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**The role of the dorsal auditory stream in auditory-motor coordination**

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**The role of the dorsal auditory stream in auditory-motor coordination**

**by**

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## **Abstract**

### **The role of the dorsal auditory stream in auditory-motor coordination**

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Rhythmic auditory stimulation is a salient cue used to guide coordinated movement. The cortical mechanism that is thought to facilitate auditory-motor coordination involves the functional and structural connections of the dorsal auditory stream. The right temporal parietal junction acts as a relay center within the dorsal auditory stream, connecting auditory and motor cortical areas. Two well studied auditory-motor coordination tasks, synchronization and syncopation are reviewed to better understand the role of the dorsal stream in motor coordination. Furthermore, the use of non-invasive brain stimulation is introduced as a possible method to modulate the flow of information through the auditory and motor cortical areas via the dorsal auditory stream. This report aims to set the stage for the investigation of the acute behavioral and cortical effects of non-invasive brain stimulation on auditory-motor coordination.

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## **The role of the dorsal auditory stream in auditory-motor coordination**

### **Introduction**

For individuals with a movement disorder, rehabilitation interventions are an important tool to address the abnormal motor movements that limit functionality and independence (Wenning et al. 2005; Hatem et al., 2016). Movement disorders refer to abnormal movements that occur as a neurologic symptom of a disease (Hallett, 2018). The motor deficits of common movement disorders, such as Parkinson's disease and Huntington's disease, are, in part, due to the disruption of sensorimotor integration (Latorre et al., 2019). Sensorimotor integration is the process by which sensory information is integrated by the central nervous system to shape motor planning and execution (Dubbioso et al., 2019) and involves communication across distributed sensory and motor brain regions (Machado et al., 2010; Wilson et al., 2017). Understanding the cortical process of sensorimotor integration and its role in facilitating movement will contribute to a general understanding of movement disorders and aid in the development of effective interventions to correct abnormal movement.

One example of sensorimotor integration is the coordination of movement with rhythmic auditory stimulation (RAS), which is thought to rely upon the rich connections between auditory and motor regions of the brain (Chen et al., 2008; Kung et al., 2013; Patel & Iverson, 2014). First introduced by Thaut and colleagues (1999), RAS has been used to aid in the coordination of movement patterns in individuals with movement disorders. It is well established that there are functional and anatomical connections between auditory and motor areas of the brain that are thought to facilitate auditory-motor entrainment. Under the concept of entrainment, the rhythmic properties of sound perceived by the auditory processing brain areas entrain a synchronized

response in motor processing brain areas. However, the neural mechanism by which auditory and motor areas of the brain interact to facilitate auditory-motor entrainment is unknown.

In this report, we provide the background of the use of RAS to improve movement and the current understanding of the neural interactions that facilitate auditory-motor entrainment, in particular, the flow of information from primary auditory processing areas to more frontal motor processing areas via the dorsal auditory stream. The role of the right temporal parietal junction (rTPJ) will also be introduced as a potential relay center within the dorsal auditory stream and as the conduit through which entrainment occurs through the auditory and motor areas of the dorsal auditory stream. The flow of information through the dorsal auditory stream is thought to have a favorable impact on rhythmic auditory-motor coordination, especially during tasks that are more unstable and that illicit increased engagement of frontal cortical areas. This concept will be introduced through the behavioral and neuronal differences identified in two common tapping tasks: syncopation (PAT) and synchronization (SYN). This report will also introduce the possible application of non-invasive brain stimulation (NIBS) to upregulate cortical activity associated with auditory-motor entrainment to enhance auditory-motor coordination. The use of NIBS to improve auditory-motor coordination through increased auditory-motor entrainment has implications for those undergoing rehabilitation for sensorimotor deficits due to neurological movement disorders (Machado et al., 2010; Oliveira et al., 2011; Patel et al., 2014; Wilson et al., 2017).

