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UNIVERSITY OF CALIFORNIA, MERCED

Sound Guides Action and Action Scaffolds Sound Perception

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor
of Philosophy

in

Cognitive & Information Sciences

by

Jessica Marie Ross

Committee in charge:

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2018

The work presented in this thesis was carried out in the Cognitive & Information Sciences (CIS) program at the University of California, Merced, U.S.A. Multiple chapters are the results of collaborations with John R. Iversen and Scott Makeig at the Swartz Center for Computational Neuroscience, a center of the Institute for Neural Computation at the University of California, San Diego, U.S.A.

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The dissertation of Jessica Marie Ross is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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University of California, Merced
2018

This dissertation is dedicated to my family.

To my parents, Dick and Cesca,
for being your cool selves.
I am thankful for all that you are,
independent of your children.

To my brothers, Patrick and Richard,
for your endless drive
for knowledge and creativity.



We are here to help each other get through this thing, whatever it is.

(Dedication stolen from Bluebeard by Kurt Vonnegut)

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- Kavli Summer Institute in Cognitive Neuroscience
- UC Music Experience Research Community Initiative (UC MERCI)
- American Psychological Association (APA)
- Center for Mind and Brain, University of California, Davis, ERP Boot Camp Scholarship

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- Graduate Dean's Dissertation Year Fellowship
- Graduate Student Fellowship Award from Mark S. Aldenderfer, Dean of the School of Social Sciences, Humanities, and Arts
- Graduate Dean's Fellowship from Marjorie Zatz, Vice Provost and Dean of Graduate Education
- Graduate Fellowship Incentive Program Award, Graduate Division
- Blum Center: *Rhythmic Skills and Reading: An Intervention Study in the San Joaquin Valley*
- Center for Human Adaptive Systems and Environments (CHASE)

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Degrees

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2015	UC MERC I Symposium/Workshop on Research on Music Experience and Communication, University of California, Los Angeles
2015	MathWorks Seminar: Data Analysis and Visualization with MATLAB
2015	Transcranial Magnetic Stimulation (TMS) Methods and Practice, Division of Biokinesiology and Physical Therapy, University of Southern California, Los Angeles
2015	Generalized Linear Model Workshop, University of California, Merced (Instructor: Bodo Winter)
2014	Advanced Training Institute on Non-Linear Methods for Psychological Science, American Psychological Association, University of Cincinnati, Ohio
2014	Dynamics of Music and Language Summer School, University of California, Merced Center for Human Adaptive Systems and Environments (CHASE)
2012	Auditory Neuroscience (Graduate Coursework), UC Davis Extension Center
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Research Articles

1. Ross, J.M., Iversen, J.R., & Balasubramaniam, R. (In review). Dorsal premotor contributions to auditory rhythm perception: Causal transcranial magnetic stimulation studies of interval, tempo, and phase.
2. Nguyen, H.M., Aravindakshan, A., Ross, J.M., & Disbrow, E. (In review). Optimizing cognitive rehabilitation in Parkinson's disease.
3. Ross, J.M., Iversen, J.R., Makeig, S., & Balasubramaniam, R. (In prep). The EEG mu rhythm and musical beat perception.
4. Ross, J.M., Iversen, J.R., & Balasubramaniam, R. (2018). The role of posterior parietal cortex in beat-based timing perception: A continuous theta-burst stimulation study. *J. Cogn. Neurosci.*, 30(5), 634-643. doi: 10.1162/jocn_a_01237
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6. Ventura, M.I., Barnes, D.E., Ross, J.M., Lanni, K.E., Sigvardt, K.A., & Disbrow, E.A (2016). A pilot study to evaluate multi-dimensional effects of dance for people with Parkinson's disease. *Contemp. Clin. Trials* 51, 50-55. doi: 10.1016/j.cct.2016.10.001
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10. Ross, J.M., & Balasubramaniam, R. (2014). Physical and neural entrainment to rhythm: human sensorimotor coordination across tasks and effector systems. *Front. Hum. Neurosci.* 8:576. doi: 10.3389/fnhum.2014.00576
11. Abney, D.H., Warlaumont, A.S., Hausman, A., Ross, J.M., & Wallot, S. (2014). Using non-linear methods to quantify changes in infant limb movements and vocalizations. *Front. Psychol.* 5:771. doi: 10.3389/fpsyg.2014.00771
12. Lanni, K.E., Ross, J.M., Higginson, C.I., Dressler, E.M., Sigvardt, K.A., Zhang, L., Malhado-Chang, N., & Disbrow, E.A. (2014). Perceived and performance-based executive dysfunction in Parkinson's disease. *J. Clin. Exp. Neuropsychol.* 36(4), 342-255. doi: 10.1080/13803395.2014.892059

Oral Presentations

1. Ross, J., Iversen, J., & Balasubramaniam, R. (2017). The role of dorsal premotor cortex in auditory timing: A continuous theta-burst stimulation study. Meeting of the Society for Music Perception and Cognition, San Diego, California, United States.
2. Balasubramaniam, R., & Ross, J. M. (2016). Human postural entrainment to the auditory environment. The Guy Van Orden UConn Workshop on Cognition and Dynamics, XI, Storrs, Connecticut, United States.
3. Ross, J.M., Warlaumont, A.S., Rigoli, L., & Balasubramaniam, R. (2015). The influence of musical groove on balance control. Meeting of the Society for Music Perception and Cognition, Nashville, Tennessee, United States.
4. Ross, J.M., Warlaumont, A.S., Rigoli, L., & Balasubramaniam, R. (2014). Using auditory noise to reduce postural sway in standing adults. Auditory Perception, Cognition, and Action Meeting, Long Beach, California, United States.

Posters

1. Ross, J., Iversen, J., & Balasubramaniam, R. (2017). Mapping out cortical contributions to auditory timing: A causal transcranial magnetic stimulation study of interval and beat-based timing perception. 2017 Neuroscience Meeting Planner. Washington, DC: Society for Neuroscience, 2017. Online.
2. Ross, J., Iversen, J., & Balasubramaniam, R. (2017). Dorsal and ventral premotor contributions to auditory timing: A continuous theta-burst stimulation study. International Multisensory Research Forum, Nashville, TN.
3. Ross, J., Iversen, J., & Balasubramaniam, R. (2017). The role of posterior parietal cortex in beat-based timing perception: a continuous theta-burst stimulation study. Cognitive Neuroscience Society Annual Meeting, San Francisco, CA.
4. Ross, J., Iversen, J., Makeig, S., & Balasubramaniam, R. (2016). An EEG examination of neural entrainment and action simulation during rhythm perception. 14th International Conference for Music Perception and Cognition, San Francisco, CA.
5. Ross, J.M., Warlaumont, A.S., Rigoli, L., & Balasubramaniam, R. (2015). Influence of high and low groove music on postural sway dynamics. 37th Annual Meeting of the Cognitive Science Society, Pasadena, CA.
6. Ventura, M.I., Ross, J.M., Lanni, K.E., Sigvardt, K.A., & Disbrow, E.A. (2015). Improving cognitive functioning and quality of life through dance for PD: A pilot intervention trial. 19th International Congress of Parkinson's Disease and Movement Disorders. San Diego, CA.
7. Ross, J.M., & Balasubramaniam, R. (2015). Contribution of auditory feedback to postural stability. Cognitive Neuroscience Society Annual Meeting, San Francisco, CA.
8. Ventura, M.I., Ross, J.M., Lanni, K.E., Sigvardt, K.A., & Disbrow, E.A. (2015). Motor and cognitive benefits of dance for people with Parkinson's disease. Cognitive Neuroscience Society Annual Meeting, San Francisco, CA.

9. Ross, J.M., Warlaumont, A.S., Rigoli, L., & Balasubramaniam, R. (2014). Influence of high and low groove music on postural sway dynamics. Advanced Training Institute on Non-Linear Methods for Psychological Science, American Psychological Association, University of Cincinnati, Ohio.
10. Dressler, E.M., Aravindakshan, A., Ross, J., Sigvardt, K., Zhang, L., Malhado-Chang, & Disbrow, E.A. (2013). Impaired motor preparation under conditions of response uncertainty in Parkinson's disease. Program No. 431.05/M18. 2013 Neuroscience Meeting Planner. San Diego, CA: Society for Neuroscience, 2013.
11. Lanni, K.E., Ross, J., Higginson, C.I., Dressler, E.M., Sigvardt, K.A., Zhang, L., Malhado-Chang, N., & Disbrow, E.A. (2013). Measuring perceived and performance-based executive dysfunction in Parkinson's disease. Program No. 431.04/M17. 2013 Neuroscience Meeting Planner. San Diego, CA: Society for Neuroscience, 2013.
12. Ross, J., Dressler, E., Sigvardt, K.A., Aravindakshan, A., Yund, E.W., Woods, D., & Disbrow, E. (2012). Cognitive neurorehabilitation of movement initiation in Parkinson's disease. Program No. 802.19. 2012 Neuroscience Meeting Planner. New Orleans, LA: Society for Neuroscience, 2012.

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2015	National Science Foundation Graduate Research Fellowship Program (NSF GRFP) Honorable Mention
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2014	Travel grant from the American Psychological Association for the Advanced Training Institute on Non-Linear Methods for Psychological Science
2010-2011	International Honor Society Phi Theta Kappa member
2009	Special Thanks for Achieving Results (STAR) award from the United States Geological Survey, Biological Resources Division
10/09	Expert of the month, Allexperts.com

Certifications

2017	Adult CPR, Child CPR, and Infant CPR, FirstAidWeb, Inc. and National Health & Safety Foundation, Valid until February 2019
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- 2017 Basic First Aid, FirstAidWeb, Inc. and National Health & Safety Foundation, Valid until February 2019
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Employment History

- 6/16-8/17 Graduate Student Researcher, (P.I.: R. Balasubramaniam), University of California, Merced
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- 1/16-6/16 Teaching Assistant, Animal Cognition (Instructor: Jeanne Milostan), University of California, Merced
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- 1/15-6/15 Graduate Student Researcher, (P.I.: R. Balasubramaniam), University of California, Merced
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- 8/14-12/14 Teaching Assistant, Perception and Action (Instructor: Ramesh Balasubramaniam), University of California, Merced.
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- 8/13-12/13 Teaching Assistant, Speech Processing (Instructor: Anne Warlaumont), University of California, Merced.
- 3/12-8/13 Psychology Technician GS-181-5, Department of Veterans Affairs, Northern California Health Care System, Martinez, California
- 4/11-8/13 Research Assistant, Elizabeth Disbrow Laboratory, Center for Neuroscience, University of California, Davis
- 8/11-10/12 Independent Living Facilitator, InAlliance, Sacramento, California
- 12/11-5/12 Science Teacher for Resident Science Program, David Lubin Elementary School, Sacramento, California
- 7/10-12/10 Junior Specialist, Petr Janata Laboratory, Center for Mind and Brain, University of California, Davis
- 1/09-7/10 Research Intern, Petr Janata Laboratory, Center for Mind and Brain, University of California, Davis
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Special Pedagogical Activities

- 04/2016 Motion capture lecture/demonstration for COGS 180: Gesture
Performed introductory lecture and training on our Vicon Bonita Motion Capture System and AMTI Force and Motion platforms (Optima BP400600-2000)
- 12/2015 TMS workshop for BIOE 113: Bioinstrumentation
Introduced and trained Bioengineering students on the safe usage of TMS

Volunteer Work

10/2015-Present	Graduate Student Representative, Advisory Committee for the UC Merced Transportation and Parking Services
Present	Ad Hoc Reviewer (Journal of Cognitive Neuroscience, Gait & Posture, Experimental Brain Research, Music Perception, PLOS ONE)
8/16/16	Experienced Teacher's Assistant Informational Panel, Graduate Student TA Orientation, Center for Engaged Teaching and Learning (CETL), UC Merced
5/30/2016	Public outreach, Mercy Hospital 5K Stroke Awareness Run Spoke with participants about brain health and balance, and discussed our research
2009-2018 7/2015	Expert, Entomology Question and Answer Service, Allexperts.com Volunteer, 37 th Annual Meeting of the Cognitive Science Society, Pasadena, CA
11/04/2014	Cognitive Science Student Association Meeting, University of California, Merced Assisted undergraduates with graduate school applications
9/2014	Volunteer, Days and Nights Festival, The Philip Glass Center for the Arts, Science, and the Environment, Big Sur, California
1/25/2014	"Child Triumphs and Troubles: Language and Learning in the Early Years" Professional Development and Research Lab Tours, University of California, Merced
2011/2012	Brain Awareness Week (K-6 brain education), Center for Neuroscience, University of California, Davis
2004-2008	Founding member of the One World Children's Fund, Davis Branch, Davis, CA

Professional Affiliations

Cognitive Neuroscience Society, Society for Music Perception & Cognition, Cognitive Science Society, American Psychological Association, Society for Neuroscience

Media Coverage

"To Hear the Beat, Your Brain May Think About Moving to it: A Brain Region Linked to Movement is Integral to Recognizing Rhythms," Science News: Magazine for the Society for Science and the Public, February 16, 2018.

