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Review article

Motor output, neural states and auditory perception

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ABSTRACT

Behavior is a complex product of interactions between sensory influx arising from the environment and the neural state of the organism. Therefore, identical sensory input can elicit different behavioral responses. Research in recent years has demonstrated that perception is modulated when an organism is engaged in active behavior – suggesting that neural activity in motor pathways is one factor governing the neural state of networks engaged in sensory processing. In the current manuscript, we focus on the auditory modality and propose a mechanism by which activity in motor cortex changes the neural state in auditory cortex through global inhibition. In turn, such global inhibition reduces auditory net population activity, sharpens auditory frequency tuning curves, shifts the auditory oscillatory state and increases the signal-to-noise ratio of auditory evoked neural activity. These changes can result in either attenuated or enhanced behavioral responses depending on the environmental context. We base our model on animal and human literature and suggest that these motor-induced shifts in sensory states may explain reported phenomena and apparent discrepancies in the literature of motor-sensory interactions, such as sensory attenuation or sensory enhancement.

1. Introduction

Biological organisms continuously interact with the environment. Therefore, behaviors and environmental context are intertwined and constantly shape each other. Although our sensory organs are designed to detect physical changes in the external world, many studies in recent years demonstrate that sensory perception is a product of complex interactions between the physical attributes of sensory stimuli and the neural state of the organism. For example, during stimulation from multiple sources, we are able to filter out irrelevant sensory inputs and extract information originating from a single source by modulating our neural state with attentional effort. In the auditory domain, this phenomenon is known as the “cocktail party effect” (Arons, 1992). Other examples in which sensory stimuli interact with neural state come from bistable perception paradigms, such as Rubin’s vase-face illusion (Rubin, 1915) and binocular rivalry (Wheatstone, 1838) in the visual modality. In such paradigms, the physical properties of the stimulus are constant, yet the percept fluctuates over time. It has been shown that subjects’ perceptual reports were dependent on spontaneous fluctuations in the neural state (Hesselmann et al., 2008; Iemi et al., 2017). Similar findings were also reported in the auditory domain, where detection of near-threshold sounds has been shown to depend on neural activity in auditory cortex preceding sound onset (Sadaghiani et al., 2009). Taken to the extreme, sensory stimulation during neural states associated with sleep can go undetected at the behavioral level.

One factor that shapes the neural state of an organism, and consequently modulates sensory processing, is activity of the motor system, for example during voluntary action execution (Händel and Schölvinck, 2017). In the tactile domain, self-applied strokes are perceived less ticklish compared with identical strokes applied by an external source (the well-known phenomenon that we are not able to tickle ourselves; Blakemore et al., 1998, 1999). Additionally, perceived loudness of auditory tones that are the consequence of voluntary actions is modulated compared with physically identical tones generated by someone else (Sato, 2008; Weiss et al., 2011a; Reznik et al., 2015b). Similar perceptual modulations in the visual domain have been reported as well (Dewey and Carr, 2013; Desantis et al., 2014). Behavioral and neural modulation of sensory-evoked responses due to activity in motor cortex has been widely reported both in humans (Horvath, 2015; Hughes et al., 2013) and animals (Poulet and Hedwig, 2007; Crapse and Sommer, 2008a, b; Schneider and Mooney, 2018), and the functional roles ascribed to such motor-induced modulations include preserving the response sensitivity of sensory organs, learning of motor-sensory contingencies and agency attribution (for elaboration on these functional roles see Box 1). Hence, delineating the parameters that govern the mechanism by which motor actions modulate sensory processing is crucial for understanding complex motor-sensory interactions and their relationship to behavior and cognition.

Although there is evidence for motor-induced sensory modulation in the visual (Bennett et al., 2013) and somatosensory (Blakemore et al., 1998) modalities, in the current manuscript we focus on the auditory modality. Our choice stems from the fact that in the auditory domain, experimental paradigms can precisely equate the physical properties of stimuli across active and passive conditions - something that is more

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Box 1
Ascribed functional roles of motor-induced sensory modulations

Preserving the dynamic range of sensory processing – some animals, such as crickets and bats, produce auditory stimuli in very high intensities as part of their natural behaviors. Singing intensity of crickets is usually greater than 100 dB SPL (Poulet and Hedwig, 2002) and the ultrasonic pulses emitted by bats are estimated to be around 110-120 dB SPL (Suga and Schlegel, 1972). Such self-produced intensive stimulation of auditory sensory apparatus can, in principle, lead to its desensitization and result in loss of sensitivity to stimuli arising from the environment. Studies that addressed this issue found suppressed neural responses during self-generated vocalizations in bats' and crickets' auditory neurons. Interestingly, such suppression was estimated to be equivalent to ~40dB reduction of self-produced vocalizations which retained auditory sensitivity to externally-produced tones during self-produced vocalizations (Schuller, 1979; Poulet and Hedwig, 2002, 2003). Thus, reduced neural auditory responses during self-produced vocalizations may serve for protecting auditory pathways from over-stimulation while maintaining sensitivity to externally-produced stimuli.

Maintaining sensory stability – in the visual domain, when we voluntarily move our eyes, the image on our retina rapidly changes, however, we perceive the world in a stable manner. Alternatively, when we gently push our eyeball through the eyelid and generate an eye movement that bypasses the oculomotor system, the change in image reflected on our retina is experienced as motion of the world. It is suggested that during voluntary eye movement, the predicted retinal image and the actual retinal image are compared and consequently nullify each other in case of full compatibility, creating the experience of visual stability of the world. In case of discrepancy, the residual is experienced as motion of the world (Sommer and Wurtz, 2002).

Agency attribution – modulated perception of self-generated stimuli is suggested to play a role in correct attribution of agency - determining whether the source of a sensory stimulus is self or other. It is suggested that during action execution, the expected sensory feedback and the actual feedback are compared, and in the case of compatibility, the sensory feedback is attributed to the self and labeled as internally-generated, otherwise, they are attributed to other and labeled as externally-generated. This notion is supported by findings that schizophrenic patients experiencing hallucinations or deficits in self-attribution (Frank, 2001; Waters et al., 2012) do not exhibit behavioral and neural modulations as healthy controls during perception of self-generated tactile and auditory stimuli (Blakemore et al., 2000; Ford et al., 2014; Shergill et al., 2014; but see Gallagher, 2004).