## **Rhythmic auditory stimulation can be used to guide coordinated movement**

Tapping with a rhythmic auditory beat reduces variability of movement and is a superior cue for guiding coordinated movement compared to other sensory modalities such as vision (Essens & Povel, 1985; Jäncke et al., 2000; Chen et al., 2002; Patel et al., 2005; Getchell et al., 2010; Rohenkohl et al., 2012). Rhythmic auditory stimulation (RAS), presented as a regularly occurring beat, has been used in therapeutic settings to facilitate motor coordination (Thaut & Abiru, 2010; Bella et al., 2015; Leow et al., 2015). Gait velocity and stride length have been shown to improve when RAS was coupled with gait training for a 3-week intervention in patients with Parkinson's disease (Thaut et al., 1996). In another example, when RAS was paired with a coordinated walking/clapping task, coordination performance improved (Getchell et al., 2010). Similar improvements to coordinated movement occur when RAS training is applied to individuals following a stroke (Thaut et al., 2007) and individuals with developmental disorders (Getchell et al., 2010; Srinivasan et al., 2015). As an intervention technique, RAS has been used to improve motor coordination.

The success of RAS based interventions on movement is attributed to the relationship between auditory and motor areas of the brain and how these regions are functionally and structurally connected (Buchsbaum et al., 2005; Friederici, 2009; Thaut, 2013; Patel & Iversen, 2014; Thaut et al., 2015). The structure of the brain areas involved in auditory processing will be introduced, followed by evidence of functional communication. Sound is perceived through the auditory system which transforms sound waves into neural activity at the auditory cortex located in the superior temporal gyrus (STG). From the primary auditory processing areas in the STG region, there is a division in which two separate pathways, which specialize in different aspects of auditory processing, terminate in the frontal cortex. The ventral pathway is often referred to as



a “what” pathway in which specific features are processed for identification of the auditory stimulus, often in context of speech based communication (Zatorre et al., 2004). The ventral stream links the STG with the inferior frontal gyrus (IFG) through the inferior fronto-occipital fasciculus (Martino et al., 2010), and is involved in identifying features of speech, speech comprehension, and the identification of the source and meaning of sound (Rauschecker & Tian, 2000; Alho et al., 2014). The dorsal pathway is referred to as the “where” pathway and is associated with sound localization (Tata & Ward, 2005; Brunetti et al., 2005) or the motion of sound in space (Belin & Zatorre, 2000; Arnott et al., 2004), but is also involved in speech and language (Hickok & Poeppel, 2000, 2007). The dorsal stream is involved with the organization of the temporal aspects of sound involved in auditory-motor integration (Zatorre et al., 2007; Hickok et al., 2011; Kornysheva & Schubotz, 2011; Sammler et al., 2015; Yang & Li, 2019). The dorsal stream initiates from the posterior STG then to the interior parietal lobule (IPL), then continues to the supplementary motor area (SMA), and premotor cortex (PMC) through the arcuate fasciculus (Catani et al., 2005; López-Barroso & Diego-Balaguer, 2017).

While the ventral and the dorsal stream both stem from the STG and terminate in the frontal cortex, the dorsal stream in particular creates a connection from the primary auditory processing cortical area to motor processing areas such as the SMA and PMC (Blakemore et al., 1998; Rauschecker & Scott, 2009). The SMA contributes to the organization of the temporal properties of actions (Mayvill et al., 2002; Shima & Tanji, 2000) and the motor planning and preparation of movements (Gerloff et al., 1997; Schubotz et al., 1999; Macar et al., 1999; Schubotz et al., 2000; Jäncke et al., 2000; Macar et al., 2006). Lesions to the SMA disrupt the coordination of movement (Stephen et al., 1999). The PMC has a role in action planning and control based on external stimuli (Hoshi & Tanji, 2006) and therefore is an important for the

integration of auditory information (Chen et al., 2006). The SMA and PMC contribute to the planning and preparation of movement guided by the temporal aspects of external stimuli.