Abstract

Action and perception are codependent processes with continuously updating bidirectional interaction, resulting in a sum that is greater than its parts. Here, I focus on the auditory and motor systems, and use musical timing to explore topics including entrainment, simulation, prediction and correction, and motor inhibition. In collaboration with numerous co-authors, I show evidence for a strong relationship between sound perception and body movements. Our auditory environment has clear and measurable impacts on subcortical and cortical movement control and planning (Chapters 2-4), and on neural signatures of movement control (Chapter 5). I show that music can be used to explore predictive and feedback-based (Chapters 2-4, 6,7), as well as inhibitory aspects of movement control (Chapter 5). I discuss claims that neural activity used for movement control and planning can causally contribute to auditory perception (Chapters 6, 7, Discussion), and I present evidence in support of these views (Chapters 6, 7). The robust synergy between human audition and action has enormous potential for clinical applications for people recovering from stroke and with movement disorders, but also for typically aging adults (Chapter 3) and healthy young adults (Chapters 2-4). However, the majority of the work presented here is intended to add insights to the fundamental understanding of the brain as a predicting and adapting organ that guides human action through a fast-paced and multisensory world. This dissertation, *Sound Guides Action and Action Scaffolds Sound Perception*, is submitted by Jessica M. Ross in the summer of 2018 in partial fulfillment of the degree Doctor of Philosophy in Cognitive and Information Sciences at the University of California, Merced, under the guidance of Ramesh Balasubramaniam.

Chapter 1 General Introduction

As a society, we recognize that some people have skilled and highly trained movements. Surgeons, athletes and musicians are reputed to have movement control that far surpasses the rest of us in dexterity and precision, both in spatial and temporal dimensions. The truth is that we often overlook how remarkable our everyday movements are; we are all experts at moving our bodies. In fact, our bodies are specialized systems that respond to and interact with our surroundings, taking into consideration the physical constraints imposed by our muscles and joints and the objects around us. Our movements need to be smooth and precise, minimize energy costs, adapt to changes in our environments, and be fast enough to keep up with these changes, whether to keep our bodies away from harm, maneuver a vehicle, or hold a conversation with another person. We are moving constantly in our speech, blinking, breathing, walking and even standing in order to maintain our balance. These movements are continuously adapting to our needs and the constraints of our bodies and the situation.

We use all of our senses, including audition, to guide and perfect our movements, even subtle movements like those we make to maintain standing balance. In this dissertation work, I explore interactions between sound perception and body movement. One aspect of movement that our motor system is particularly adapted for is timing. Precise and accurate timing is usually necessary for effective movement control. Sounds inform temporally appropriate movement control by providing feedback about the environment that we can then respond to and also by providing structured cues that allow our nervous system to make predictions that can be used for optimally fast movements. Timing of this type, with intervals in the sub-second range, is critically important for everyday movements, but there are gaping holes in knowledge of the networks and mechanisms involved.

Perception of and mechanisms used for sub-second timing are studied using paradigms of sensorimotor timing, although classical timekeeping models assume independence from motor influences. The Wing-Kristofferson model describes timing as having two parts: a centrally represented timekeeper, referred to as a “clock”, and the peripheral motor system that implements signals from the clock but is an independent system from the clock (Wing & Kristofferson, 1973). More recent work, however, supports that this division may be an oversimplification (see Ross & Balasubramaniam, 2014 for a review). It is likely the case that there are both centrally controlled clock-like mechanisms of timing as well as motor affordances and specialization in sensorimotor guidance that influence timing. Many suggest that timekeeping is interactive with the motor system, and some hypothesize that timekeeping mechanisms are reliant on motor system specializations or contingent on motor context.

Sensorimotor timing paradigms observe voluntary and involuntary synchronization between our brains, bodies and the environment. A commonly used approach in this neuroentrainment research is to study temporal relationships between body movements and rhythmic stimulation in the environment, such as musical rhythms (Balasubramaniam, 2006; Keller & Repp, 2008). Measuring this temporal coupling is useful for understanding (1) variability, stability, and adaptability of entrainment, (2)

coordination between multiple effectors during entrainment and (3) neural basis of rhythmic timekeeping (Ross & Balasubramaniam, 2014). Finger tapping to an auditory metronome can provide insight into timekeeping “clock” mechanisms, and although finger tapping is a movement with limited degrees of freedom, it is still subject to motor constraints. For example, finger movement trajectories in this paradigm demonstrate timing asymmetries between flexion and extension that are negatively correlated with timing accuracy (Balasubramaniam, Wing, & Daffertshofer, 2004). Specifically, we make faster movements before the beat to aid in accurate synchronization and slower movements after the beat when preparing for the next beat to aid in period accuracy (Balasubramaniam, Wing, & Daffertshofer, 2004). This literature using finger tapping describes two separate cognitive processes involved with timing that may rely on distinct cognitive control mechanisms and possibly different brain circuits (Repp, 2005a; Repp, 2005b): phase and period timing. Phase timing is based on events and the intervals between events. Period timing is based on ongoing oscillators that can be sped up or slowed down. From this work, it has been deduced that sub-second timekeeping involves both phase and period maintenance, and both processes require motor planning for sensorimotor entrainment accuracy (Mayville, Jantzen, Fuchs, Steinberg, & Kelso, 2002; Krause, Schnitzler, & Pollok, 2010).

Relatedly, we can use circle drawing movements instead of finger tapping to measure timing in a slightly more demanding motor context. Continuous movement, such as circle drawing, requires more sensory guidance for accurate movement than in limited dimensional and discrete finger tapping tasks (Studenka, Zelaznik, & Balasubramaniam, 2012; Torre & Balasubramaniam, 2009). Circle drawing shows preservation with cerebellar damage that compromises finger tapping (Spencer, Zelaznik, Diedrichsen & Ivry, 2003) because, it is thought, that circle drawing dynamics emerge from sensory-neuromuscular interactions more than finger tapping dynamics.

Drawing a line with one hand and a circle with the other make the line appear more curved and the circle appear more like a line (Franz, Zelaznik, & McCabe, 1991). This phenomenon, called the magnet effect, is unintentional movement interference that is seen when two limbs perform spatially dissimilar tasks, as known to anyone who has tried simultaneously patting their head and rubbing their belly. The magnet effect is robust in typical populations and also in patients with an amputated and phantom limb (Franz & Ramachandran, 1998). In this work, patients who experience subjective but vivid feelings of movement in a phantom limb (arm/hand) also show the magnet effect in their preserved limb when asked to perform orthogonal tasks with both limbs (tapping with one hand and circle drawing with the other). This effect is not seen if the patient does not experience phantom movement in their amputated limb or when control participants (non-amputees) are asked to do one task with one hand and imagine moving their hand to do the orthogonal task; imagined movement does not create a magnet effect but phantom movement does (Franz & Ramachandran, 1998). Although movement imagery and phantom movement may have overlapping properties, there are neural mechanisms of bimanual coupling that are specific to phantom or actual movement, including efference copies and motor interference.

Work from our lab demonstrates that rhythmic entrainment can create magnet effect spatial interference when performing eye and hand movements simultaneously

(Richardson, Cluff, Lyons, & Balasubramaniam, 2013). In one experiment, subjects performed finger tapping entrainment to a pacing stimulus while simultaneously making repetitive horizontal saccadic eye movements. The finger trajectories showed lateral shift to the right when making rightward saccades and to the left when making leftward saccades-- vertical finger movements are unintentionally attracted in the direction of concurrently executed horizontal eye saccades when responses are planned or timed together. In a second experiment, participants performed finger tapping but were instructed to make reactive horizontal saccades following target jumps at unpredictable times. Here, with reduced predictability of concurrent movements, the lateral shift that accompanied the saccades was weak and occurred only in the hand ipsilateral to the direction of the saccade. These results suggest recruitment of a common timekeeping mechanism that can create spatial interference in effectors that are innervated by distinctly different neurophysiological tracts (Richardson, Cluff, Lyons, & Balasubramaniam, 2013).

This interaction between top-down (clock) and bottom up (sensorimotor) contributions to timing has been described in detail in sensorimotor models of state estimation. State estimation is the process of determining an approximate state of a system, which in terms of human movement would be estimating some parameters of state of an effector (bottom up), taking into consideration motor commands (top down). This type of state estimation uses knowledge of motor commands and the predicted sensory state of these actions. Accurate motor and sensory state estimation is necessary for appropriate motor control, and can be undermined by inaccurate information about the motor command or sensory consequences of action, as demonstrated by the Lombard effect and escalation effect (for more on these, see Therrien, Richardson, & Balasubramaniam, 2011; Therrien, Lyons, & Balasubramaniam, 2012). In short, the motor system adapts if the sensory consequences are not as expected, supporting that sensorimotor context influences top-down control. In further support that sensorimotor context impacts timing, it has been shown that unambiguous sensory feedback and successful multisensory integration are crucial to minimizing timing variability (Studenka, Elias, Shore, & Balasubramaniam, 2014; Keller, Ishihara, & Prinz, 2011), and that brain activations during rhythm perception following an entrainment task can show persistent patterns specific to the modality of entrainment (Jantzen, Steinberg, & Kelso, 2005).

Collectively, this work shows that there may be clock-like timekeeping as well as interaction from sensorimotor context for timing. Effector movement parameters should be considered for a complete and accurate understanding of timekeeping mechanisms (Ross & Balasubramaniam, 2014). Further, some evidence, including that which is presented in chapters 6 and 7 and discussed in chapter 8 here, suggests that the motor system is used critically for timing perception and is necessary for accurate timing (Grahn & Brett, 2009; Ross, Iversen, & Balasubramaniam, 2018; Ross, Iversen, & Balasubramaniam, in review; Ross & Balasubramaniam, 2014).

It should be mentioned that although entrainment to environmental rhythms is possible with any sensory modality, synchronization to sound may be easiest for humans. Most work comparing entrainment in different sensory modalities focuses on auditory and visual, and this work shows that auditory-motor entrainment is more precise and

accurate than visual-motor entrainment (Hove, Fairhurst, Kotz, & Keller, 2013). This is not to say that auditory-motor entrainment has some modality specific privilege, but that the mechanisms of entrainment might be better suited for time sensitive proficiency (Comstock & Balasubramaniam, 2018; Comstock, Hove, & Balasubramaniam, 2018). The time scales of operation and feedback loops that work in error detection may simply be different between visual and auditory modalities. Visual-motor entrainment can improve with stimuli that are moving targets, but there is still a timing advantage for auditory-motor over moving target visual-motor entrainment (Hove, Spivey, & Krumhansl, 2010; Hove, Iversen, Zhang, & Repp, 2013). In addition, the neural structures that sub-serve auditory-motor and visual-motor entrainment may differ, with auditory-motor more strongly activating structures associated with internal motor control, including ventral premotor cortex, inferior parietal lobule, supplementary motor areas, and right inferior cerebellum (Jäncke, Loose, Lutz, Specht, & Shah, 2000).

In the work presented here, my co-authors and I show that the sounds we hear have a strong relationship with our motor planning and behavior. Chapters 2 and 4 show that anticipatory and feedback-based movements used for balance control are influenced by sounds that are unstructured (i.e. white noise, Ross & Balasubramaniam, 2015) and sounds that are rhythmic (i.e. varying degrees of musical Grooviness, Ross, Warlaumont, Abney, Rigoli, & Balasubramaniam, 2015), respectively. In Chapter 3, we suggest this auditory-motor relationship may be under-utilized clinically and have potential for movement optimization and rehabilitation for typically aging adults with balance variability (Ross, Will, McGann, & Balasubramaniam, 2016). In Chapter 5, we show that rhythmic sounds have a causal effect on neural signatures of motor behavior and motor inhibition (Ross, Iversen, Makeig, & Balasubramaniam, in prep). We then show, in Chapters 6 and 7, evidence that the auditory-motor relationship is bidirectional and that movement planning may be critically important for auditory perception (Ross, Iversen, & Balasubramaniam, 2018; Ross, Iversen, & Balasubramaniam, in review). The Discussion summarizes the findings presented in Chapters 2-7, and positions them in relation to models of motor and auditory simulation and prediction, and proposes future directions for auditory-motor timing investigations.