Sensorimotor learning – evaluating the difference between the actual and expected sensory feedback plays a crucial role also in shaping and fine-tuning behaviors. For example, in male songbirds, learning of singing behavior emerges through several developmental stages. In the first "sensory" stage, the juvenile bird listens to the songs of adult birds and stores the song-template in memory. In the second "sensorimotor" stage, the juvenile bird begins to sing spontaneously with gradually refining variable and noisy singing until it approximates the memorized template (Brainard and Doupe, 2000). In this stage, the juvenile bird monitors its own singing and adjusts its vocalizations according to the errors estimated by comparing the reafferent feedback to the internalized song-template. In the final "crystallization" stage, the singing is stabilized and rarely changes through the bird's adulthood.

difficult in the somatosensory modality. In the case of vision, to the best of our knowledge, there is no detailed description for direct anatomical connections between motor and visual cortices. On the other hand, direct anatomical connections between motor and auditory cortices, allow us to build a physiologically parsimonious model for motor-auditory modulation.

We start by describing the anatomical connectivity between motor and auditory regions in rodents and primates. Next, we review evidence showing that engagement of motor cortex results in a shift of the neural state in auditory cortex and how responsiveness of auditory neurons depends on environmental context. We continue by describing how motor cortex engagement and environmental context interact to shape auditory cortical responses and perception. To support our proposed mechanism with empirical evidence, we review both animal and human literature. We conclude by pointing to open questions and future research directions.

Although within the auditory modality it is appealing to focus on speech and natural vocalization as the most ecologically relevant type of self-generated auditory stimuli, a few limitations arise. A crucial limitation lies in an inherent methodological difficulty to equate the physical properties of active vocalizations and their passive replay. During vocalization, auditory pathways are stimulated through both bone and air conduction (Reinfeldt et al., 2010). Moreover, vocalizations are associated with stretch of the inner ear muscles ("attenuation reflex") which reduces the amount of auditory input to the central nervous system (Salomon and Starr, 1963; Borg and Zakrisson, 1975; Suga and Jen, 1975; Hennig et al., 1994; Poulet and Hedwig, 2001). Conversely, during passive perception of recorded playback, the sound is perceived only through air conduction and there are no frequency/intensity shifts associated with stretch of the inner ear – making the two types of stimuli inherently different. Therefore, to avoid potential confounds due to mere differences in physical aspects of the stimulus, we deliberately refrain from discussing paradigms involving speech/vocalizations (e.g., Eliades and Wang, 2003, 2008; Chen et al., 2011; Greenlee et al., 2011), and focus on studies in which physical attributes of the stimuli can be controlled across conditions. These studies typically involve pure tones perceived in the presence or absence of motor cortex engagement (e.g., during voluntary movements or neural stimulations).

2. Anatomical connectivity between the motor and auditory cortices

Although to date, there is no evidence for direct connections between primary motor cortex and primary auditory cortex, functional-anatomical evidence from rodents and primates point to bi-directional connections between secondary motor regions and associative auditory regions.

In mice and rats, reciprocal connections between secondary motor cortex and the auditory cortex and auditory thalamus have been reported (Reep et al., 1984, 1987; Nelson et al., 2013; Schneider et al., 2014). Moreover, neurons in rodent secondary motor cortex make direct excitatory connections with both auditory pyramidal cells and auditory inhibitory interneurons (Nelson et al., 2013; Schneider et al., 2014). In non-human primates, motor-auditory anatomical connectivity has been reported between pre-motor areas dorsal to the inferior limb of the arcuate sulcus (area 45) and associative auditory regions, such as superior temporal gyrus (STG) and the upper bank of superior temporal sulcus (Deacon, 1992; Pandya and Vignolo, 1971; Petrides and Pandya, 2002). Weak anatomical connections were also reported between the medial portion of area 6 (pre-supplementary motor area; pre-SMA) and superior temporal sulcus (Luppino et al., 1993). (For reports of connections in the reverse direction, i.e. from auditory to motor regions, see Pandya et al., 1969; Jones and Powell, 1970; Hackett et al., 1999; Romanski et al., 1999; Petrides and Pandya, 1988.)

In humans, diffusion tensor imaging (DTI) studies provide non-invasive means to describe anatomical connectivity, however, without the possibility to indicate directionality. Using DTI, it was found that the dorsolateral and ventrolateral frontal cortices (areas 8 and 6) are connected via the arcuate and superior longitudinal fascicle to the posterior portion of the STG. The inferior frontal gyrus (IFG; area 45; ventral pre-motor cortex) and anterior portion of the STG are also connected via the extreme capsule (Frey et al., 2008; Saur et al., 2008; Glasser and Rilling, 2008; Catani and Jones, 2005). In addition to direct anatomical connectivity, reports of functional coupling between primary and supplementary motor cortices and the auditory cortex in primates suggest the existence of indirect anatomical connections between motor and auditory systems (Möttönen and Watkins, 2009; Morillon et al., 2015; see also Lima et al., 2016).