From the SMA and PMC, information is sent to the primary motor cortex (M1) which generates the neural signals to control the execution of movement through the activation of skeletal muscle (Natali et al., 2020). Fibers of the corticospinal tract originate from the M1, SMA and PMC. This tract is the direct pathway from the cortex to the spine and the main pathway for the control of voluntary movement. Subcortical areas are also involved in coordinating sensory and motor neurons and in generating signals that correspond to movement by interacting with motor planning and execution areas of the cortex (Leaver et al., 2009). The cerebellum and basal ganglia, along with the thalamus, are involved the timing aspect of motor control (Mayville et al., 2002). The basal ganglia organizes the structure of motor tasks. The basal ganglia receives input signals from the cerebral cortex. The signals are processed, and an output signal is projected to motor neurons of the frontal lobe via the thalamus or to the motor neurons of the brainstem. The projected signal contributes to the planning and execution of movement. The cerebellum modulates movement and aids in coordination and balance. It receives input from the cerebral cortex and the spinal cord. The cerebellar output projections to motor planning and execution areas of the cortex via the thalamus. The basal ganglia and cerebellum are active during auditory-motor coordination and involved in temporal processing (Mayville et al., 2002).

These components of the dorsal auditory stream are thought to communicate through the entrainment of low frequency cortical oscillations across auditory and motor areas (Kandylaki et al., 2016). Cortical oscillations are related to the excitability of populations of neurons across the cortex (Sanchez-Vives & McCormick, 2000; Lakatos et al., 2005) and neuronal excitability entrained to stimulus onset indicates that sensorimotor neural resources are allocated towards

stimulus processing (Lakatos et al., 2008; Henry & Obleser, 2012). Sensorimotor rhythmic entrainment may aid in sensorimotor integration, or the process in which sensory input is integrated by the central nervous system for motor processing and execution, by enhancing the neural processes involved in sensory processing (Henry & Obleser, 2012; Sowinski & Dalla Bella, 2013; Tierney & Kraus, 2013; Dalla Bella & Sowinski, 2015; Tierney & Kraus, 2015; Colling et al., 2017).

During RAS, cortical oscillatory activity is entrained with the onset of the stimulus through sensory and motor areas of the cortex (Schroeder & Lakatos, 2009; Cravo, Rohenkohl, Wyart, & Nobre, 2013). Synchronous event-related activity in the beta frequency band (15-30Hz) occurs in the PMC and SMA as well as the sensorimotor cortex (SMC) and A1 (Pollok et al., 2005; Fujioka et al., 2009; Fujioka et al., 2012; Arnal et al., 2014). The SMC is part of the motor system in which movements are controlled through the integration of feedback signals from afferent sensory neurons and feedforward signals to descending motor neurons to the skeletal muscle (Eskandari et al., 2004). The SMA and PMC are frontal regions of the dorsal auditory stream, structurally linked to the A1 through the IPL. The entrainment of cortical oscillations across auditory and motor areas facilitates the coordination of movement with RAS (Kandylaki et al., 2016).

### **The right temporal parietal junction acts as a relay center within the dorsal pathway**

The temporal and frontal regions of the dorsal auditory stream are linked via the inferior parietal regions, which is a multimodal integrative hub involved in multisensory processing (Hickok & Poeppel, 2000; Hickok et al., 2003; Buchsbaum et al., 2005). One inferior parietal region in particular, the right temporal parietal junction (rTPJ), has been identified as a relay

center between sensory and motor regions (Corbetta & Shulman, 2002; Jakobs et al., 2012; Hill et al., 2017).

The manipulation of brain activity or altered brain activity due to damage at the rTPJ has allowed for inferences to be made of the role of this particular brain region. Individuals with lesions at the rTPJ exhibited increased attention to cues that were essentially distractor cues compared to individuals with no rTPJ damage (Pedrazzini & Ptak, 2019). Based on this finding, the rTPJ plays a role in prioritizing behaviorally relevant stimuli over distractor stimuli that may interfere with performance. In another study, NIBS was used to facilitate cortical excitability at the rTPJ, this increased the participant's ability to identify if two rhythmic sequences were the same. These findings implicate the role of the rTPJ in processing auditory stimuli (Schaal et al., 2017). Of interest, is the role of the rTPJ in facilitating the flow of information through the dorsal auditory stream. A1 and SMC are two key brain areas activated during RAS that are proposed to be connected through the rTPJ. Previous unpublished findings from our lab indicate the rTPJ is an intermediate site within the dorsal auditory stream recruited during RAS.