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Chapter 2

Auditory white noise reduces postural fluctuations even in the absence of vision.

The contributions of somatosensory, vestibular and visual feedback to balance control are well documented, but the influence of auditory information, especially acoustic noise, on balance is less clear. Because somatosensory noise has been shown to reduce postural sway, we hypothesized that noise from the auditory modality might have a similar effect. Given that the nervous system uses noise to optimize signal transfer, adding mechanical or auditory noise should lead to increased feedback about sensory frames of reference used in balance control. In the present experiment, postural sway was analyzed in healthy young adults where they were presented with continuous white noise, in the presence and absence of visual information. Our results show reduced postural sway variability (as indexed by the body's center of pressure) in the presence of auditory noise, even when visual information was not present. Nonlinear time series analysis revealed that auditory noise has an additive effect, independent of vision, on postural stability. Further analysis revealed that auditory noise reduced postural sway variability in both low and high frequency regimes ($>$ or $<$ 0.3Hz) of sway, suggesting that both spontaneous and feedback driven aspects of postural fluctuations were influenced by acoustic noise. Our results support the idea that auditory white noise reduces postural sway, suggesting that auditory noise might be used for therapeutic and rehabilitation purposes in older individuals and those with balance disorders.

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Introduction

Postural stability relies on active motor adjustment and control of a distributed system of muscles (Balasubramaniam & Wing, 2002). Successful control relies on prediction and feedback from the somatosensory, vestibular and visual modalities (Dozza, Horak, & Chiari, 2007). Postural sway is sensitive to subtle changes in feedback (Yeh, Boulet, Cluff, & Balasubramaniam, 2010), and increased availability of information from these systems has been shown to improve balance, as in the case of light touch (Jeka, Schöner, Dijkstra, Ribeiro, & Lackner, 1997; Wing, Johannsen, & Endo, 2011). Although multisensory feedback is essential for postural control, individuals differentially depend on combinations of somatosensory, vestibular, and visual feedback for postural stability. The dominant dependence can change with circumstance, including impairment of one or more of the senses (Dozza et al., 2007; Hegeman, Honegger, Kupper, & Allum, 2005). Partial compensation occurs in these systems to ensure balance not only for major impairment, but also temporary interruptions, such as when we close our eyes. In this situation, sway variability increases but balance can be maintained. Postural stability is greatest for healthy, young people

who have intact somatosensory, vestibular and visual function and strong multisensory compensation (Juntunen et al., 1987; Tanaka, Kojima, Takeda, Ino, & Ifukube, 2001).

The mechanisms for postural control include two components that work on different timescales (Yeh et al., 2010). Lower frequencies in postural sway reflect feedback based corrective processes, and higher frequencies reflect open loop and exploratory processes (Yeh, Cluff, & Balasubramaniam, 2014). Postural sway frequency spectra do not show two distinct ranges of higher power, but changes in feedback have been shown to influence the two frequency components differentially (Yeh et al., 2010), and the best fit cut-off frequency between the two timescales is estimated to be 0.3 Hz (van den Heuvel, Balasubramaniam, Daffertshofer, Longtin, & Beek, 2009). In a study that explored the relationship between the velocity of sway and the velocity of sub-threshold vibrating somatosensory references during light touch, they found that head and body sway coupled to the oscillating reference, and that coupling was nearly in-phase to frequencies of 0.2 Hz and lower, and had a significant lag for higher frequencies. This supports that lower frequency sway relies more on feedback than higher frequency sway when there is a cut-off frequency of slightly over 0.2 Hz (Jeka et al., 1997).

Auditory feedback has been shown to influence postural sway, but is less documented than other modalities of feedback. Impairment of vision, proprioception or vestibular systems leads to more reliance on audition (Dozza et al., 2007; Hegeman et al., 2005; Palm, Strobel, Achatz, Luebken, & Friemert, 2009), and hearing loss has been shown to increase variability in postural sway, although the explanation for this is unclear. Juntunen et al. proposed that subclinical damage to the vestibular system with noise-induced hearing loss could explain the effect on stability, but there is no corroboration for vestibular damage in their participants because of the difficulty in examining damage too subtle for current clinical detection (Juntunen et al., 1987). Imbalance and hearing loss co-occur in a number of disorders, including Ménière's disease, multiple sclerosis, viral infections and vestibular schwannoma (Mangiore, 2012). Reduction of sway with auditory feedback has also been shown in people without visual, proprioceptive or vestibular deficits (Dozza et al., 2007); audition might be utilized for postural stability even in people without impairment of other perceptual systems.

The aspect of auditory feedback that is most influential for balance is unknown. Attempts to encode position and velocity information in auditory feedback have resulted in mixed and confusing results. Hegeman et al. found very small improvements in stability with sound that provided information about position, but only when participants had their eyes open and were standing on a hard surface; they found no effect when participants' eyes were closed, when participants were standing on a foam surface designed to reduce somatosensory feedback from the feet, or when the sound provided velocity information (Hegeman et al., 2005). In contrast, Dozza et al. found a reduction in sway when the sound provided information about position, but only when participants' eyes were closed and participants were standing on a foam surface (Dozza et al., 2007). They also found a lot of inter-subject variability, possibly indicating that participants were responding to the feedback in individualized ways (Dozza et al., 2007). It is possible that the acoustic properties of the auditory stimuli might be more influential in reducing sway than any position or velocity information encoded in the stimuli. Auditory stimuli with changing acoustic properties, as in Hegeman et al. (2005) and Dozza et al.

(2007), could result in mixed and inconsistent effects on sway if the acoustic properties themselves influence sway. Palm et al. found no effect on sway with music from a fixed location (Palm et al., 2009). Deviterne et al. found reduced sway when participants listened to speech, but not when they listened to a single sustained tone (Deviterne, Gauchard, Jamet, Vançon, & Perrin, 2005). Acoustic properties of the sound stimuli might be more influential than the sound producing event, and informational feedback that event provides about how stable the stance is. The major differences between stimuli with changing acoustic properties and white noise are that noise is a complex sound, with many frequencies occurring at the same time, and noise can be presented continuously with acoustic properties that are held constant over the course of the experiment.

Noise in the somatosensory modality has been shown to reduce sway variability. Subsensory mechanical noise chips applied to the soles of the feet have been shown to reduce postural sway in healthy aging adults, adults with sensorimotor deficits of central and peripheral causes (Priplata et al., 2006; Priplata, Niemi, Harry, Lipsitz, & Collins, 2003), and in healthy young adults (Priplata et al., 2002). This shows that the presence of mechanical noise can reduce sway variability, which is thought to be a result of stochastic resonance (SR). SR describes the amplification of signals when adding noise to a threshold based system, such as the nervous system. Subsensory mechanical noise was shown to increase sensory feedback from the feet. Because somatosensory noise improves postural sway (Priplata et al., 2006; Priplata et al., 2003; Priplata et al., 2002), we hypothesized that auditory noise would also improve postural sway, due to a similar SR mechanism. There is evidence that auditory noise from a fixed location can improve postural stability in patients with cochlear implants, and that this could be due to the sound serving as an auditory field anchor (Mangiore, 2012). In the current experiment, postural sway was analyzed in healthy young adults without somatosensory, vestibular, visual or auditory deficits during silence and sustained white noise. Participants were examined with their eyes open and closed. It was hypothesized that sway variability would be reduced with exposure to auditory white noise, and that this effect would be greater in the eyes open condition than the eyes closed condition because of the reliance on multisensory feedback for postural stability.

Methods

Participants

Nineteen healthy participants (7 men, 12 women; aged 18-25) of similar height (64.8 ± 4.2 inches) and weight (146.5 ± 36.7 lbs.) were recruited from the University of California, Merced undergraduate and graduate student populations. Participants with hearing loss, neurological disorder, arthritis, orthopedic conditions, recent injury, and/or balance disorders were not included in the study. The protocol was approved by the Institutional Review Board and participants gave informed written consent prior to the experiment.

Experimental Protocol

Participants were asked to stand on a force platform in a relaxed, comfortable standing position with their arms at their sides while wearing headphones. The headphones worn were designed to reduce noise from any other external source.

Participants were instructed to keep their eyes on a black crosshair stimulus posted on the wall 229.0 cm in front of them at approximately eye level for the eyes-open trials and to keep their head facing forward and their eyes closed for the eyes-closed trials. Noise and silence conditions were presented in a randomized order. Trials lasted 30 seconds and were either accompanied by auditory white noise (10 trials at 75 dB) or silence (10 trials). Postural sway data were collected in a single session with twenty 30-second trials of the four conditions (5 trials each with eyes closed during silence, eyes open during silence, eyes closed during noise, eyes open during noise). The noise stimulus was generated using MATLAB to be a random signal with a constant spectral density. Participants were exposed to the noise stimulus prior to the experiment to verify that the noise stimulus was not uncomfortable for them.

CoP Acquisition and Analysis

Center of pressure (CoP) was sampled at 2000 Hz with an AMTI Force and Motion force platform (Optima BP400600-2000). The first four seconds of each trial were removed to eliminate any potential startle response the participants might have had to the stimulus onset. Radial sway (r) of the CoP was calculated for each time step (i) using anterior-posterior (x) and medial-lateral (y) components of sway following

$r_i = \sqrt{x_i^2 + y_i^2}$. Average radial sway was calculated for each trial, and was used to assess standing stability during the trials (Lafond, Corriveau, Hébert, & Prince, 2004a; Lafond, Corriveau, & Prince, 2004b). Detrended fluctuation analysis (DFA) and recurrence quantification analysis (RQA) were used to quantify the sway patterns over time. The data was down sampled for these analyses to 50 Hz. RQA measures used were percent determinism, percent recurrence, and entropy (delay = 40, embedding dimension = 4, radius = 10) and the standard largest box size was used (Richardson, Schmidt, & Kay, 2007). Radial sway in low and high frequency ranges was examined separately to assess changes in slow and fast timescales of postural control (Yeh et al., 2010; Yeh et al., 2014; van den Heuvel et al., 2009). Filtering was performed using a dual-pass, second-order Butterworth filter with a cutoff frequency of 0.3 Hz. The filter cutoff was chosen based van den Heuvel et al. 2009. We used low and high-pass Butterworth filtering routines, as in Yeh et al. 2010 and Yeh et al. 2014, to decompose sway into low (< 0.3 Hz) and high (> 0.3 Hz) frequency sway.

Results

Analysis of variability

Postural sway variability was reduced with the addition of auditory noise, and wandering behavior in both medial-lateral and anterior-posterior directions was reduced. The sway paths from representative trials from each condition for one subject are shown in Figure 2.1.

Radial sway variability was compared using a 2 EYES (Closed vs. Open) \times 2 NOISE (No noise vs. Noise) analysis of variance (ANOVA) with repeated measures on the visual and auditory feedback conditions. We found a main effect of vision ($F(1,18)=9.472$, $p=.006$) and noise ($F(1,18)=6.873$, $p=.017$), as shown in Figure 2.2. These results support that variability in postural sway decreases when eyes are open and

with the addition of noise, contributing to more stability in standing balance. We also found a vision \times noise interaction ($F(1,18)=5.885$, $p=.026$), which supports that visual and auditory feedback contribute interactively to sway variability.

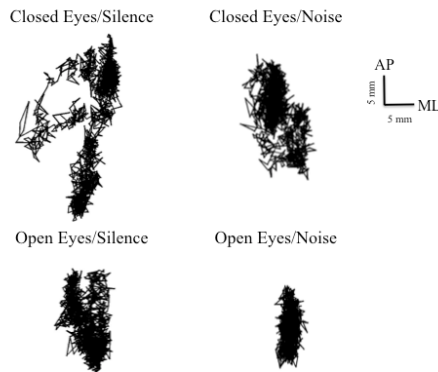


Figure 2.1. Center of pressure displacement exhibited by one subject in eyes closed/open and silent/noise conditions

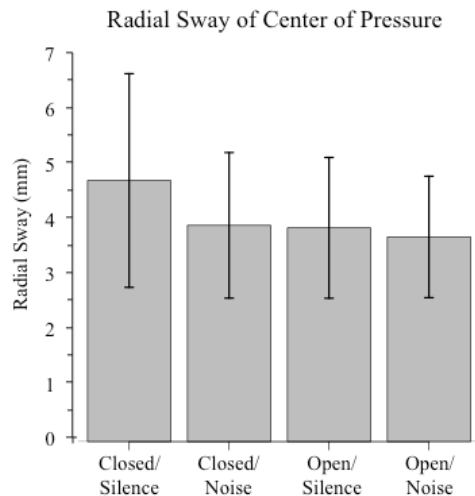


Figure 2.2. Radial sway variability in eyes closed/open and silent/noise conditions. Error bars represent ± 1 standard deviation from the mean

Nonlinear analyses

Detrended fluctuation analysis (DFA) revealed that the sway patterns exhibit antipersistent fBm ($1 < \beta < 1.5$), which is consistent with previous work on postural sway (Blázquez, Anguiano, de Saavedra, Lallena, & Carpena, 2010; Delignières, Deschamps, Legros, & Caillou, 2003). This means the sway moves in successive steps in random directions (a semi-random walk), and does not tend toward the same direction. This was the pattern in all four experimental conditions. There were no effects of eyes ($F(1,93) = .039$, $p = .844$), noise ($F(1,93) < .0001$, $p = .990$), or an interaction between them ($F(1,93)$

= 1.118, $p = .293$). Neither vision nor noise changed this random walk pattern typical of postural sway.