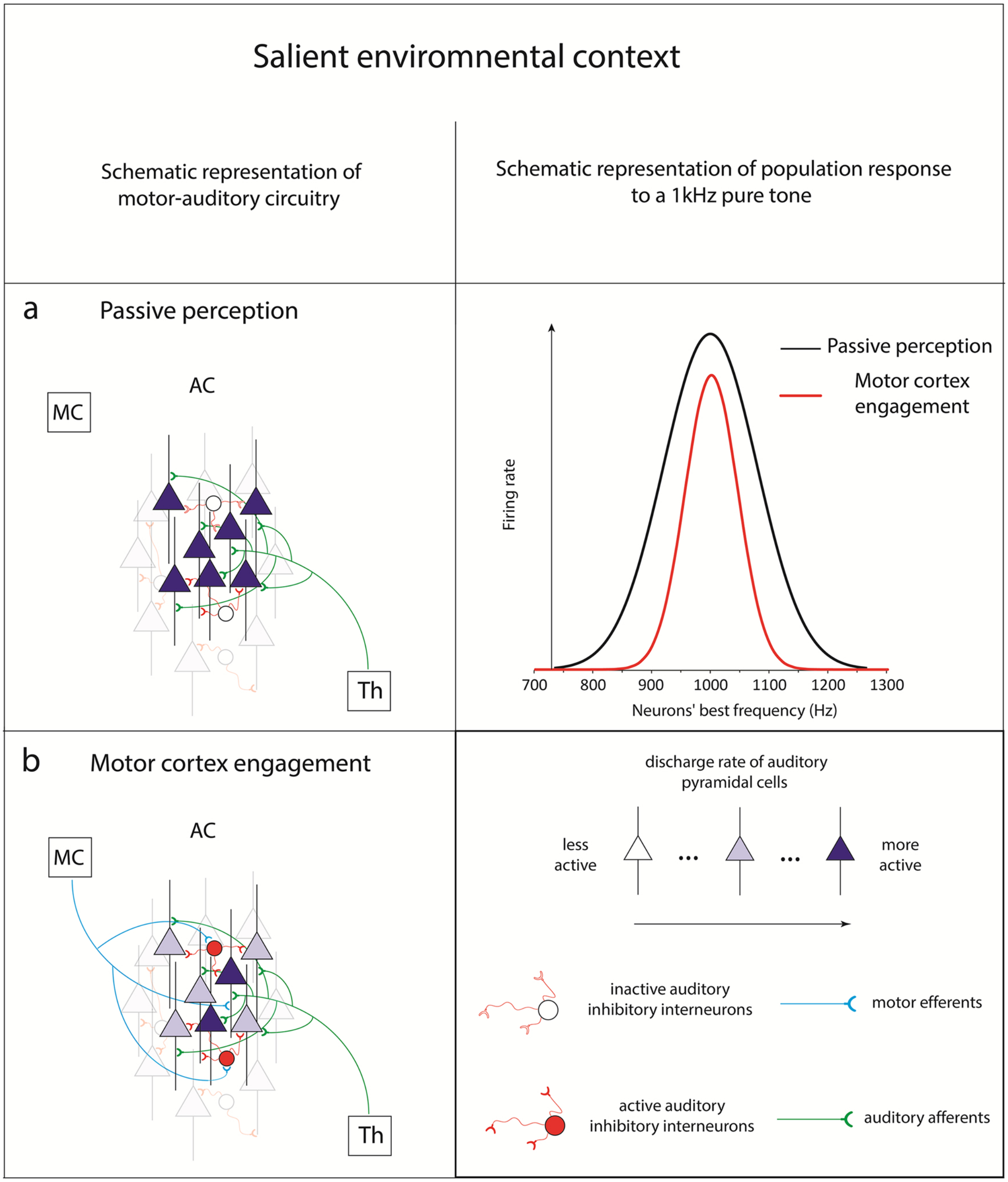

Fig. 1. Salient Environmental Context. In salient environmental contexts, the thalamus provides extensive auditory input (green lines) that targets large population of cells with corresponding and nearby best-frequency. During passive perception (**a**) auditory stimulation is associated with broad frequency tuning curves. Thus, a 1 kHz tone at 75 dB sound pressure level (SPL) evokes strong neural responses in neurons with 1 kHz best frequency and also in neurons with nearby best frequencies (e.g. 0.9 and 1.1 kHz), although to a lesser extent. When the same auditory input is coupled with motor engagement (**b**), motor-induced inhibition results in reduced net population response and in sharpening of auditory frequency tuning curves. That is, a 1 kHz tone still evokes neural responses in neurons with 1 kHz best frequency, but almost no responses in neurons with 0.9 and 1.1 kHz best frequencies. Schematic representation of motor-auditory circuitry depicting motor efferent neurons that make direct synapses on both pyramidal cells and inhibitory interneurons in auditory cortex (cyan lines). Note that motor-auditory connectivity targets more inhibitory interneurons than pyramidal cells. Such modulation of neural state in auditory cortex may be associated with the behavioral phenomenon of attenuation of perceived sound loudness and enhanced frequency discrimination. MC – motor cortex; AC – auditory cortex; Th – thalamus.