### **Synchronized and syncopated movement with rhythmic auditory stimulation mediate different neural and behavioral outcomes**

Synchronized (SYN) and syncopated (PAT) tapping are two well defined RAS motor coordination tasks. These tasks are simple enough to be performed by most adults yet provide insight into how RAS informs and facilitates motor planning and coordinated motor execution (Repp et al., 2005). SYN requires the subject to move with a beat while PAT requires the subject to move between beats without switching to a SYN pattern. Based on prior evidence, PAT requires greater cognitive effort and resource demands compared to SYN (Scholz & Kelso, 1990; Mayville et al., 1999). It is not known how the rTPJ contributes to the increased demands of PAT

over SYN. However, there is evidence to suggest the dorsal auditory stream is more heavily recruited during PAT as discussed later in the section.

PAT performance is a less stable than performance during SYN (Kelso et al., 1990; Kelso et al., 1992). The main measure of stability in SYN and PAT is the standard deviation of relative phase (Jantzen et al., 2009). In other words, how consistent the timing of movement is relative to the intended target time of movement (on the beat for SYN, off the beat for PAT). Furthermore, the kinematics of the finger flexion phase of tapping is more variable for PAT than SYN (Pabst & Balasubramaniam, 2018). PAT performance is also more susceptible to reorganization, or changing to a new tapping pattern, than SYN performance (Mayville et al., 2002; Repp, 2005; Repp & Su, 2013). SYN task performance can be maintained within a frequency range of 0.5-4Hz, while PAT tasks become increasingly unstable and shift to a SYN pattern around 1.75 – 2.0 Hz (Bove et al., 2007; Mayville et al., 2001).

Decreased tapping stability is associated with increased activity in bilateral PMC and SMA (Debaere et al., 2004; Jantzen et al., 2009). Furthermore, connectivity between premotor and motor cortices increases as movement became more variable (Jantzen et al., 2002; Mayville et al., 2002; Jantzen et al., 2004; Jantzen et al., 2009). The cortical activity underlying PAT reflects increased planning and preparation demands due to the timing constraint of the off-beat pattern (Mayvill et al., 2002). Activity in the basal ganglia and cerebellum also increases for PAT compared to SYN (Mayville et al., 2002; Jantzen et al., 2005). When compared to SYN, the underlying cortical activity during PAT indicates increased motor planning and preparation demands via the recruitment of the frontal regions of the dorsal auditory steam (Jantzen, et al., 2009; Oullier et al., 2006). A less stable task places a greater demand on the internal processes

that organize the temporal aspects of coordinated movement (Debaere et al., 2004; Jantzen et al., 2009).

In addition to the heavier recruitment of cortical and subcortical regions, a larger event related desynchronization (ERD) in the beta frequency bands occurs in auditory and motor regions during PAT compared to SYN (Mayville et al., 2001; Oullier, Jantzen, Steinberg & Kelso, 2005). The ERD is captured by the induced response which is time-locked to the event but may occur before or after the event, therefore is not phase-locked to the event. The ERD is associated with a decrease of synchronized populations of neurons firing in a given frequency band (Pfurtscheller & Silva, 1999). A comparatively more robust ERD is also associated with the recruitment of additional cortical resources (Jantzen et al., 2001; Pollok et al., 2014) and may perhaps relate to the enhanced recruitment of the dorsal auditory stream. These findings demonstrate the differences in cortical activation for SYN and PAT, indicating that SYN engages a subset of cortical resources engaged during PAT and that PAT is dependent upon the recruitment of additional frontal regions to coordinate sound with movement (Carson & Kelso, 2004; Mayville et al., 2002).