Recurrence quantification analysis (RQA) was used to quantify complexity of the sway over the last 26 seconds of each trial. The parameters we examined were percent determinism, percent recurrence, and entropy (Marwan, Romano, Theil, & Kurths, 2007). Each RQA parameter was compared across conditions using a 2 EYES (Closed vs. Open) \times 2 NOISE (No noise vs. Noise) analysis of variance (ANOVA) with repeated measures. As shown in Figure 2.3A, percent determinism decreased when eyes were open and when noise was present. There was a main effect of eyes ($F(1,92)=9.400$, $p=.003$) and noise ($F(1,92)=4.112$, $p=.045$). Having eyes open and hearing noise reduces determinism of radial sway movements. There was no eyes \times noise interaction ($F(1,92)=1.080$, $p=.301$), indicating that noise has an additive effect on the random nature of postural sway. As shown in Figure 2.3B, percent recurrence decreases in the noise conditions. There was a main effect of noise ($F(1,93) = 4.806$, $p = .031$), but no effect of eyes ($F(1,93) = .249$, $p = .619$). There was no eyes \times noise interaction ($F(1,93) = .426$, $p = .516$). As shown in Figure 2.3C, entropy decreased when eyes were open and when noise was present. There was a main effect of eyes ($F(1,93) = 6.314$, $p = .014$) and noise ($F(1,93) = 7.813$, $p = .006$). There was no eyes \times noise interaction ($F(1,93) = 1.413$, $p = .238$).

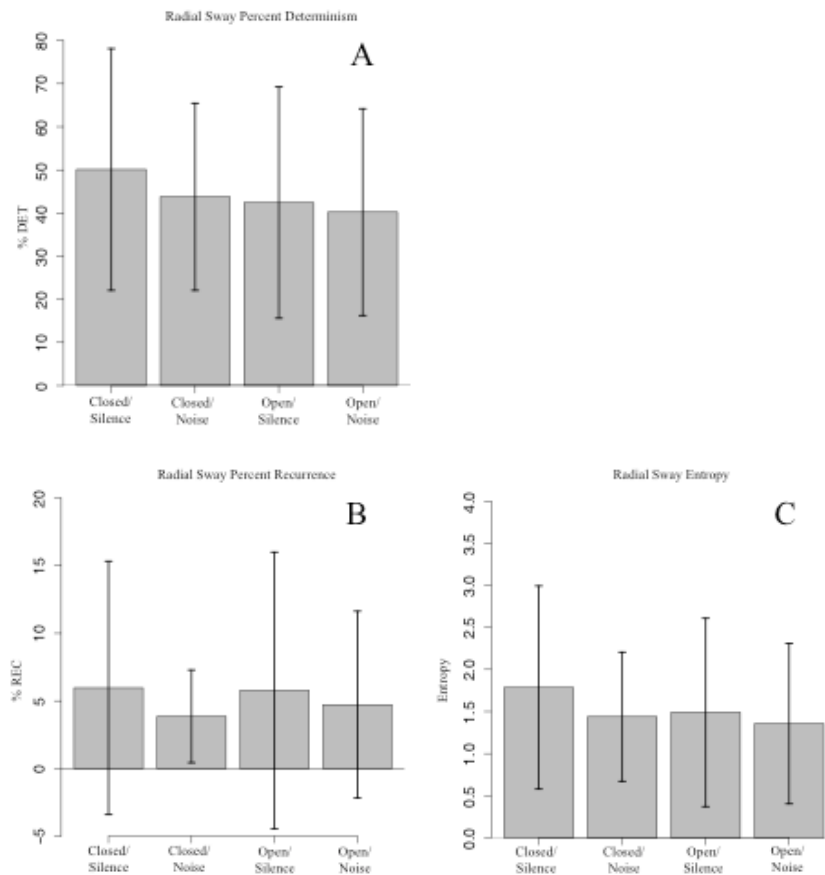


Figure 2.3. Nonlinear measures of sway in eyes closed/open and silent/noise conditions. Error bars represent ± 1 standard deviation from the mean

Variability in high and low frequency ranges

In low frequency sway (<0.3 Hz), there was a main effect of vision ($F(1,92)=7.082, p=.009$) and noise ($F(1,92)=6.539, p=.012$). Both vision and noise reduced radial sway variability in the low frequency band, as summarized in Figure 2.4. The vision \times noise interaction was also significant ($F(1,92)=9.375, p=.003$), indicating that visual and auditory feedback interactively influenced feedback based postural control mechanisms. In high frequency sway (>0.3 Hz), there was a main effect of vision ($F(1,92)=37.992, p<.001$) and noise ($F(1,92)=19.558, p<.001$). Vision and noise reduced radial sway variability in the high frequency band, as shown in Figure 2.4. There was no interaction between vision \times noise ($F(1,92)=.919, p=.340$), indicating that visual and auditory feedback independently influenced exploratory postural control mechanisms. In low frequency sway, noise interacts with vision, but in high frequency sway, the effect of noise is additive.

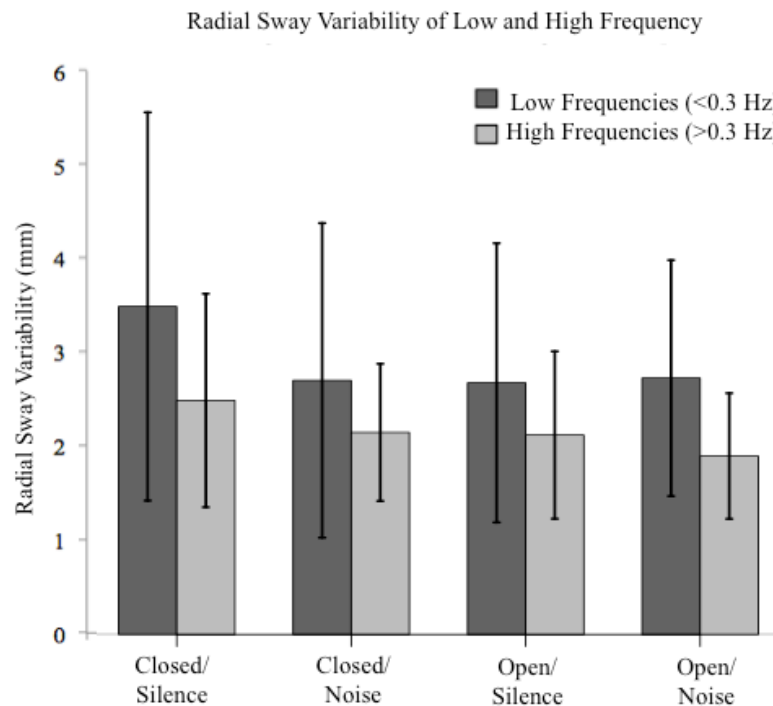


Figure 2.4. Radial sway variability in low and high frequencies in eyes closed/open and silent/noise conditions. Error bars represent ± 1 standard deviation from the mean

Discussion

We show improved postural stability with auditory noise in healthy young adults using headphones. However, it is important to note that somatosensory noise presented to participants in the previous experiments were subthreshold, in that it was not actively detected by the participants. In our experiment, the auditory noise presented to participants was well within audible range (75 dB). The presented results support the idea

that variability in postural sway decreases when eyes are open and with the addition of noise, contributing to more stability in standing balance. All postural sway exhibits antipersistent fractional Brownian motion, but the patterns of complexity are influenced by visual and auditory stimulation. Having eyes open and hearing noise reduces determinism of radial sway movements, and the effect of noise is additive. Percent recurrence decreases with noise, and entropy decreases with vision and noise independently.

One explanation for the noise effect on postural sway is that the sound provides an orienting reference when it comes from a fixed location (Zhong & Yost, 2013). This is an argument that has also been used with regard to light touch. Somatosensory contact with an object provides the participant with a sensory reference frame that helps them stabilize their posture. Although acoustic noise can provide information about directionality, it is unlikely that it provides information about a sensory reference frame in the same way that light touch does. Also, with light touch, somatosensory contact with a moving object can also reduce sway variability (Jeka et al., 1997; Wing et al., 2011). It seems to be that increasing somatosensory feedback, whether the source is stationary or not, improves balance. Similarly, auditory stimulation from stationary and moving sources has been shown to reduce sway variability (Deviterne et al., 2005).

It is not the case that sound source does not matter in postural sway, but that it is not necessarily the driving force behind the noise effect. Pure tone and conversation from a fixed source on one side of the body during an eyes closed condition actually has a destabilizing effect on postural sway (Raper & Soames, 1991). Moving sound sources can lead to illusions of self-motion, especially with limited spatial feedback from vision, but feedback from sensory modalities other than hearing about the reference frame ruin this illusion (Väljamäe, 2009; Lackner, 1977). Directionality of a moving sound source alone does not seem to matter in reducing sway; clockwise and counter-clockwise moving auditory stimuli reduce postural sway variability (Tanaka et al., 2001). However, sound that moves from the front towards the back of participants can result in participants leaning toward the approaching sound (Agaeva, Altman, & Kirillova, 2006), which helps explain why Soames and Raper reported a destabilizing effect of a sound stimulus that jumped between speakers anterior and posterior to participants (Soames & Raper, 1992). In the current study, we used headphones to eliminate the possibility of the noise stimulus indicating a single fixed or moving location.

Another explanation is that increased attentional arousal during the noise condition could explain the improved stability. McNevin and Wulf (2002) show that an external focus of attention (on the results of an effector on an object) when compared to an internal focus of attention (on the movement of the effector) can lead to reliance on more automatic control processes, which results in improved stability. Others have found that adding a cognitively demanding task leads to more automaticity in balance processes (Cluff, Gharib, & Balasubramaniam, 2010). Because passively listening to auditory noise does not involve performance related (external or internal) attention and is not cognitively demanding, we would not predict that attention in the noise condition would drive a stabilizing effect. However, we cannot summarily rule out the possibility of attentional arousal being involved in some way. Further experimentation is required to shed more light on this.

Stochastic resonance (SR) is an explanation for the noise effect on postural sway that fits appropriately and describes the results of much of the literature. SR describes the amplification of signals with the addition of noise. Noise is often viewed in signal processing as something that obscures a signal, but evidence shows that in some systems noise can contribute to signal optimization. The concept of SR originated in the field of physics (Benzi, Sutera, & Vulpiani, 1981), where it was used to explain weather patterns in which an accumulation of noise, in the form of heat, leads to certain types of climate shifts. The mechanism has been explained in general theoretical terms as a result of 1) background noise 2) a weak signal 3) a threshold system in which a barrier must be reached for signal transfer (Hänggi, 2002). The mechanism was then studied in biological systems because of the prevalence of noise, weak signals, and action potential firing thresholds. It has been demonstrated in nonhuman (Douglass, Wilkens, Pantazelou, & Moss, 1993; Levin & Miller, 1996; Russell, Wilkens, & Moss, 1999; Bezrukov & Vodvanov, 1995; Schmid, Goychuk, & Hänggi, 2001; Jung & Shuai, 2001) and human (Hidaka, Nozaki, & Yamamoto, 2000; Collins, Imhoff, & Grigg, 1996; Richardson, Imhoff, Grigg, & Collins, 1998; Simonotto et al., 1997) nervous systems. These studies show that sensory perception in a number of species utilizes noise to optimize performance. SR has been studied in vision, audition and mechanical sensory perception and could be an integral part of sensory perception across species.