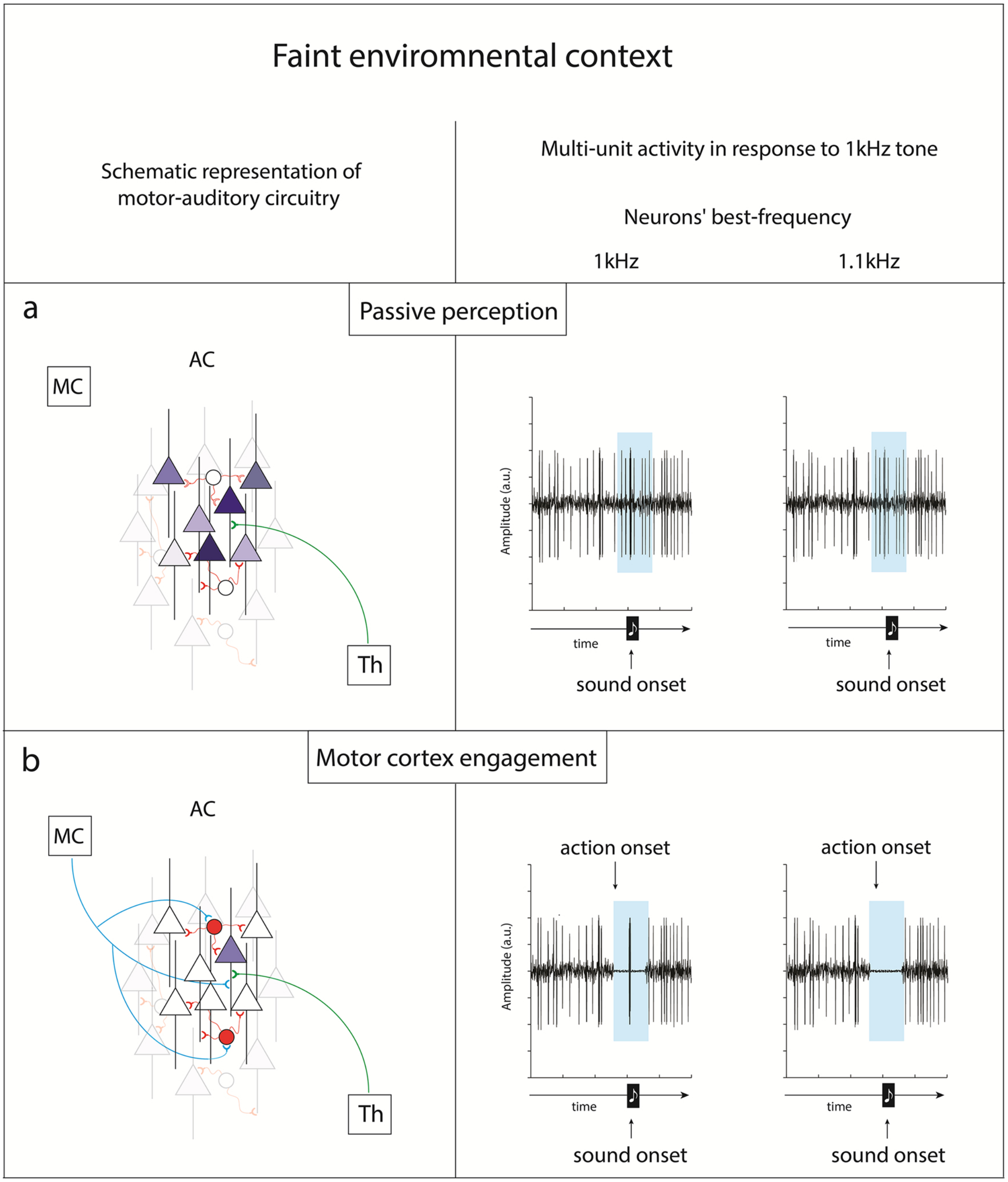

Fig. 2. Faint Environmental Context. In faint environmental contexts, the thalamus provides weak auditory input (green line) that selectively targets small population of cells with corresponding best-frequency. Thus, low amplitude auditory stimulation (for instance, 1 kHz tone delivered at 5 dB SPL) is associated with narrow tuning curves. Under such circumstances, during passive perception (**a**), only neurons with best frequency of 1 kHz will respond weakly, and the level of evoked activity will be hard to distinguish from the background spontaneous activity. When the same auditory input is coupled with motor engagement (cyan lines; **b**), motor-induced inhibition attenuates both the evoked and the background activity. That is, neurons with best frequency of 1 kHz still respond, but neurons with nearby best-frequency are silenced. This results in increased auditory signal-to-noise ratio, which may be associated with improved sound detectability in faint environmental contexts. MC – motor cortex; AC – auditory cortex; Th – thalamus; symbols as in Fig. 1.

3. Motor cortex engagement changes the neural state in auditory cortex

As mentioned above, neurons in mice secondary motor cortex make direct (i.e., monosynaptic) excitatory connections with auditory pyramidal cells and auditory inhibitory interneurons (Nelson et al., 2013; Schneider et al., 2014). The inhibitory interneurons in turn make local connections with auditory pyramidal cells (see Figs. 1 and 2 for schematic representation of motor-auditory circuitry during motor engagement). Therefore, activity in motor regions exerts direct excitation and indirect inhibition (mediated by interneurons) of auditory pyramidal cells.

How does engagement of motor cortex affect the net population activity in auditory cortex? Although neocortical neurons comprise mostly excitatory pyramidal cells (Markram et al., 2004), according to Nelson and colleagues (Nelson et al., 2013), neurons in mice secondary motor cortex (M2) target predominantly inhibitory parvalbumin-positive (PV^+) interneurons in auditory cortex. Therefore, neural activity in motor cortex results in much greater inhibition compared with excitation of auditory pyramidal cells (Nelson et al., 2013; Zhou et al., 2014), and leads to a reduction in net population activity. At the single cell level, this motor-induced inhibition hyperpolarizes and stabilizes membrane potential of auditory pyramidal cells (Schneider et al., 2014). When auditory stimulation is coupled with motor cortex engagement, motor-induced inhibition reduces activity of both background and sound-evoked activity in auditory cortex. Although in absolute terms the magnitude of the sound-evoked response (signal) is reduced, relative to background activity (noise) it is enhanced, thus having a higher signal-to-noise ratio (SNR; we assume similar magnitude of motor-induced inhibition for sound-evoked and background activity). In addition to the reduction in net population activity and increase in auditory SNR, motor-induced inhibition results in sharpening of frequency tuning curves. Broad frequency tuning curves are associated with high firing rate of neurons with "best-frequency" that matches the stimulus and also of neurons with neighboring "best-frequencies", resulting in evoked responses in large populations of neurons and blurred tonotopic discrimination due to overlapping responses of neurons with different "best frequencies". Conversely, narrow frequency tuning curves are associated with reduced number of responding neurons (i.e., only neurons with "best-frequency" that match the stimulus) and thus, better tonal representation. It has been shown in rodents' and bats' auditory cortex that increased inhibition results in sharpening of frequency tuning curves (Chen and Jen, 2000; Wang et al., 2002).

How does motor-induced inhibition affect the state in auditory cortex at the level of neural oscillations? Theoretical analysis has shown that strong correlations between inhibitory and excitatory inputs lead to suppression of synchronized, low-frequency fluctuations of neural activity. More specifically, correlated inhibition and excitation results in reduced pairwise correlations between neurons' firing activity (Renart et al., 2010) and shifts the networks' firing pattern from phasic to tonic. This transition in firing pattern results in a corresponding shift in the networks' power spectrum from low-frequency bands (synchronized) to high-frequency bands (desynchronized). During motor engagement, correlated excitatory and inhibitory activity via direct stimulation of auditory pyramidal neurons and PV^+ interneurons results in a corresponding shift in oscillatory state. Supporting this notion, during quiescence or anesthesia (in the absence of both evoked auditory and motor activity), auditory local field potentials (LFP) are characterized by synchronized, spatially-correlated low-frequency (< 10Hz) activity patterns (Noda et al., 2013; Zhou et al., 2014; Pachitariu et al., 2015). During movement, the power spectrum of LFP recorded from rodents' auditory cortex transitions from synchronized to a desynchronized cortical state. Specifically, during movement, the power of high-frequency oscillations (> 20 Hz) in auditory cortex increases, whereas the power of low-frequency oscillations (< 10 Hz) decreases (Zhou et al., 2014; McGinley et al., 2015a, b). During auditory stimulation, it has been shown that auditory-evoked responses in desynchronized state are characterized by reduced amplitude, lower variance, increased reliability and greater signal-to-noise ratio compared with synchronized state (Curto et al., 2009; Pachitariu et al., 2015). Therefore, by bringing the auditory cortex to a desynchronized state, motor cortex engagement results in more precise and reliable representation of auditory input (von Trapp et al., 2016).