Based on the literature, PAT is associated with both the recruitment of additional cortical areas through the dorsal auditory stream compared to SYN. SYN does not have the same task demands and recruits fewer frontal resources compared to PAT and is regarded as a more automatic task that is not as dependent on frontal motor planning and execution regions. SYN and PAT may serve as proxies for more automatic and more effortful motor tasks in future investigation sensorimotor integration and its impact on sensorimotor coordination.

## **Theta burst stimulation has lasting cortical and behavioral effects**

Non-invasive brain stimulation (NIBS) is a tool that has been used to understand the impact of cortical areas on cortical functions and behaviors. This report aims to introduce NIBS as a potential tool to have an effect on auditory-motor entrainment and auditory-motor coordination. Particularly in those tasks that are more reliant on the frontal motor planning and execution areas connected to auditory processing areas through the dorsal auditory stream.

Transcranial magnetic stimulation (TMS) is a common type of NIBS in which a magnetic field, directed at brain tissue, depolarizes nerve cells via induced electric currents. When applied repetitively (rTMS), it causes acute changes in the post-synaptic response to stimulation, resulting in long-term potentiation and depression like effects (LTP/LTD) (Siebner & Rothwell, 2003; Teo et al., 2007; Huang et al., 2007; Wankerl et al., 2010; Cardenas-Morales et al., 2011). The after-effects of rTMS, to suppress or facilitate corticospinal excitability, is dependent on the location, frequency, duration, intensity, and pattern of pulses. (Chen et al., 1997; Chen & Seitz, 2001; Quartarone et al., 2005; Rounis et al., 2005; Huerta & Volpe, 2009; Fitzgerald; 2006). Additionally, variability in baseline cortical and behavioral levels between subjects has been used to account for the after-effects of rTMS (Lopez-Alonso et al., 2014; Vallence et al., 2015).

A well reported measure of the after-effects of rTMS is the motor -evoked potential (MEP), a measure of corticospinal excitability through the corticospinal tract which connects M1 to a corresponding muscle. MEPs are a measurable twitch in the muscle due to descending volleys in corticospinal neurons (Burke et al., 1993). They are used as a peripheral indicator of corticospinal excitability. A single TMS pulse is delivered to the corresponding M1 connected upstream from the muscle of interest, creating a MEP which can be measured at the muscle using electromyography (EMG). An increase in MEP size indicates increased corticospinal excitability

and a facilitated response while a decrease indicates suppressed corticospinal excitability (Maeda et al., 2000; Peinemann et al., 2004). While, MEPs provide insight to cortical activity they are limited to M1 interpretation and can also be modulated by interneurons and corticospinal tract excitability. The MEP is limited in that it is a peripheral measure and can only be used to measure corticospinal at the muscle. The MEP not only reflects the neuromuscular synapses but also the synapses onto corticospinal neurons and the synapses onto motor neurons of the spinal cord. Measures of cortical activity across the cortex have also been used to address this limitation and provide a more direct measure of after-effects of rTMS on cortical activity (Chen et al., 1997; Hallett, 2000; Maeda et al., 2000; Nyffeler et al., 2006; Lefaucheur et al., 2014). Furthermore, the data gathered from neuroimaging can be used to assess cortical excitability across the cortex as well as changes within a distributed cortical network (Esser et al., 2006; Yoo et al., 2008).

Theta burst stimulation (TBS), a type of patterned rTMS, has been shown to maximize post-stimulus effects compared to other forms of rTMS. It can also be applied in a shorter amount of time while eliciting similar effects (Cárdenas-Morales et al., 2010; DiLazzaro et al., 2011; Veniero et al., 2019). TBS is a sub-maximal (70-90% of resting or active motor threshold) is most commonly used (Suppa et al., 2016) intensity burst of 3 pulses at 50Hz repeated 5 times per second continuously (cTBS) or intermittently (iTBS). TBS is also well tolerated, with the most common reported side effect being a mild headache that dissipates soon after stimulation (Oberman et al., 2011). TBS induced changes have been reported at the behavioral level (He et al., 2013; Mancini et al., 2017), peripheral level (Zafar, Paulus & Sommer, 2008; Chung et al., 2016), and cortical level (Marshall et al., 2015; Chung et al., 2017). We will discuss the



conception of TBS along with findings that contribute to the current understanding of its effect of brain and behavior.