SR has been explored for clinical purposes to enhance sound detection in cochlear implant users (Morse & Evans, 1996) and in improving postural stability for people with balance problems. Subsensory mechanical noise chips on the bottoms of the feet reduce sway in clinical and typical populations (Priplata et al., 2006; Priplata et al., 2003; Priplata et al., 2002). The explanation for this could be that noise increases somatosensory feedback from the feet. More specifically, the mechanical noise could be contributing to reaching action potential firing thresholds needed for somatosensory feedback, resulting in increased feedback and increased postural control. Similarly, auditory noise can improve postural stability in patients with cochlear implants (Mangiore, 2012), which could be the result of increased auditory feedback. Our data show that visual and auditory feedback interactively contribute to overall sway variability. However, upon examining sway separately in low (<0.3 Hz) and high (>0.3 Hz) frequency bands, it was demonstrated that vision and auditory noise reduce radial sway variability in low frequencies interactively and in high frequencies independently. Therefore, the effect of noise is utilized with vision for feedback based processes, but is additive for open-loop or exploratory processes in postural sway. Further investigation is needed to determine whether the noise effect and its differential influence on the two balance control timescales holds if the auditory signal is sub-threshold or masked by other sounds. This work would contribute to a deeper understanding of the mechanisms involved but would also have implications for practical implementation in clinical practice.

Although SR explains our results, as well as the results others have found, it will take a series of targeted studies to determine whether noise is the critical component driving improved stability, whether this is due to SR mechanisms, and specifically how SR works in the auditory modality. We present SR as a possible explanation and do not intend to overextend our interpretation. However, whether or not the effects are due to

SR, the current findings have profound implications for improving balance in clinical populations. Auditory noise has the potential for fall prevention for people with instability due to visual, vestibular or somatosensory deficits. Peripheral sensory deficits can lead to more reliance on audition for balance (Dozza et al., 2007; Hegeman et al., 2005; Palm et al., 2009), and auditory noise can reduce postural fluctuations, so auditory noise should be tested for its ability to improve balance in these populations.

If it is the case that SR is the reason auditory noise reduces sway, then auditory noise also has the potential for fall prevention for people with instability due to central causes. The support for this is that mechanical noise can reduce sway both in people with peripheral and central deficits (Priplata et al., 2006; Priplata et al., 2003) and SR is a mechanism that works both in somatosensory (Douglass et al., 1993; Levin & Miller, 1996) and auditory system signal transfer (Mangiore, 2012). It should be explored whether auditory noise can reduce sway variability in people with instability due to central nervous system damage. Future research should investigate the influence of auditory noise on postural sway in people with centrally caused balance disorders. Finding reduced postural sway in this population would provide further support for SR as an explanation and could easily be extended to clinical applications.

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Chapter 3

Auditory White Noise Reduces Age-Related Fluctuations in Balance

Fall prevention technologies have the potential to improve the lives of older adults. Because of the multisensory nature of human balance control, sensory therapies, including some involving tactile and auditory noise, are being explored that might reduce increased balance variability due to typical age-related sensory declines. Auditory white noise has previously been shown to reduce postural sway variability in healthy young adults. In the present experiment, we examined this treatment in young adults and typically aging older adults. We measured postural sway of healthy young adults and adults over the age of 65 years during silence and auditory white noise, with and without vision. Our results show reduced postural sway variability in young and older adults with auditory noise, even in the absence of vision. We show that vision and noise can reduce sway variability for both feedback-based and exploratory balance processes. In addition, we show changes with auditory noise in nonlinear patterns of sway in older adults that reflect what is more typical of young adults, and these changes did not interfere with the typical random walk behavior of sway. Our results suggest that auditory noise might be valuable for therapeutic and rehabilitative purposes in older adults with typical age-related balance variability.

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Introduction

With aging comes an increased risk of falling. Falls lead to declines in health and reduced independence and mobility, especially in adults over 65 years of age (Priplata, Niemei, Harry, Lipsitz, & Collins, 2003; Tinetti, 2003). It has long been posited that postural variability is greater in older adults, although the reasons for that are varied (Balasubramaniam & Wing, 2002). In recent years, researchers have looked into ways of reducing this variability using a variety of means (Priplata et al., 2002; Priplata et al., 2003; Priplata et al., 2006; Ross & Balasubramaniam, 2015; Dozza, Horak, & Chiari, 2007; Hegeman, Honegger, Jupper, & Allum, 2005). Balance control relies on continuous streams of multisensory information from visual, vestibular, somatosensory and auditory modalities (Dozza et al., 2007; Hegeman et al., 2005; Palm, Strobel, Achatz, Luebken, & Friemert, 2009), and is sensitive to changes in feedback in any of these modalities (Balasubramaniam & Wing, 2002; Dozza et al., 2007; Hegeman et al., 2005; Palm et al., 2009; Yeh, Boulet, Cluff, & Balasubramaniam, 2010; Ross, Warlaumont, Abney, Rigoli, & Balasubramaniam, 2016; Jeka, Schöner, Dijkstra, Ribeiro, & Lackner, 1997; Wing, Johannsen, & Endo, 2011). It has been observed that tactile and auditory noise can both lead to reductions in sway variability (Priplata et al., 2002; Priplata et al., 2003; Priplata et al., 2006; Ross & Balasubramaniam, 2015).

A seminal study looked at the potential of stochastic resonance for incorporation into fall prevention technologies (Priplata et al., 2002; also Priplata et al., 2003; Priplata et al., 2006; Ross & Balasubramaniam, 2015). Stochastic resonance is when uncorrelated noise boosts transmission of weak signals in threshold-based systems (Benzi, Sutera, & Vulpiani, 1981; Hänggi, 2002), and is known to play a role in enhancing weak signals in the peripheral nervous system (Hidaka, Nozaki, & Yamamoto, 2000; Collins, Imhoff, & Grigg, 1996; Richardson, Imhoff, Grigg, & Collins, 1998; Simonotto et al., 1997; Morse & Evans, 1996). Priplata and colleagues used vibrating insoles to reduce sway variability in healthy elderly adults and adults with sensorimotor deficits due to peripheral and central causes (Priplata et al., 2002; Priplata et al., 2003; Priplata et al., 2006). The mechanical noise produced by these insoles is at 90% of sensory threshold, but these insoles are designed to use stochastic resonance to increase sensory feedback from the feet. The increased feedback from the feet gets incorporated into complex balance control processes, leading to less variability in standing balance.

In a manner similar to somatosensory noise, auditory noise has also been shown to reduce sway variability in cochlear implant users (Mangiore, 2012) and healthy young adults (Ross & Balasubramaniam, 2015), possibly due to a mechanism similar to stochastic resonance. Auditory noise has not been used previously to reduce sway variability in older adults, but has the potential to compensate for reduced sensory feedback due to visual, vestibular, somatosensory or auditory deficits (Dozza et al., 2007; Hegeman et al., 2005; Juntunen et al., 1987; Tanaka, Kojima, Takeda, Ino, & Ifukube, 2001) that lead to postural instability in this age group (Yeh, Cluff, & Balasubramaniam, 2014).

In the current experiment, we examined sway variability during silence and while listening to auditory noise, with and without vision, in young adults and adults over 65. We hypothesized that auditory noise would lead to reduced sway variability, even in the absence of vision in both age groups. In addition, we expected the reduction to be greater in adults over 65 because of more variable sway (Yeh, Cluff, & Balasubramaniam, 2014) in all four conditions.

Methods

Participants

Fifteen healthy young adults (mean age 19.87 ± 2.10 years) and fifteen adults over the age of 65 (mean age 78.67 ± 7.73) of similar height ($t(28) = 2.92$, $p = 1.44$) and weight ($t(28) = 2.43$, $p = .13$) were recruited from the University of California, Merced student population and the Merced local population, respectively. The older adult participants had a range of typical age-related impairments including mild hearing loss (that did not interfere with conversational speech), mild vision impairment (with corrective lenses), arthritis, orthopedic conditions, nerve pain and history of heart attack. Young adult participants had no hearing impairments, arthritis, orthopedic conditions, or neurological disorder. No subjects reported recent injuries or skeletomuscular disorders and all could stand unassisted during the experiment. The experimental protocol was carried out in accordance with the Declaration of Helsinki, reviewed by the UC Merced IRB, and all participants gave informed consent prior to testing.

All participants were screened for vision impairment using the Rosenbaum Pocket Vision Screener, and were asked to complete a standing balance test (balancing on one leg at a time, three times per leg) to screen for major balance problems that would put participants at increased risk for injury during the experimental protocol. Experimenters and all participants were comfortable participating and did not feel unsafe completing the protocol. However, there were group differences in ability to stand on one leg at a time, which we believe is representative of real-world differences between young and older adults. Young adults and older adults differed in the average amount of time they could balance on the left leg ($t(28) = 9.84$, $p = .004$) and on the right leg ($t(28) = 8.62$, $p = .007$). The older adult participants completed the Falls Efficacy Scale- International (FES-I), a standard questionnaire designed to quantify daily fear of falling in older adults (Yardley et al., 2005; Kempen et al., 2008). Scores averaged 25.28 ± 9.18 , indicating a range of fear spanning low concern, moderate concern, and high concern. Fear of falling is a common concern for adults over 65, and the amount of fear varied in our participant group. The protocol was approved by the Institutional Review Board.

Experimental Protocol

Participants were asked to stand on a force platform in a relaxed, comfortable standing position with their arms at their sides while wearing headphones designed to reduce noise from external sources. Participants were instructed to keep their eyes on a black crosshair stimulus posted on the wall 229.0 cm in front of them at approximately eye level for the eyes-open trials and to keep their head facing forward and their eyes closed for the eyes-closed trials. Conditions were presented in a randomized order. Trials lasted 30 s and were either accompanied by auditory white noise (10 trials) or silence (10 trials). Postural sway data were collected in a single session with 20 30-second trials of the four conditions (five trials each with eyes closed during silence, eyes open during silence, eyes closed during noise, eyes open during noise). The noise stimulus was generated using MATLAB to be a random signal with a constant spectral density, presented at 75 dB through the headphones. Participants were exposed to the noise stimulus prior to the experiment to verify that the noise stimulus was not uncomfortable for them.

Analyses

Center of pressure (CoP) was sampled at 2000 Hz with an AMTI Force and Motion platform (Optima BP400600-2000). The first 4 s of each trial were removed to eliminate any potential startle response the participants might have had to the stimulus onset. Raw data was down sampled to $FS = 50$ Hz and normalized. Standard deviation from mean CoP of anterior-posterior (A-P) and medial-lateral (M-L) sway was calculated for each time step, and radial sway (r) of the CoP was calculated for each time step (i) using A-P (x) and M-L (y) components of sway following

$$r_i = \sqrt{x_i^2 + y_i^2}$$

Average A-P, M-L, and radial sway were calculated for each trial and were used to assess variability in postural sway during the trials (Lafond, Corriveau, Hébert, &

Prince, 2004a). Trial outliers outside ± 2 standard deviations from each subject's mean were removed.

Radial sway in low- and high-frequency ranges was examined separately to assess changes in slower and faster timescales of postural control (Yeh et al., 2010; Yeh et al., 2014; van den Heuvel, Balasubramaniam, Daffertshofer, Longtin, & Beek, 2009). Filtering was performed using a dual-pass, second-order Butterworth filter with a cutoff frequency of 0.3 Hz. The filter cutoff was chosen based on van den Heuvel et al. 2009. We used low- and high-pass Butterworth filtering routines, as in Yeh et al. 2010 and Yeh et al. 2014, to decompose sway into low (<0.3 Hz)- and high (>0.3 Hz)-frequency sway. Detrended fluctuation analysis (DFA) was used to quantify the sway patterns over time. The data were down sampled for this analysis to 25 Hz.

Results

Analysis of postural variability

A-P, M-L, and radial sway variability were reduced with the addition of auditory noise (Figure 3.1). Standard deviation in the A-P and M-L sway and radial sway was compared across condition and between groups using two-way analyses of variance (eyes closed vs. open and silence vs. noise) with repeated measures, with age group as the between subjects factor. We found main effects of vision ($F(1,28) = 9.36$, $p = .005$) and noise ($F(1,28) = 5.93$, $p = .022$) on A-P sway, a main effect of noise ($F(1,28) = 8.86$, $p = .006$) on M-L sway, and main effects of vision ($F(1,28) = 10.47$, $p = .003$) and noise ($F(1,28) = 9.01$, $p = .006$) on radial sway. We did not find any vision \times noise interactions. We found greater A-P sway ($F(1,28) = 21.27$, $p < .001$) and radial sway ($F(1,28) = 9.03$, $p = .006$) in the older adults than in the young adults. See Figure 3.2 for radial sway of young and older adults.