Taken together, motor cortex engagement results in sharpening of auditory tuning curves, reduction in net population response, transition of oscillatory activity from synchronized to desynchronized state and increase in SNR. Next, we turn to describe how different environmental contexts shape the responsiveness of neurons in auditory cortex,

4. Responsiveness of auditory neurons depends on environmental context

One characteristic of the immediate sensory environment is its saliency. At one end are salient environmental contexts in which bottom-up sensory stimulation is well above threshold, easily detectible or can even induce over-stimulation of sensory pathways. At the other end are faint environmental contexts in which sensory inputs are at the organisms' threshold of detection.

Auditory stimulation results in afferent input to auditory cortex and evoked responses in auditory neurons. Importantly, the width of auditory neurons' frequency tuning curves depends on sound amplitude and broadens with increase in sound intensity (Tan et al., 2004; Guo et al., 2017; Zhou et al., 2014; Pachitariu et al., 2015). Therefore, salient environments are associated with broad frequency tuning curves and spatially overlapping responses of neural populations with different 'best-frequency' (Schreiner, 1998; Guo et al., 2017). Conversely, faint environmental contexts, in which an organism is exposed to stimuli delivered near the hearing threshold, are associated with narrow frequency tuning curves characterized by weak and more selective neural responses. Under such circumstances, signals arising from bottom-up auditory pathways can remain indistinguishable from the background neural activity and therefore have lower probability to be detected at the behavioral level.

In what follows we present empirical evidence describing how these environmentally-dependent changes in responsiveness of auditory neurons, interact with changes in auditory neural states associated with motor cortex engagement. Importantly, we show how such interactions can result in different modulations of auditory perception.

5. Motor cortex engagement and environmental context shape responsiveness of auditory cortex and perception

Motor-induced inhibition results in change in auditory neural state irrespective of environmental context. However, since different environmental contexts are associated with tasks that emphasize different aspects of the neural representation of auditory stimuli, the consequences of motor-induced inhibition may change across environmental contexts. For example, perception of sound loudness (usually performed in salient environmental contexts) may be governed by the amount of responding neurons, while detection tasks (typically performed in faint environmental contexts) may be governed by SNR. Frequency discrimination tasks (which can be performed in any environmental context) may be governed by response selectivity and the width of auditory frequency tuning curves. In what follows, we describe how auditory neural states, environmental contexts and stimulus attributes may interact and give rise to different behavioral phenomena.

5.1. Motor-auditory modulations in salient environmental contexts

In a series of studies, the effects of motor cortex engagement on perception of sound amplitude were examined by comparing perceived loudness of self- vs. externally-generated auditory stimuli. Human subjects were presented with two consecutive salient tones delivered at random time delays (usually ranging between 800–1200 ms). The first tone was presented in a fixed amplitude and across trials the amplitude of the second tone varied several dBs around the amplitude of the first. After presentation of the second tone, subjects were asked to report which one of the two tones was louder - first or second. In the active condition, subjects triggered the first tone by button press, while in the passive condition, the first tone was triggered either by an experimenter or by a computer. The second tone in both conditions was always triggered by an external source. Subjects' responses across trials are converted to a proportion of times the second (or first) tone was reported to be louder, and fit to a logistic curve. The sound amplitude at which the curve is at 50% (indicating equal number of trials in which the first or the second tone was reported to be louder) was defined as subjects' point of subjective equality (PSE). Comparing the PSE in active and passive conditions indicates that self-generated auditory stimuli are perceived as less loud compared with identical stimuli perceived passively (i.e., sensory attenuation; Sato, 2008, 2009; Weiss et al., 2011a, b; Weiss and Schutz-Bosbach, 2012; Reznik et al., 2015b; but see Cao and Gross, 2015 for no difference in PSE). Taken together, these studies demonstrating reduction of perceived loudness for self-generated sounds are in agreement with reduced net population response in auditory cortex during motor engagement.

Other studies that manipulated engagement of motor cortex during sound perception report that pitch discrimination was better when subjects were engaged in silent finger tapping compared with passive listening (Morillon et al., 2014; Morillon and Baillet, 2017). More specifically, pitch discrimination was best when finger taps were synchronous with presented sounds (vs. sounds that were asynchronous to the finger taps; Morillon et al., 2014). Interestingly, subjects' finger taps were not the triggering source of the presented sounds, suggesting that mere temporal co-occurrence of motor activity (irrespective of intentional motor-sensory coupling) is sufficient to induce modulation of auditory responses. Although the studies by Morillon and colleagues were not originally designed to address the effect of motor engagement on pitch discrimination, the reported results are compatible with the notion of sharpening of auditory frequency tuning curves and more selective response in auditory cortex following motor-induced inhibition.

At the physiological level, studies using electroencephalography (EEG) have focused on the auditory evoked N1 and P2 components recorded from midline electrodes Fz, FCz and Cz. The major finding arising from these experimental protocols is that the amplitude of the auditory evoked N1 component is attenuated in self-generated compared with passive trials (Baess et al., 2011; Sowman et al., 2012; Horvath, 2013, 2015; but see Poonian et al., 2015). For the P2 component, similar attenuation effects for self-generated sounds were also reported (Horvath, 2013; Sanmiguel et al., 2013). Additional evidence from magnetoencephalography (MEG) studies support these findings and demonstrate suppressed M100 amplitudes (an MEG equivalent of the EEG N1 evoked response) in STG for self-generated sounds (Martikainen et al., 2005; Aliu et al., 2009; Horvath et al., 2012).

