys produce similar deficits, namely the inability to shape the hand in an appropriate configuration to grasp an object.<sup>52,75</sup> The difficulty in dissociating the contributions of each region has led to the suggestion that the F5-AIP circuit as a whole plays a crucial role in mediating these visuomotor transformations, but that area F5 might dominate as it has a more prevalent motor role than AIP, which has more sensorydominant neurons.<sup>1,76</sup>

On the other hand, literature from the domain of speech is not as clear. Auditory-motor interactions are highly relevant in the context of directly mapping heard speech sounds, such as phonemes onto articulatory representations, and the vPMC (along with Broca's regions), has been shown to be an important neural substrate for this process, often more so than posterior auditory areas.<sup>77–85</sup> For example, TMS to the left vPMC impairs subjects' ability to perform a phonetic discrimination task whereas, in contrast, TMS to the left STG has no effect.<sup>80</sup> These findings are also in accordance with those of studies in patients where electrical stimulation of vPMC interferes with speech, causing dysarthria,<sup>86,87</sup> an inability to articulate or coordinate muscles of the mouth. Together, these findings support the motor theory of speech.<sup>88</sup> In contrast to Liberman's theory, the argument has also been made that posterior auditory regions are important for speech production: Damage to these regions results in conduction aphasia, where patients are still able to comprehend speech, but have difficulty in production at the phonemic level.<sup>45</sup> This has lead Hickok and Poeppel to suggest that this disorder stems from impairment of auditorymotor integration.<sup>45</sup> Last, recent work in persons who stutter, a disorder of motor-speech fluency, shows reduced neural activity in both the left vPMC and left Heschl's gyrus compared to that in control subjects, and furthermore the integrity of the white matter underlying the vPMC is also reduced.<sup>89</sup> Given that the vPMC is anatomically connected with auditory regions, these findings suggest that disruption of these connections may hinder the integration of acoustic inputs with motor outputs, thereby affecting speech fluency.<sup>89</sup>

# Auditory–Motor Interactions: A Role for Mirror Neurons?

Mirror neurons were first studied in the visual domain in monkeys, and they are located in area F5 of the monkey's premotor cortex. Mirror neurons become active when an individual performs an action, such as grasping a peanut, and when the individual observes someone else performing the same action.<sup>90,91</sup> In the domain of sound, auditory mirror neurons, also known as echo neurons, are engaged when the monkey breaks a peanut and when he/she hears the sound of a peanut being broken.<sup>92,93</sup> Therefore, these neurons are engaged during action and action observation. Since their discovery, the mirror neuron theory has been widely applied to explain a variety of phenomena, including their involvement in action-recognition of musical sounds,<sup>41,42,94</sup> that is, the association of sounds to a motor program, which we have suggested involves the vPMC. However, it is unclear whether mirror neurons do indeed form the basis for auditory-motor integration.

In humans, core regions of the mirror neuron system are purported to include the vPMC as well as the adjacent pars opercularis,<sup>95</sup> although involvement of the pars triangularis has also been reported. It is critical to state that three types of neurons have been characterized

within area F5 of the macaque: motor neurons, visuomotor neurons, and mirror neurons, all of which have distinct anatomic locations.<sup>96</sup> The evidence on which we have based our proposal stems from findings of the visuomotor neurons that were previously discussed in the context of direct sensorimotor mappings and the F5-AIP circuit. While mirror and visuomotor neurons are indistinguishable in terms of their motor properties as both discharge when an action is executed on an object, 1,97 it is the difference in their sensory properties that leads to their different functions. Critically, mirror neurons do not discharge at the mere sight of an object as importantly, they are only active when there is an interaction between a biological effector (e.g., hand) and the object (e.g., a peanut) of its manipulation. Thus, a mirror neuron becomes engaged at the observation of an action performed on an object.