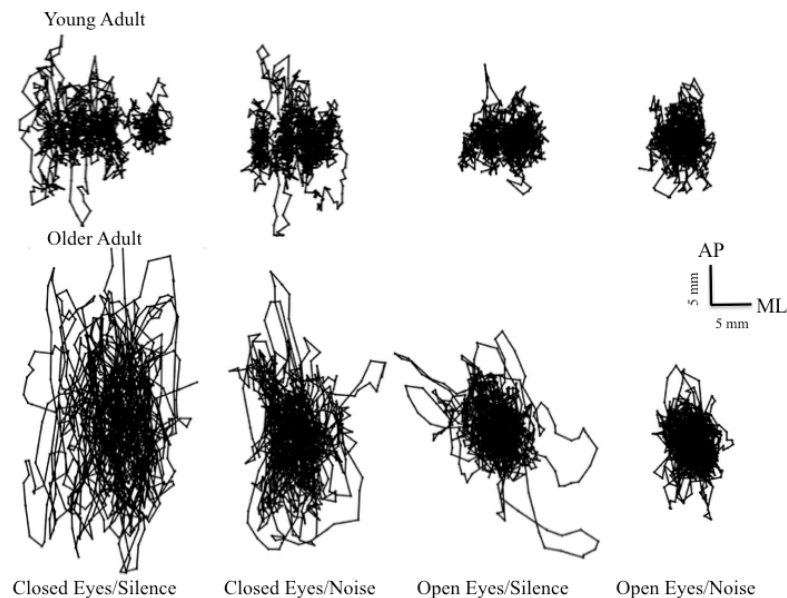


Figure 3.1. Center of pressure displacement exhibited by representative young and older adult subjects with eyes closed and open and in silent and noise conditions.

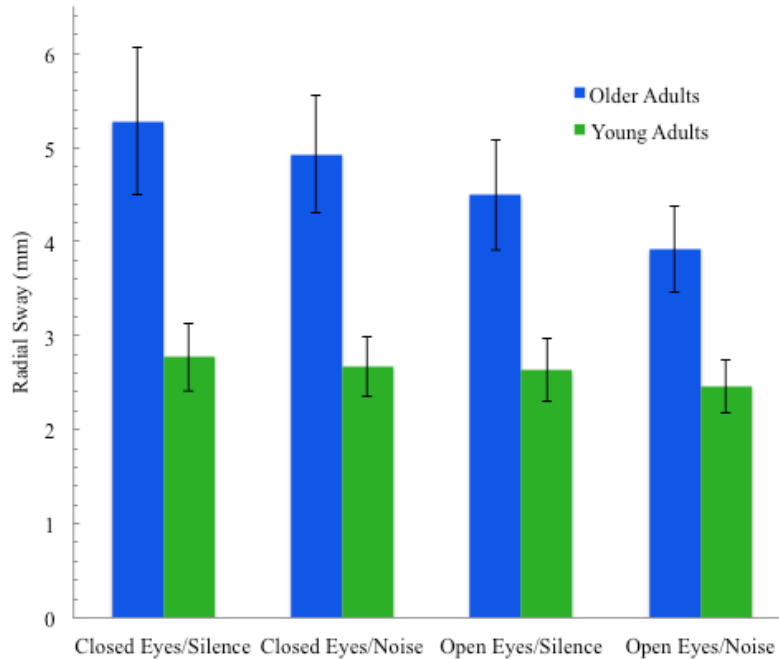


Figure 3.2. Radial sway variability in eyes closed/eyes open and silent/noise conditions for young and older adults. Error bars represent ± 1 standard error from the mean.

When variability in low (< 0.3 Hz) and high-frequency (> 0.3 Hz) sway was analyzed separately, we found reductions in sway variability in both frequency bands, indicating that vision and noise can influence both feedback based and exploratory balance processes. We found a main effect of vision on low frequency A-P sway ($F(1,28) = 5.91, p = .022$) and on high frequency A-P sway ($F(1,28) = 20.11, p < .001$), a marginal effect of noise on low frequency A-P sway ($F(1,28) = 2.19, p = .073$), and a strong effect of noise on high frequency A-P sway ($F(1,28) = 11.03, p = .003$). There was a vision \times noise interaction in high frequency A-P sway, a between subjects effect in low frequency A-P sway ($F(1,28) = 13.69, p = .001$) and marginally in high frequency A-P sway ($F(1,28) = 3.72, p = .064$), with more A-P sway in older adults than young adults.

We found a main effect of noise on low frequency ($F(1,28) = 8.41, p = .007$) and high frequency ($F(1,28) = 4.31, p = .047$) M-L sway, and a between subjects effect in low frequency M-L sway ($F(1,28) = 6.77, p = .015$), with no vision \times noise interactions.

In radial sway, there were main effects of vision on both low ($F(1,28) = 4.37, p = .046$) and high ($F(1,28) = 14.58, p = .001$) frequency radial sway, and main effects of noise on both low ($F(1,28) = 7.91, p = .009$) and high ($F(1,28) = 8.01, p = .008$) frequency radial sway. There were no vision \times noise interactions, and there was a between subjects effect in low ($F(1,28) = 13.21, p = .001$) frequency radial sway, with a marginal between subjects effect in high ($F(1,28) = 3.71, p = .064$) frequency radial sway. See Figure 3.3 for radial sway of young and older adults in low and high frequencies.

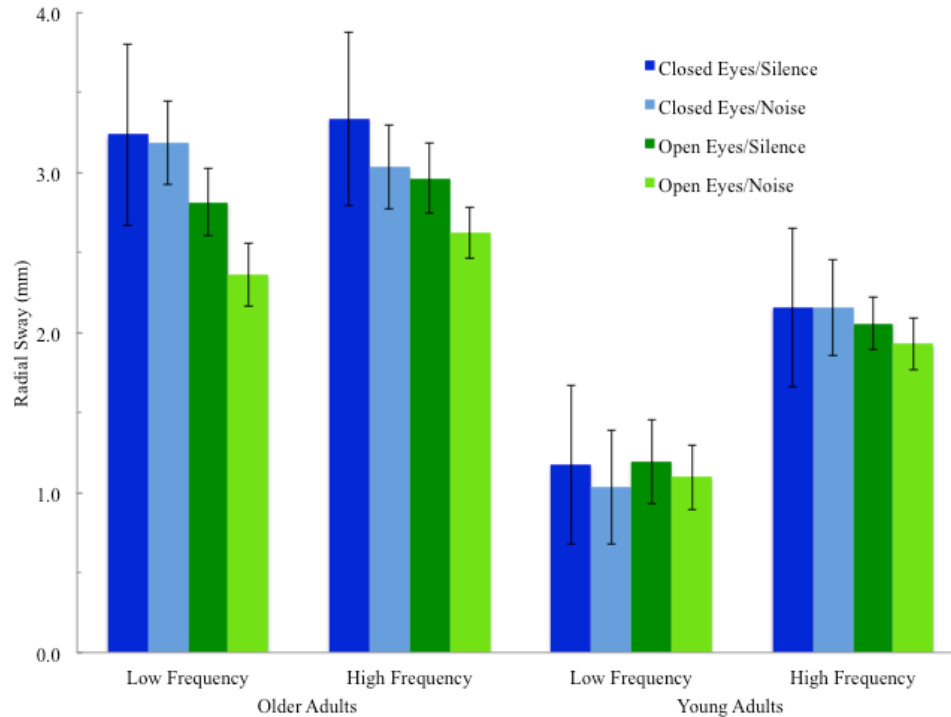


Figure 3.3. Radial sway variability in low (<0.3 Hz) and high (>0.3 Hz) frequency ranges in eyes closed/eyes open and silent/noise conditions for young and older adults. Error bars represent ± 1 standard error from the mean.

Detrended fluctuation analysis

Detrended fluctuation analysis showed that all sway measures (A-P, M-L, and radial) exhibit anti-persistent fractional Brownian motion (fBm, $1 < \beta < 1.5$). This semi-random walk pattern is characteristic of postural sway (Blázquez, Anguiano, de Saavedra, Lallena, & Carpena, 2010; Delignières, Deschamps, Legros, & Caillou, 1993; Collins & De Luca, 1994). Within this 1 to 1.5 range, there were differences between conditions and subjects in β . The value of β was compared across conditions and age group using a two-way ANOVA (eyes closed vs. open and silence vs. noise) with repeated measures, with age group as the between subjects factor. We found higher β in older adults than in younger adults for A-P sway ($F(1,28) = 11.21$, $p = .002$) and radial sway ($F(1,28) = 7.63$, $p = .010$). We found a main effect of noise on radial sway β ($F(1,28) = 4.71$, $p = .039$), and marginal effects of noise on A-P β ($F(1,28) = 3.65$, $p = .066$) and M-L β ($F(1,28) = 2.98$, $p = .095$), and a vision \times noise interaction for A-P β ($F(1,28) = 12.15$, $p = .002$). Vision and noise reduce β so sway is more similar to that of healthy young adults, while not interfering with the typical random walk pattern of postural sway.

Discussion

We clearly demonstrate reduced postural sway variability in young and older adults over 65 with auditory noise. This reduction in variability was present with and without vision. Standing balance has been described using an inverted pendulum model, where sway movements are dictated by the dynamics of the joints and muscles of the

lower limbs (Gurfinkel, Lipshits, & Popov, 1974; Winter, Patla, Prince, Ishac, & Gielo-Perczak, 1998). However, a large body of literature on postural sway shows that sensory information is incorporated into balance maintenance in real time (Balasubramaniam & Wing, 2002; Dozza et al., 2007; Hegeman et al., 2005; Palm et al., 2009; Yeh et al., 2010; Ross et al., 2016; Jeka et al., 1997; Wing et al., 2011; Loram & Lakie, 2002), and that sensory feedback delays effect low and high frequency components of sway differentially in both young (Yeh et al., 2010; van den Heuvel et al., 2009) and older adults (Yeh et al., 2014), supporting that there are two timescales of sway that reflect different balance processes (van den Heuvel et al., 2009; Gurfinkel et al., 1974). Slower timescales of sway are thought to reflect drift of the inertial mass of the body, at the center of mass (Winter et al., 1998), and are more susceptible to changes in sensory feedback (Yeh et al., 2010; Yeh et al., 2014; van den Heuvel et al., 2009). Faster timescales of sway are thought to reflect smaller adjustments around the center of mass that are more directly related to joint rigidity and muscle tone (Kiemel, Oie, & Jeka, 2005; Peterka, 2002). Some researchers have argued that the faster timescale movements could be representative of anticipatory or exploratory processes (van den Heuvel et al., 2009). Using low- and high-pass Butterworth filters with a cut-off frequency of 0.3 Hz, these two timescales of sway can be examined separately (Yeh et al., 2010; Yeh et al., 2014; van den Heuvel et al., 2009). Our results show that auditory noise and vision can influence both slower and faster timescale components of sway. We also show changes with auditory noise in nonlinear patterns over time in older adults to reflect what is more characteristic of young adults while maintaining the typical random walk pattern. These results support that auditory noise could be a valuable aid for adults over 65 who suffer from instability by improving balance without disrupting healthy balance processes.

Balance control relies on both exogenous and endogenous fluctuations--fluctuations with sources external to the body and fluctuations that are inherent in the control of balance (Kelty-Stephen & Dixon, 2013). Sources that have been shown to influence postural control that are exogenous include changes in visual, auditory and tactile feedback (Dozza et al., 2007; Hegeman et al., 2005; Palm et al., 2009; Yeh et al., 2010; Ross et al., 2016; Jeka et al., 1997; Wing et al., 2011; Juntunen et al., 1987; Tanaka et al., 2001; Soames & Raper, 1992; Agaeva, Altman, & Kirillova, 2006). Sources that could be considered endogenous include cognitive load (Yeh et al., 2010; Deviterne, Gauchard, Jamet, Vancon, & Perrin, 2005; Cluff, Gharib, & Balasubramaniam, 2010) and attention (McNevin & Wulf, 2002). The temporally correlated nature of postural sway patterns is a reflection of endogenous influences on balance control. Because stochastic resonance also relies on both endogenous and exogenous fluctuations, the strength of the effect is influenced by a range of individual differences and environmental factors. In addition, the strength of the effect is also influenced by interactions between exogenous signals and the temporal correlations of endogenous fluctuations (Kelty-Stephen & Dixon, 2013). It would be very interesting to see the effect of cognitive load on postural fluctuations in the presence of auditory noise.

In a re-analysis of Priplata et al., 2003 by Kelty-Stephen & Dixon (2013), older adults' postural sway patterns show an increase in temporal correlations when compared with younger adults, and temporal correlations in sway patterns moderate the stochastic

resonance effect of the vibrating insoles. Our data show a proportionally greater reduction in sway variability when noise was presented to older adults than young adults.