Evidence for activity in motor regions being the source of such modulations of auditory processing comes from functional magnetic resonance imaging (fMRI). Using the advantage of whole-brain coverage, functional connectivity analysis suggests that fMRI signal in STG during active conditions is coupled with activity in primary motor cortex (M1) and SMA (Reznik et al., 2015a). Although to date there is no evidence in primates for direct anatomical connections between M1 or SMA and STG, the functional coupling suggests that these motor pathways may exert modulations through indirect anatomical connections (see section 2). Further support for the functional coupling between motor and auditory systems comes from the finding that the magnitude of fMRI signal modulation in STG correlated with the rate of subjects' sound-triggering actions (Reznik et al., 2015a). In other words, higher rate of subjects' sound-triggering actions (and stronger neural output from motor cortex) resulted in stronger fMRI signal modulation in STG.

Modulation of fMRI signal in STG by voluntary actions has been reported in both directions, namely attenuation (Straube et al., 2017) and enhancement (Reznik et al., 2014, 2015a). A possible reconciliation of these opposite directions of modulation may reside in the fact that the fMRI paradigms reporting enhancement used trains of auditory stimuli delivered in a fixed rate (either 1 Hz or 2 Hz) while the study reporting attenuation used single stimuli delivered as discrete events. Repetitive low stimulation rate has been reported to entrain auditory oscillatory activity (Lakatos et al., 2005) resulting in high power in low-frequency range. This stimulus-induced power increase in low-frequency bands is expected to be lower during active repetitive sound generation (relative to passive listening) due to motor-induced inhibition of auditory activity (as described above). A previous report showed that fMRI BOLD signal and LFPs at low frequencies in auditory cortex are *negatively* correlated (Mukamel et al., 2005). Therefore, it is plausible that the enhanced fMRI signal in STG during active repetitive low rate stimulation, corresponds with attenuated low-frequency neural oscillations. Taken together, the electrophysiological and fMRI data in humans described above point to reduced auditory population evoked responses that is coupled to activity in motor cortex.

Evidence from animal studies provide an opportunity to examine the motor-induced inhibition of auditory cortex directly at the level of single cell activity and activity of localized neural populations. For example, when mice actively generated auditory tones, firing rate of single neurons in auditory cortex was reduced compared with firing rate evoked by passive perception of identical sounds (Carcea et al., 2017). Similarly, motor-induced inhibition was also observed in the amplitude of evoked LFP (Rummell et al., 2016). These results are in agreement with reports of attenuated evoked LFPs when auditory cortex is in desynchronized compared with synchronized oscillatory states (Curto et al., 2009; Marguet and Harris, 2011; Pachitariu et al., 2015), simulating the desynchronization it undergoes during motor cortex engagement.

Interestingly, motor-induced inhibition of auditory responses occurs also when there is no intentional link between motor actions and auditory stimuli. Thus, in mice, sounds that temporally coincide with animal movement (but are not triggered by it), are associated with reduced sound-evoked LFPs compared with those evoked by identical sounds delivered during quiescence (Zhou et al., 2014; Rummell et al., 2016). The notion that intentional motor-sensory coupling is not a necessary requisite for sensory modulation is further supported by optogenetic and pharmacological studies. Such interventions can simulate signals propagating through motor pathways in the absence of voluntary control by modulating neural activity in motor or auditory cortex. When optogenetic stimulation of motor cortex in anesthetized mice was coupled with auditory stimuli, excitatory neurons in auditory cortex exhibited reduced evoked firing rates compared with firing rates in the absence of optogenetic stimulation (Nelson et al., 2013; Schneider et al., 2014).

Optogenetic and pharmacological interventions have been also applied directly to the auditory cortex, thus mimicking its activation by motor engagement. For example, direct optogenetic activation of PV^+ interneurons in auditory cortex resulted in reduced auditory-evoked firing rates (Hamilton et al., 2013). Consistent findings were reported using pharmacology to deactivate auditory interneurons (including PV^+ interneurons). When auditory interneurons were deactivated, thus reducing the level of inhibition they exert, sound-evoked firing rate of auditory pyramidal cells increased and their frequency tuning curves broadened (Chen and Jen, 2000; Wang et al., 2002; see also Pi et al., 2013). Thus, the optogenetic and pharmacological studies described above suggest that activation of interneurons that make direct connections to auditory pyramidal cells increases the inhibition they exert, resulting in reduced evoked activity in auditory cortex. On the other hand, de-activation of interneurons reduces the inhibition they exert on pyramidal cells resulting in enhanced evoked responses in auditory cortex.

Taken together, physiological and behavioral evidence reviewed so far suggest that the level of motor cortex engagement can gate the level of inhibition exerted by auditory interneurons and thus influence evoked responses and auditory perception through sharpening of frequency tuning curves and reduction in the net population response (Fig. 1). In tasks comparing sound amplitude, the reduction in population response is associated with attenuation of perceived loudness. However, in tasks requiring selective neural representation (e.g., pitch discrimination) sharpening of tuning curves can result in enhanced performance due to better separation of population responses with different best-frequencies. The effect of motor-induced inhibition on other stimulus attributes, such as spatial (Lee and Middlebrooks, 2011) or temporal (Lu et al., 2001) representations needs to be examined in further studies. In what follows, we describe the neural and behavioral implications of motor-induced inhibition in faint environmental context.

5.2. Motor-auditory modulations in faint environmental contexts

During motor cortex engagement, global inhibition reduces activity of both background and evoked activity, thus increasing signal-to-noise ratio (SNR) of the sound-evoked responses. In salient environmental contexts, the same increase in SNR has no effect on sound detectability which by definition is at ceiling. However, in faint environmental contexts, increase in SNR can make near-threshold sound-evoked activity more easily detectable from the spontaneous background activity (Fig. 2). We now review the empirical evidence supporting the notion that motor-induced inhibition can enhance behavioral responses in faint environmental contexts.

Experimental paradigms that used near-threshold auditory stimuli point to enhanced auditory sensitivity favoring self-generated sounds. This increased sensitivity was found in the amplitude and temporal domains. In the amplitude domain, when subjects were asked to compare perceived loudness of weak sounds delivered at intensities near their perceptual threshold, they rated self-generated sounds to be louder than identical sounds that were delivered passively (Reznik et al., 2015b). Similarly, detectability of self-generated sounds was better compared with identical-amplitude sounds delivered in a passive manner (Reznik et al., 2014). Importantly, increased detectability was not due a change in response bias but rather a true increase in sensitivity.