iTBS is a common type of TBS and consists of a 2s train of pulses followed by 8s of rest while cTBS is one long train of stimulation (Huang et al., 2005). TBS was designed to mimic the theta discharge pattern of hippocampal cells in exploring rats (Skaggs et al., 1996; Suppa et al., 2016) and has been shown to lead to long-term potentiation (LTP), or a lasting increases in synaptic strength measured by electrical stimulation of pre-synaptic neurons, in the rodent hippocampus (Larson & Munkacsy, 2015) and motor cortex (Hess et al., 1996). A single TMS pulse activates both excitatory and inhibitory interneurons that synapse on corticospinal cells. An excitatory post-synaptic potential (EPSP) occurs due to the release of pre-synaptic glutamate which activates  $\alpha$ -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) receptors and depolarizes the neuron. An inhibitory post-synaptic potential (IPSP) occurs due to the release of pre-synaptic gamma-aminobutyric acid (GABA) binding to the post-synaptic GABA-A receptors and hyperpolarizing the cell. As the theta pulses continue, the release of GABA is suppressed and IPSPs are reduced. This allows for the EPSPs to have a prolonged depolarizing effect, which induces an influx of  $\text{Ca}^{2+}$  through the post-synaptic NMDA receptor to the postsynaptic dendrite spine, leading to further depolarization and long-lasting changes in synaptic strength (Larson & Munkacsy, 2015; Suppa et al., 2016). The summation of excitatory effects outweigh the inhibitory effects and are proposed to contribute to the LTP-like effects of iTBS (Larson & Munkacsy, 2015). When theta burst pulses are applied in a continuous long train, as with cTBS, the inhibitory effects are thought to outweigh the excitatory effects leading to LTD-like synaptic suppression (Suppa et al., 2016). This is supported by stimulation of hippocampal slices in which the same number of theta burst pulses facilitated the synaptic response after iTBS but suppress

the synaptic response after cTBS (Larson & Munkascy, 2015). Additionally, when NMDA receptors and  $\text{Ca}^{2+}$  are blocked so too are the effects of TBS, indicating that TBS is involved in LTP/LTD (Teo et al., 2007; Huang et al., 2007; Wankerl et al., 2010). The post-synaptic response used to assess LTP and LTD is recorded on the cellular level between a presynaptic stimulation and a post-synaptic response.

MEPs have been used to infer LTP and LTD like effects of TBS in humans (Suppa et al., 2016). Huang and colleagues (2005) were the first to establish the effects of TBS in humans. CTBS was applied to the primary motor cortex (M1) for a continuous 40s while iTBS was applied for 2s every 10s for a total of 192s. Corticospinal excitability was assessed post-TBS by applying a TMS pulse to the stimulated M1 and measuring the motor evoked potential (MEP) via EMG amplitude in a small muscle of the hand. MEPs were suppressed after cTBS and facilitated after iTBS, indicating LTD and LTP-like effects respectively. Similar findings have been reported in adults and children (Teo et al., 2007; DiLazzaro et al., 2008; Suppa et al., 2008; DiLazzaro et al., 2011; Doeltgen & Ridding, 2011; Cardenas-Morales et al., 2011; Nettekoven et al., 2014; Chung et al., 2015; Pedapati et al., 2015). The generalization that iTBS elicits LTP-like effects by facilitating synaptic transmission, while cTBS generates LTD like effects by suppressing synaptic transmission is mainly supported by MEP responses after stimulation of the motor cortex (Suppa et al., 2008; Chung et al., 2016).