On the other hand, visuomotor neurons, also called canonical neurons, are engaged when an object is manipulated and when the same object is merely observed.<sup>96</sup> Importantly, these neurons discharge when the shape and size of the object is congruent with the type of grasp used to acquire it. These findings have led to the interpretation that there must be a close correspondence between objects and the actions implemented on them, that the sight of an object automatically evokes an action to be implemented on that object, regardless of whether the action is actually carried out.<sup>96</sup> This has led to the idea that the "visuomotor coupling shown by canonical neurons could be at the basis of the sensorimotor transformation that adapt the hand to a given object" (p. 517).<sup>97</sup> This interpretation is consistent with others that have suggested that vPMC neurons match sensory information with a motor act, and are considered to be involved in direct sensorimotor mappings.<sup>51,54</sup> In particular, important evidence comes from a study in macaques that showed that inactivation of visuomotor neurons resulted in impaired hand shaping according to the visual characteristics of the object to be grasped; however, inactivation of mirror neurons had no effect on hand shaping.<sup>52</sup> These findings clearly demonstrate that mirror neurons are not engaged in actual sensorimotor transformations. Instead, "the visuomotor discharge that characterizes mirror neurons could be at the basis of action imitation and action understanding" (p. 517),<sup>97</sup> or, in the words of Rizzolatti and Fadiga,<sup>98</sup> mirror and visuomotor neurons are engaged in "grasping action meaning versus grasping objects," respectively. In sum, mirror neurons match self-action with an observed action, while visuomotor neurons match an observed object with its corresponding action.<sup>1,51,97</sup>

In the domain of sound, an unanswered question is: What population of neurons within the vPMC might be implicated in sensorimotor integration for sounds and actions? From what was reviewed in the prior paragraphs, it seems that visual mirror neurons are not engaged in the actual "co-ordinate" transformation or mapping of sensory information onto motor representations, as this is the role of the visuomotor neurons. Is it valid, then, to extrapolate these findings to the auditory domain, and therefore conclude that auditory mirror neurons (i.e., echo neurons) do not perform such transformations, but that a population of auditory-motor neurons that would be equivalent to visuomotor neurons does? Importantly, it has not been demonstrated whether there are indeed auditory-motor neurons.

## Auditory–Motor Interactions: Clinical Applications

Much research is still required to fully understand the neuroanatomic and neurophysiological basis for interactions between the auditory and motor systems, namely, how they integrate information. However, we have reviewed evidence to suggest that this process involves the posterior STG and the premotor cortex. These findings may help us understand why rhythmic auditory cueing is an efficacious technique that improves movement coordination and fluency in those with motor impairments,

manifested in a variety of different clinical disorders, such as head injury, stroke, and Parkinson's disease.<sup>3,99–102</sup> It is tempting to rationalize that this type of therapy is successful across patient populations because it taps into an intact auditory-premotor system. For example, unilateral stroke affecting the dPMC,<sup>103</sup> or a virtual lesion created by TMS<sup>104</sup> to the dPMC, impairs this region's role in the selection of visually guided movements. However, the unaffected hemisphere can quickly reorganize and take over the function of the lesioned one.<sup>103,104</sup> In a critical manipulation, O'Shea et al. then showed that TMS to the unaffected hemisphere, which had originally taken over the role of the lesioned one, subsequently impaired subjects' ability to select visually guided movements.<sup>104</sup> This study therefore shows that sensory cues are able to influence movements by specifically accessing the unaffected premotor cortex.

In Parkinson's disease, a disorder of the basal ganglia, rhythmic auditory cueing may similarly be effective in organizing coordinated actions because these cues are accessing a functional auditory-premotor circuit such that the premotor cortex is in a position to receive auditory information relevant for the temporal organization of movements. An interesting point, though, is that Jessica Grahn's work, also presented in this volume, has demonstrated that beat perception involves the basal ganglia<sup>8</sup> and that people with Parkinson's disease are in fact impaired at perceptually detecting the beat when only relying on temporal cues.<sup>105</sup> Thus, if the basal ganglia are important for beat perception, this begs the question of how can people with Parkinson's disease nonetheless use "the beat" to facilitate their movements, as has been behaviorally demonstrated.<sup>100,106,107</sup> Perhaps in these cases, there might be a greater role for nontemporal cues, such as timbre or pitch, that can be used to detect the beat. Nonetheless, to shed light on this topic, one avenue of future research might address the role of the premotor cortex and its interaction with the basal ganglia in beat perception and synchronization. One possibility is that the former has a more cognitive or top-down modulatory role in the selection of auditorily guided actions, whereas the latter is more concerned with a bottom-up analysis that facilitates subjects' experience of "feeling the beat" (Jessica Grahn, personal communication).

# Conclusions

In order to understand why auditory cues can influence movements, we used musical rhythm as a tool to probe how interactions between the auditory and motor systems take place. We have presented three studies that highlight the role of the premotor cortex in auditory-motor interactions, and have reviewed the role of this region along with the posterior STG in the transformation of sound information into temporally organized motor actions. While these studies were conducted in the context of music perception and production, we believe that these findings transcend the domain of music and can be generalized to account for sensorimotor interactions relevant for speech. It is clear that many outstanding questions remain and we hope that this review will motivate more research in an effort to resolve them.

## **Conflicts of Interest**

The authors declare no conflicts of interest.

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