Modulated processing of self-generated auditory stimuli has been also reported in the temporal domain. Iordanescu and colleagues (Iordanescu et al., 2013) presented subjects with three consecutive sounds delivered at the intensity that was slightly above the constant background noise. In the active condition, the three tones were initiated by subjects' button press, while in the passive condition the tones were triggered by the experimenter. The temporal distance between the first and third tones was constant, but the onset of the middle tone varied. Subjects' task was to report whether the middle tone was closer in time to the first or the last tone. Subjects showed reduced just-noticeable-difference (indicating greater sensitivity) during the active compared with passive trials. Although the neural representation of time-intervals is not yet clear (Lu et al., 2001) and there are no known equivalents of frequency tuning-curves in the time domain, these results suggest that enhancement of auditory processing in faint environmental contexts associated with motor cortex engagement, can be expressed not only in the amplitude domain but also in the temporal domain. Whether such increased sensitivity is due to motor-induced inhibition and increased SNR, as proposed by our model, remains to be seen.

Unlike the behavioral studies described above, to the best of our knowledge there are no human physiological studies performed under faint environmental context. Therefore, to date, only animal models provide the physiological basis for delineating the mechanism behind modulated processing of actively-generated auditory stimuli in faint environmental contexts. For example, a study by Buran and colleagues (Buran et al., 2014), showed that spontaneous firing rate in rodent auditory cortex was lower during motor engagement (active nose-poke) compared with spontaneous activity during quiescence. Importantly, sound-evoked activity was higher in active compared with passive trials when calculated relative to the corresponding baseline (Buran et al., 2014). In other words, signal-to-noise ratio of sound-evoked activity, defined as the ratio between the evoked firing rate and the background firing rate, is actually increased when motor cortex is engaged (Zhou et al., 2014; Busse, 2018). The notion of increased auditory SNR during motor engagement is also supported by findings that auditory neurons exhibit higher firing rates relative to their spontaneous firing rates in the desynchronized compared with synchronized network states (Pachitariu et al., 2015). Moreover, auditory-evoked responses during synchronized state are characterized by greater variance and poorer reliability compared with desynchronized state (Curto et al., 2009; Pachitariu et al., 2015). This suggests that auditory stimuli are more faithfully and reliably represented during desynchronized compared with synchronized auditory network state (as occurs with or without motor cortex engagement, respectively; Marguet and Harris, 2011; Pachitariu et al., 2015; von Trapp et al., 2016). Furthermore, simulation of motor-induced activation of auditory interneurons by direct optogenetic stimulation was associated with increase in auditory SNR and sharpening of auditory tonal representation (Hamilton et al., 2013; Li et al., 2014; see also Wehr and Zador, 2003 and Sohal et al., 2009).

Finally, auditory field potentials recorded during delivery of weak auditory input, show little change of their spontaneous slow-wave oscillatory activity pattern and poor coherence to the envelope of the auditory input (Marguet and Harris, 2011). Therefore, during quiescence, when auditory cortical state is characterized by slow, low-frequency and spatially correlated oscillations, weak auditory stimuli are simply "filtered out" and masked by ongoing background activity (Marguet and Harris, 2011; Guo et al., 2017; Pachitariu et al., 2015). Thus, the main factor which governs the ability to reliably detect a near-threshold auditory stimulus lies in its *relative* saliency to the ongoing background/spontaneous activity. Since ongoing auditory spontaneous activity is inhibited during motor actions (via the top-down inhibitory network, mediated by interneurons), the saliency of near-threshold stimuli relative to the background activity is increased. While the relationship between increase in neural SNR due to motor engagement and behavioral performance is not fully understood, it is plausible that increased SNR may improve detectability and temporal precision of near-threshold sounds (Buran et al., 2014; McGinley et al., 2015b; Iordanescu et al., 2013; Reznik et al., 2014; Carcea et al., 2017). This relationship requires further investigation.

6. Discussion and open questions

We outline a new perspective on a behavioral and neurophysiological phenomenon of sensory modulation and propose a plausible neurophysiologic model that can reconcile apparent discrepancies in the literature. The reviewed body of literature suggests that motor actions result in (1) reduced auditory net population activity, (2) narrowing of auditory frequency tuning curves, (3) increase in auditory-evoked SNR and (4) shift of the oscillatory activity from synchronized to desynchronized sate. Such motor-induced changes lead to different behavioral phenomena under different environmental contexts (Harris and Thiele, 2011).

Modulated processing of self-generated stimuli has been previously addressed by different theoretical models of motor control. For example, during execution of voluntary actions, it has been suggested that the motor system sends an "efference copy" of the motor commands (von Holst, 1954) that results in a "corollary discharge" (Sperry, 1950) in sensory cortex representing the expected sensory outcomes. Based on the current state and the efference copy, a forward model simulates the neural representation of the *expected* feedback which is then compared with that of the *actual* reafferent feedback conveyed by the sensory system (Wolpert et al., 1995). When there is a match between the expected and reafferent feedback, the neural and behavioral responses are attenuated.

The model we propose in the current manuscript aligns broadly with the ideas of "efference copy" and "corollary discharge" implemented in the forward model in terms of top-down propagation of motor signals to auditory cortex during motor cortex engagement. The forward model uses efference copies to generate sensory expectations and therefore relies on an intentional link between actions and their sensory consequences. Reports in the literature demonstrating sensory modulation following stimulation of motor cortex, or following actions that are disengaged from sensory consequences but simply temporally coincide, suggest that intentional coupling between the action and sensory stimulus is sufficient but not necessary in order to induce modulations of sensory processing. Thus, it seems that engagement of motor cortex modulates sensory processing irrespective of intentional coupling. It is an open question whether the degree of behavioral and physiological modulation of sensory responses depends on the degree of intentional coupling with preceding actions (see also open question 6.1 below).