Neuroimaging tools allow for more direct measures of cortical activity at the site of stimulation and have been used to investigate the distributed effects of TBS. iTBS to the dorsolateral prefrontal cortex (DLPFC) increases evoked theta (4-8Hz) band power in the prefrontal region in response to a single TMS pulse, while theta power decreased in response to cTBS (Chung et al., 2017). iTBS to the DLPFC has also been shown to modulate theta band

power in frontal and parietal cortical areas paired with improved performance on a working memory n-back task (Hoy et al., 2016). iTBS over the motor cortex has been shown to enhance choice reaction time and decrease the cortical response in bilateral primary motor cortex (M1) and primary sensory cortex (S1) during the reaction time motor response (Cardenas-Morales et al., 2011). The results suggest that the transmission of neural activity from the motor cortex to the muscle was facilitated by iTBS modulation of neural activity as explained by the decrease cortical response. While these studies provide evidence that iTBS facilitates the transmission of information throughout cortical regions that may contribute to a task specific network, little is known about the potential to modulate network activity through the dorsal auditory stream.

Furthermore, the application of iTBS results in different outcomes depending upon the stimulation parameters. The most common application of TBS is based on the methods put forward by Huang and colleagues (2005) – the intermittent or continuous theta burst pattern for a total of 600 pulses at 80% of active motor threshold (Oberman et al., 2012; Suppa et al., 2016). Increasing stimulation duration has had mixed results. Multiple doses of iTBS, applied in three blocks of 600 pulses each separated by 15 minutes, has been shown to have an additive effect on MEP amplitude (Nettekoven et al., 2014). In another study, increasing the total number of pulses from 600 to 1200 using a prolonged method with no separation reversed the effects on MEP after iTBS/cTBS to the M1 (Gamboa et al., 2010). However, the reversal of MEP effects after 1200 pulses of iTBS/cTBS to the M1 did not occur in a study by Hsu and colleagues (2011). The differences may have been due to pre-TBS activities. In the first study isometric muscle contraction occurred for five minutes before the application TBS. Contraction immediately before (Iezzi et al., 2008) or after (Huang et al., 2008) TBS has been shown to reverse the expected effects of TBS to the M1 on MEP. This effect may be due to rapid polarity-reversing

meta-plasticity, in which changes in synaptic efficacy (LTP or LTD) occur (Genttner et al., 2008; Suppa et al., 2016).

The other parameters of TBS that have been manipulated are the stimulation intensity and the frequency of stimulation. These parameters can be adjusted based on the individual. Not all individuals are considered “responders” to a given NIBS intervention. NIBS effects may be mediated by human factors such as menstrual cycle phase (Smith et al., 1999) or cortical thickness (Conde et al., 2012) which contribute to variability of results. In the case of TBS, there are reports of both inter and intra-variability responses to iTBS (Lopez-Alonso et al., 2014; Hinder et al., 2014; Vallence et al., 2015). It is common to have a standardization of stimulation intensity based on the individual’s active or resting motor threshold (Suppa et al., 2016). For iTBS, stimulation intensity has been shown to have an effect on outcome. iTBS applied over prefrontal cortex at 50, 75, and 100% of resting MT had the greatest effect on neurophysiological changes and changes to working memory at 75% resting MT (Chung et al., 2018). Inter-participant variability has also been addressed by matching the frequency of stimulation to an individualized target frequency (Brownjohn et al., 2013).

### **Concluding remarks**

The auditory dorsal stream facilitates the pairing of sensory and motor signals (Rauschecker, 2007; Rauschecker & Scott, 2009). RAS promotes sensorimotor integration processing and the coordination of motor responses by entraining neuronal excitability to the stimulus onset through functionally and structurally connected auditory and motor areas of the dorsal stream. Communication through the dorsal auditory stream may be a contributing factor in the coordination of movement with RAS. It is thought that the rTPJ is involved in relaying information from auditory to motor regions in the dorsal auditory stream. Further research is

needed on the involvement of the rTPJ in the communication between auditory and motor brain regions and the implication of such involvement on RAS-mediated changes on coordinated behavior. One possible avenue is the implementation of non-invasive brain stimulation, namely iTBS, to investigate facilitatory auditory-motor neural mechanisms with the added goal of upregulating auditory-motor activity associated with sensorimotor integration and the coordination of movement with RAS.

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