It is important to underscore that variability and stability in standing balance do not necessarily have an inverse relationship, as variability in sway patterns may be needed for adaptability and increased control in the presence of perturbations (Balasubramaniam, Riley, & Turvey, 2000; Balasubramaniam & Torre, 2012). However, increased variability in standing balance has been linked with increased likelihood of falls (Ferne, Gryfe, Holliday, & Llewellyn, 1982; Liu-Ambrose et al., 2004; Lord, Ward, Williams, & Anstey, 1994; Maki, Holliday, & Fernie, 1990; Overstall, Exton-Smith, Imms, & Johnson, 1977). Our results support that a reduction in variability with auditory noise is accompanied by changes in nonlinear patterning that is more typical of healthy young adults. Auditory noise reduces variability in young and older adults and leads to sway patterns more typical of younger adults while still maintaining a random walk pattern.

Stability can be understood as the coadjustment of local variability and serial correlation properties (Torre & Balasubramaniam, 2011). Amoud et al., 2007 found a similar pattern of group differences when analyzing COP in young and older adults. In this study, DFA of sway from young and older adults revealed higher H in the older adults' sway than in the younger adults' sway. Higher H indicates more persistence, or more correlation between successive points, and a lower H indicates more anti-persistence in a signal. Anti-persistence can be interpreted as more tightly controlled, or less resistant to changes in COP displacement direction, which reflects adaptability of the signal to change. Due to the direct relationship between H and β , a lower β can be interpreted in the same way as a lower H. Our DFA results contribute to the question of variability and adaptability by suggesting that the reduction in sway variability with noise in the older adults is accompanied by increased adaptability. Importantly, however, we emphasize that β was between 1 and 1.5 in all conditions; all sway was anti-persistent and the differences between groups show only differences between degree of anti-persistence within this range. Auditory white noise did not interfere with the random walk property of sway, but might have influenced adaptability as well as variability leading to increased postural stability.

It should be explored whether auditory white noise can be used to reduce variability and adaptability in older adults with centrally caused balance disorders, such as due to stroke or Parkinson's disease. Finding similar variability reduction in these groups would provide evidence for the generalizability of the noise effect on balance variability of different causes. It would also lend further support for stochastic resonance as a valid mechanistic explanation. Finally, practical application of auditory white noise for balance should be explored for therapeutic and rehabilitation purposes for adults who suffer from balance instability.

Authors' contributions All authors read and approved the final manuscript. JR, RB, design of experiment; JR, OW, ZM, collection of data; JR, RB, analyses; RB, project supervision; JR, OW, ZM, RB, joint contribution to writing the manuscript. The authors have no conflict of interest to declare.

Chapter 4 Influence of Musical Groove on Postural Sway

Timescales of postural fluctuation reflect underlying neuromuscular processes in balance control that are influenced by sensory information and the performance of concurrent cognitive and motor tasks. An open question is how postural fluctuations entrain to complex environmental rhythms, such as in music, which also vary on multiple timescales. Musical groove describes the property of music that encourages auditory-motor synchronization and is used to study voluntary motor entrainment to rhythmic sounds. The influence of groove on balance control mechanisms remains unexplored. We recorded fluctuations in center of pressure (CoP) of standing participants (N=40) listening to low and high groove music and during quiet stance. We found an effect of musical groove on radial sway variability, with the least amount of variability in the high groove condition. In addition, we observed that groove influenced postural sway entrainment at various temporal scales. For example, with increasing levels of groove, we observed more entrainment to shorter, local timescale rhythmic musical occurrences. In contrast, we observed more entrainment to longer, global timescale features of the music, such as periodicity, with decreasing levels of groove. Finally, musical experience influenced the amount of postural variability and entrainment at local and global timescales. We conclude that groove in music and musical experience can influence the neural mechanisms that govern balance control and discuss implications of our findings in terms of multiscale sensorimotor coupling.

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Introduction

Within the context of sensorimotor control, entrainment describes body synchronization with environmental rhythms. Entrainment is commonly seen in multiple modalities to rhythmic sounds, such as music and speech. Research on voluntary entrainment has looked at variability, stability and adaptability of entrainment, coordination between multiple effectors, and timekeeping mechanisms (Balasubramaniam, 2006; Ross & Balasubramaniam, 2014). It is clear that humans can easily entrain body movements to auditory rhythms (Janata, Tomic, & Haberman, 2012). Involuntary entrainment in neural oscillations is thought to be involved in beat and meter perception (Large & Snyder, 2009; Nozaradan, Peretz, Missal, & Mouraux, 2011; Nozaradan, Peretz, & Mouraux, 2012) and primes us for voluntary motor entrainment to rhythmic sounds (Iversen, Repp, & Patel, 2009; Patel & Iversen, 2014).

A common paradigm for studying entrainment is to measure simple voluntary movements, such as finger tapping. Although some attempts have been made to study more distributed body movements (Burger, Thompson, Luck, Saarikallio, & Toiviainen,

2012; Janata et al., 2012), like the complex ensembles of dance (Burger, Thompson, Luck, Saarikallio, & Toiviainen, 2014), distributed control of various joints and muscles within and between body segments has been difficult to describe and quantify (Balasubramaniam & Turvey, 2004). In this paper, we look at the control of upright balance and its susceptibility toward entrainment to musical rhythms (Yeh, Boulet, Cluff, & Balasubramaniam, 2010; Yeh, Cluff, & Balasubramaniam, 2014; Riley, Balasubramaniam, & Turvey, 1999; Balasubramaniam & Wing, 2002).

Postural control and entrainment

It is now well known that visual, vestibular, and sensory information are incorporated into balance control processes (Balasubramaniam & Wing, 2002). Postural sway can exhibit frequency coupling with rhythmically oscillating visual displays (Dijkstra, Schöner, Giese, & Gielen, 1994; Dijkstra, Schöner, & Gielen, 1994), and with rhythmically moving contact surfaces (Jeka, Schöner, Dijkstra, Ribeiro, & Lackner, 1997). Sounds have also been shown to influence postural sway, but the role of auditory feedback in balance control processes is less understood. The existing research supports the idea that balance control can incorporate auditory information (Ross & Balasubramaniam, 2015; Dozza, Horak, & Chiari, 2007; Hegeman, Honegger, Kupper, & Allum, 2005; Tanaka, Kojima, Takeda, Ino, & Ifukube, 2001). However, there is no consensus on which types of sounds reduce sway (Ross & Balasubramaniam, 2015; Dozza et al., 2007; Hegeman et al., 2005; Tanaka et al., 2001) and which increase sway (Agaeva, Altman, Kirillova, 2006; Soames & Raper, 1992). However, it is clear that balance control mechanisms can use auditory information including multisensory compensation and a dynamically changing sensory strategy (Dozza et al., 2007; Forti, Filipponi, Di Bernardino, Barozzi, & Cesarani, 2010). We seek to test whether rhythmic sounds, such as music, can lead to entrainment in sway timing and patterns.

The most common measure of postural control is the center of pressure (CoP). CoP consists of anterior-posterior and medial-lateral coordinates of the location on the standing surface of the force vector. This singular point reflects the sum of all forces and can reveal changes in balance processes (Balasubramaniam & Wing, 2002). One complication with using postural sway to study entrainment is that CoP is the outcome of complex balance processes and is non-stationary, so assessing entrainment requires tapping into multiple dimensions of entrainment like phase locking, frequency matching, and other aspects of sway patterns. Entrainment can occur with shorter timescale features of the music, such as beat and meter, which is reflected in tight phase or frequency locking. For the purposes of this study, we will refer to shorter timescales of entrainment as “local”. Entrainment can also occur with longer timescale features of the music, such as changes in periodicity and variability in rhythmic patterning, which means that larger scale features of sway match or vary with changes in larger scale features in a stimulus. For the purposes of this study, we will refer to larger timescales of entrainment as “global”.

Musical groove and sensorimotor coupling

Groove describes how some music more than others makes us want to move, and has been shown to feel enjoyable and improve entrainment in the listener. Groove in

music has been used to investigate sensorimotor entrainment (Hurley, Martens, & Janata, 2014; Janata et al., 2012; Stupacher, Hove, Novembre, Schütz-Bosbach, & Keller, 2013). Groove spontaneously induces a sense of wanting to move and is consistently perceived and rated by musician and nonmusician listeners, regardless of musical style (Madison, 2006; Madison, Gouyon, Ullén, & Hörnström, 2011; Janata et al., 2012; Witek, Clarke, Wallentin, Kringelbach, & Vuust, 2014). Increasing groove, as determined perceptually, has been shown to lead to increases in spontaneous body movement (Janata et al., 2012), but has not previously been used to study entrainment in postural sway. Music has both local rhythmic and global multiscale features that can be entrained to, which makes it a viable candidate for studying entrainment in postural sway.

In the present experiment, postural sway of participants was recorded during exposure to high and low groove music, as defined by Janata et al. (2012). Because groove in music can induce spontaneous entrainment, and because postural sway is sensitive to auditory information, musical groove should influence spontaneous entrainment in postural sway. Increased corticospinal excitability following rhythmic regularity in musical groove (Stupacher et al., 2013) should contribute to regularity in intermittent muscular activity in the distributed control of balance. We hypothesized that groove in music would induce regularity in postural sway, and that the level of groove (high vs. low) would influence the rhythmic nature of postural sway to varying degrees. More specifically, it was proposed that high groove music would have a stronger effect than low groove music on spontaneous rhythmic regularity in postural sway following the rhythmic properties of the music. We expected that this increase in rhythmic regularity of sway would be reflected in reduced overall sway variability and tighter local and global entrainment. In addition, we expected nonmusicians to be more susceptible than musicians to changes in postural sway with auditory information because nonmusicians have greater groove-induced corticospinal excitability (Stupacher et al., 2013).

Methods

Participants

Forty healthy participants (25 women, 15 men) of similar age (22.25 ± 4.00 yrs.), height (65.68 ± 4.21 in.), and weight (156.30 ± 39.95 lbs.) were recruited from the University of California, Merced undergraduate and graduate student populations. Exclusionary criteria were hearing loss, neurological disorder, arthritis, orthopedic conditions, recent injury, and/or balance disorders at the time of testing. 20 participants had 3 or more years of musical training and/or experience and were considered musicians for this study. The other 20 participants had fewer than 3 years of musical training or experience and were considered nonmusicians. This protocol was approved by the Institutional Review Board and participants gave informed written consent prior to the experiment.

Stimuli

Six musical stimuli were selected from a collection of songs ranked for level of groove (Janata et al., 2012): three high groove musical clips and three low groove musical clips (matched for vocals, meter, and tempo; cf. Stupacher et al., 2013). See Table 4.1 for details about the musical stimuli. The 30 s free samples available on the

iTunes website were used. These stimuli were normalized to control for maximum amplitude using custom MATLAB scripts. Stimuli were analyzed using an auditory salience model that is based on how humans process onsets and offsets of sounds (Coath, et al., 2007; Coath, et al., 2009; Denham, 2008). According to the auditory salience model, the high groove stimuli had greater salient event density ($M=.097$ salient events per second, $SD=.003$) relative to the low groove stimuli ($M=.068$, $SD=.011$); $t(2) = -4.546$, $p = .034$. Event density has previously been linked with perception of groove (Madison et al., 2011), supporting that the stimuli selected for this study are perceived as having differing levels of groove. Stimuli were also analyzed for audio features using the MIRToolbox (Lartillot & Toivainen, 2007). High groove stimuli had greater event density ($M=3.945$, $SD=1.025$) than low groove stimuli ($M=1.553$, $SD=.508$); $t(2.926)=-3.622$, $p=.038$, greater RMS energy ($M=.290$, $SD=.015$) than low groove stimuli ($M=.247$, $SD=.017$); $t(3.979)=-3.330$, $p=.029$, greater spectral flux ($M=107.807$, $SD=14.542$) than low groove stimuli ($M=65.967$, $SD=8.264$); $t(3.170)=-4.333$, $p=.020$, and nominally greater spectral flux in the lowest frequencies (0-800 Hz) ($M=32.888$, $SD=2.089$) than in the low groove stimuli ($M=21.494$, $SD=6.073$); $t(2.467)=-3.073$, $p=.070$.

Table 4.1. Musical stimuli. Information taken from the groove library compiled and rated by Janata et al. (2012).