An additional framework that addressed motor modulations of sensory processing is that of active sensing (Schroeder et al., 2010;

Ahissar and Assa, 2016). Perhaps counterintuitively, active sensing postulates that perception is not a passive process, but rather an active process in which sensory information is actively sampled from the environment by either covert or overt motor/attentional engagement that results in beneficial sensory processing (Schroeder et al., 2010). It has been proposed that rhythmic oscillatory activity within the motor cortex entrains the sensory pathways involved in sensory perception (e.g., sniffing during exposure to odors), thus contributing to more precise sensory processing (Arnal, 2012; Fujioka et al., 2012). In the auditory domain, "active sensing" implies that top-down modulations originating in the motor cortex result in increased temporal prediction and therefore, in beneficial processing of auditory input (Arnal, 2012; Morillon et al., 2015, 2016; Morillon and Baillet, 2017).

The framework of "active sensing" is compatible with the model we propose, that is, we postulate that overt motor activity during active sound generation provides a temporal framework in which modulated neural and behavioral responses to auditory stimuli occur. Additionally, in agreement with "active sensing", our model postulates that motor engagement modulates auditory cortex activity in a global fashion that does not depend on expected sensory consequences. However, reports in the literature point to potentially differential sensory modulation occurring during intentional and non-intentional motor-sensory coupling (Desantis et al., 2012; Rummell et al., 2016). Therefore, expanding the framework of "active sensing", it might be that motor activity provides informative priors that relate not only to the temporal occurrence of self-generated stimuli ("when" the stimuli is going to occur), but also to its expected sensory identity ("what" stimuli is going to occur; see open questions 6.1 and 6.3 below).

Motor-sensory interactions were also addressed by the active inference model proposed by Brown et al. (2013; see also Friston and Kiebel, 2009 for the general predictive coding framework). This model postulates that sensory attenuation and reduction in sensitivity are necessary features of self-generated movements. Our model, on the other hand, suggests that inhibition (as a mechanism) not only doesn't always result in dampening of behavioral responses, but in some cases, can even enhance performance. Such is the case during sound detection in faint environmental contexts. Furthermore, the active inference model addresses perceptual properties of stimulus attributes that relate only to intensity, such as sound loudness or tactile pressure. Our model expands motor-related modulations to other auditory attributes by demonstrating that motor-induced inhibition of auditory cortex can also affect frequency and temporal processing. Additionally, similar to the forward model, the active inference model suggests that self-generated actions result in attenuation of sensory processing only if motor actions are causally and intentionally linked to the generated sensory stimuli. Contrary to this notion, as we mentioned above, intentional motor-sensory coupling is a sufficient but not necessary component of motor-sensory modulations (Juravle and Spence, 2011; see also open question 6.1 below).

Next, we enumerate some open questions and future research directions that can further elucidate the nature of motor-sensory interactions:

6.1. The role of intention in motor-induced modulations

Some of the reviewed studies suggest that motor actions modulate auditory processing even in the absence of intentional coupling with the auditory stimuli (e.g., during finger tapping performed in synchrony with auditory stimulation in humans or during optogenetic activation of motor cortex in anesthetized rodents; Morillon et al., 2015; Schneider et al., 2014). These results suggest that intention is not a necessary component of such modulations. However, other reports suggest that the magnitude of sensory modulation is different when subjects subjectively attribute self-generated sounds to themselves rather than to an external source (Desantis et al., 2012; see also differences in "intentional" and "non-intentional" modulations in Rummell et al., 2016). Therefore, it is possible that while both intentionally and non-intentionally coupled actions result in sensory modulation (relative to passive sensory stimulation), the modulation patterns are different between the two.

6.2. Selectivity of motor-induced modulations

In the current framework, we assumed that motor actions result in global and non-selective inhibition of auditory cortex. However, the selectivity of such inhibition is another open question. Does it target specific neural populations depending on expected stimulus attributes such as modality, frequency etc., or rather has a global non-selective effect? It can be speculated, for instance, that one of the functional properties of voluntary actions is to prime the auditory cortex by shifting its neural state and to gate auditory processing. It can be further speculated that the process of sensorimotor learning involves a shift from global and non-selective motor-induced inhibition, to a more selective and specific inhibition that depends on the expected sensory consequences. This might provide an explanation as to why people tend to learn better from active engagement than from passive perception of someone else's performance (Ossmy and Mukamel, 2018).

6.3. The role of sensory expectations in motor-induced modulations

In the current framework, we assume that modulation of auditory cortex does not depend on expected sensory consequences. However, recent evidence show that motor preparatory activity is modulated by expected sensory consequences of voluntary actions (Reznik et al., 2018; Vercillo et al., 2018). Therefore, it is plausible, that sensory expectations also change the degree of motor-induced inhibition. For example, when faint auditory stimuli are expected, motor-induced inhibition may be higher in order to increase SNR (relative to motor-induced inhibition when salient stimuli are expected).

6.4. Motor-induced inhibition of auditory cortex in primates

Most of the direct physiological and anatomical evidence for motor-induced inhibition comes from studies performed on rodents and detailed functional evidence from primates in this regard is still lacking. Furthermore, to date, there is no direct physiological evidence for motor-induced sharpening of tuning curves in primates. Possible future lines of research should address the mechanism of motor-auditory interactions in primates in order to delineate its functional and anatomical properties, such as selectivity of motor output and cell types involved in the circuit.

6.5. Additional brain circuitries and additional behavioral/environmental contexts

In the current review we addressed only the involvement of cortico-cortical connections in auditory cortex modulation. However, it has been shown that also midbrain (Singla et al., 2017), thalamus (Guo et al., 2017) and basal forebrain (Nelson and Mooney, 2016) contribute to modulation of auditory responses. Furthermore, although to the best of our knowledge there are no reports showing a direct role of the cerebellum in modulation of auditory activity, there is evidence that it is involved in forward motor state estimation during voluntary actions (Ebner and Pasalar, 2008; Miall et al., 2007; Mulliken et al., 2008). Therefore, the role of the cerebellum and other brain regions in modulating auditory responses during motor engagement awaits further investigation.

Here we focused on environmental saliency as one domain in which motor-induced inhibition results in differential auditory processing. However, additional contextual factors, such as timing of auditory stimulation (Guo et al., 2017) and animals' arousal level (McGinley et al., 2015a, b), should be taken into consideration as well when discussing modulated auditory responses to otherwise identical stimuli. Therefore, future research is needed to further delineate the interactions between neural states, and physical attributes of stimuli and their relationship to behavior and cognition.

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