	<u>Artist</u>	<u>Groove Category</u>	<u>Groove Rating (0-127)</u>	<u>Vocals</u>	<u>Meter</u>	<u>BPM</u>
Superstition ⁺	Stevie Wonder	High	108.7	Male	4/4	101
Look-Ka Py Py [#]	The Meters	High	92.5	None	4/4	87
Bad Tune ^{\$}	Earth, Wind & Fire	High	86.2	None	4/4	118
Beauty of the Sea ⁺	The Gabe Dixon Band	Low	32.1	Male	4/4	113
Ray Dawn Balloon [#]	Trey Anastasio	Low	38.5	None	4/4	80
Bryter Layter ^{\$}	Nick Drake	Low	40.4	None	4/4	119

Note. Each high groove clip was matched with a low groove clip for similar vocals, meter, and tempo (beats per minute, BPM), following the example of Stupacher et al. (2013), and these matched pairs are indicated by superscript symbols.

Procedure

Participants were presented with the 6 musical clips (3 low groove and 3 high groove) three times each and three trials of silence, for a total of 21 trials each lasting 30 s. These trials were randomized for each participant and presented using noise minimizing headphones. The volume was adjusted to be loud but not uncomfortable, as determined by each participant. For each trial, the start of the stimulus and the initiation of the force platform recording were simultaneous and controlled by an external trigger.

Participants were asked to wear noise-minimizing headphones and to stand still on a force platform facing away from the experimenters. They were also asked to keep their eyes on a black crosshair stimulus posted on the wall 229.00 cm in front of them at approximately eye level. Headphone volume was adjusted for participant comfort. Participants were given an opportunity for a break halfway through the experiment (after approximately 15 minutes). Stimuli were presented through headphones as CoP was sampled by the AMTI Force and Motion platform (Optima BP400600-2000) at 1000 Hz.

Analyses

Sway variability

Radial sway is a measure that can be used to examine multidirectional variability in postural sway, and is often used to assess CoP maintenance (Lafond, Corriveau, Hébert, & Prince, 2004a; Lafond, Corriveau, & Prince, 2004b). Radial sway of CoP was calculated for each time step (i) using anterior-posterior (x) and medial-lateral (y) components of sway (Lafond et al. 2004a; Lafond et al. 2004b) following

$$r_i = \sqrt{x_i^2 + y_i^2}.$$

In previous work, we found that it takes a few seconds for an auditory stimulus to influence postural sway, so we removed four seconds from the beginning of each trial (Ross & Balasubramaniam, 2015) before calculating an average radial sway for each trial. Average radial sway variability was compared between condition and group. It should be mentioned that although variability in unperturbed standing might indicate less stability, variability in sway does not necessarily indicate less balance control or less stability (Riley & Turvey, 2002; Balasubramaniam, Riley, & Turvey, 2000). Variability in postural sway may be needed to ensure adaptability, and therefore control (Balasubramaniam et al., 2000; Balasubramaniam & Torre, 2012). We used radial sway as a measure of variability, which can but does not necessarily measure stability in standing balance.

Local entrainment

Three measures were used to assess local entrainment: Cross-correlation analysis, spectral coherence, and the normalized pairwise variability index (nPVI). Entrainment between postural sway and beat and/or meter in the stimuli was analyzed using cross-correlation analysis and spectral coherence analysis. Entrainment between the sequential contrasts of postural sway and musical stimuli was analyzed using the nPVI.

Cross-correlation analysis was used to assess whether there was a relationship between events in radial sway and events in the stimuli, and to compare across condition and group. We discretized the radial sway and stimuli in order to have time series of events that were comparable. Radial sway was discretized using a distance from mean CoP threshold of 1.5 mm, with an event indicating this threshold was crossed. The stimuli were discretized using event detection (mironsets function of the MIRToolbox, Lartillot & Toiviainen, 2007). See Figure 4.2 for an example of the stimulus time series extraction method. Cross correlations at lag zero between the stimuli and postural sway traces were calculated and correlation coefficients were transformed to z scores using the

Fisher r-to-z transform. Cross correlations at multiple lags were calculated (± 500 ms), but because there was no lead or lag, lag zero coefficients were chosen for the analysis.

Entrainment between stimuli and sway was examined using spectral coherence. To isolate components of the stimuli with which entrainment was expected to occur we extracted the temporal envelopes using a Hilbert function, as implemented by the MIRTtoolbox (Lartillot & Toiviainen, 2007). The resulting time-varying amplitude waveforms and the radial sway were passed through a Butterworth low-pass filter with a cut-off frequency of 10 Hz to isolate rhythm-related signal. The filtered amplitude waveforms and filtered radial sway were then transformed into the frequency domain using a discrete Fourier transform. See Figure 4.3 for one trial's amplitude envelope spectrum plotted against the radial sway spectrum and Figure 4.4 for amplitude envelope spectra plotted against the radial sway spectra of all trial types for all subjects. Musical beats and meter were identified by a human listener for each stimulus, and beat and meter frequencies are included in Figures 4.3 and 4.4. The stimuli amplitude envelope spectra and radial sway spectra were then compared using magnitude squared coherence. Coherence estimates were transformed to z scores using the Fisher r-to-z transform.

The normalized pairwise variability index (nPVI) measures the average degree of surface contrast (or variability) between two successive inter-event interval durations in a time series of discretized events, and can therefore be considered a measure of local variability. The nPVI first computes the absolute difference between two successive inter-event interval durations and is then normalized by the mean duration of the pair. All normalized values are averaged and multiplied by 100, which yields the nPVI estimate. Time series with higher (e.g., closer to 100) nPVI estimates are interpreted as having larger durational contrasts between successive inter-event intervals, relative to lower nPVI estimates. The nPVI has typically been used to study speech and musical rhythm (Grabe & Low, 2002; Low, Grabe, & Nolan, 2000; Patel & Daniele, 2003; Ramus, 2002), but can be applied to any time series. For each trial, we created an nPVI matching score, $nPVI_{\text{difference}}$, which is the absolute difference between an nPVI estimate for postural sway and an nPVI estimate for the auditory stimuli. A smaller $nPVI_{\text{difference}}$ value indicates more matching between postural sway and the auditory stimuli. We used the $nPVI_{\text{difference}}$ for each trial to test for differences across condition and group.

Global entrainment

Two measures were used to assess global entrainment of postural sway to properties of the stimuli: normalized multiscale coefficient of variation (nMSCV), and a resonator model that extracts periodicity profiles. The nMSCV measures the distance between local coefficient of variation estimates at particular timescales and the overall coefficient of variation across all time samples. The average coefficient of variation was computed for increasing time scales starting at bin size=2, and increased in multiples of two up to bin size=128 (i.e. 7 bin sizes: 2 (40 msec), 4 (80 msec), 8 (160 msec), 16 (320 msec), 32 (640 msec), 64 (1280 msec), and 128 (2560 msec)). For each timescale, coefficient of variation was estimated across a sliding non-overlapping window from the start to the end of each time series. For each trial, the average coefficient of variation values at each bin size were summed, normalized by the overall coefficient of variation, and then divided by the total number of bins (i.e., 7 bins; 2, 4, 8, 16, 32, 64, 128). Figure

4.5 is an example of an MSCV profile, which is used to compute the nMSCV estimates. The nMSCV is not bounded by a specific range but generally spans from 0.0 to 1.0, where higher nMSCV estimates indicate that the coefficient of variation at small bin sizes (e.g., bin size=2) are approximating the overall coefficient of variation, whereas smaller nMSCV estimates indicate that the coefficient of variation across increasing bin sizes increases slower toward the overall coefficient of variation. A random time series will have an nMSCV value of 1.0, which indicates that there is little heterogeneity of variability across various temporal scales. Smaller nMSCV values suggest more heterogeneity of variability across temporal scales and are interpreted as having more multiscale structure. The nMSCV is a novel analysis of the multiscale structure of a time series. Similar to assessing matching for the nPVI estimates, for matching of nMSCV estimates, we created a matching score, $nMSCV_{\text{difference}}$, which is the absolute difference between an nMSCV estimate for postural sway and an nMSCV estimate for the auditory stimulus in a particular trial.

The resonator model generates a periodicity spectrum and a mean periodicity profile (MPP), which is an average amplitude spectrum of periodicities over time (Tomic & Janata, 2008). MPPs can be generated for musical stimuli and movement data and have been used to measure entrainment to multiple periods between music and movement (Janata et al., 2012; Hurley et al., 2014). We consider this a global measure of entrainment because it abstracts the peak periodicities from the frequency spectrum and averages those peak periodicities over the duration of the time series (in contrast with spectral coherence, which includes all frequencies within the specified frequency range, and does not involve averaging over time). Cross-correlations were transformed to z scores using the Fisher r -to- z transform. We compared z -transformed cross-correlations between stimulus MPPs and sway MPPs to quantify multi-period matching between stimuli and postural sway.

Results

Sway variability

Radial sway was reduced with increasing levels of groove: radial sway was greatest in the silent condition and least in the high groove condition (musicians/silence $M=4.32$, $SE=.49$, musicians/low groove $M=3.69$, $SE=.32$, musicians/high groove $M=2.97$, $SE=.17$, nonmusicians/silence $M=4.61$, $SE=.48$, nonmusicians/low groove $M=3.83$, $SE=.16$, nonmusicians/high groove $M=3.15$, $SE=.10$), as shown in Figure 4.1A. Radial sway was compared using a 3 condition (silence, low groove, high groove) \times 2 group (musicians, nonmusicians) analysis of variance (ANOVA) with repeated measures. We found a main effect of condition ($F(2,19) = 9.315$, $p < .001$), with no significant group effect ($F(1,19) = .608$, $p = .445$) and no significant condition \times group interaction ($F(2,19) = .030$, $p = .970$). Pairwise tests using the Bonferroni adjustment for multiple comparisons revealed a decrease in radial sway between silence and high groove conditions ($p = .007$) and between low groove and high groove conditions ($p = .003$). Radial sway of the individual stimuli did not vary as a function of groove rating, as shown in Figure 4.1B (musicians/Beauty of the Sea $M=3.23$, $SE=.25$, musicians/Ray Dawn Balloon $M=3.75$, $SE=.40$, musicians/Bryter Layter $M=4.09$, $SE=.53$, musicians/Bad Tune $M=2.77$, $SE=.20$, musicians/Look-Ka Py Py $M=3.20$, $SE=.26$,

musicians/Superstition $M=2.92$, $SE=.24$, nonmusicians/Beauty of the Sea $M=3.42$, $SE=.25$, nonmusicians/Ray Dawn Balloon $M=3.56$, $SE=.22$, nonmusicians/Bryter Layter $M=4.50$, $SE=.44$, nonmusicians/Bad Tune $M=2.92$, $SE=.20$, nonmusicians/Look-Ka Py $M=3.28$, $SE=.19$, nonmusicians/Superstition $M=3.24$, $SE=.19$).

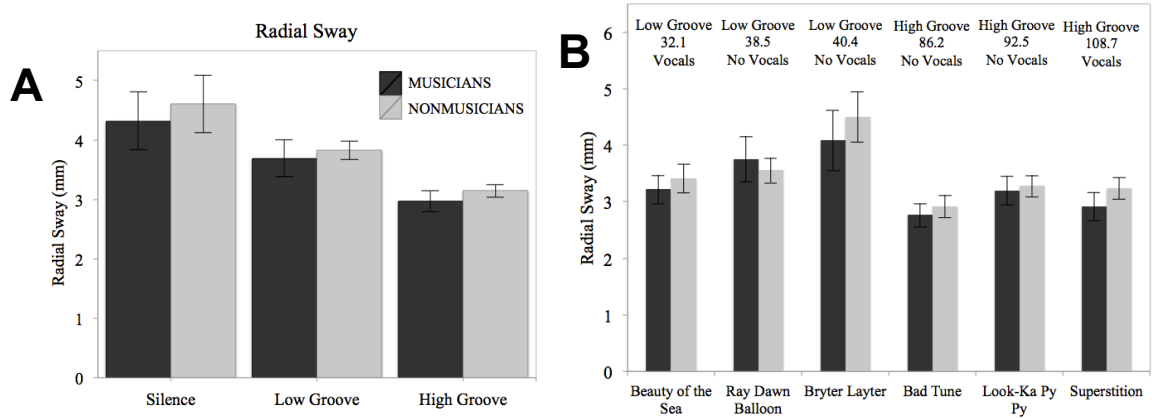


Figure 4.1. (A) Radial sway variability of CoP by condition. Error bars represent ± 1 standard error from the mean. (B) Radial sway variability of CoP by stimulus, in order of ascending groove rating. Groove category, groove ratings (Janata et al., 2012), and information about vocals are included for each stimulus. Error bars represent ± 1 standard error from the mean.

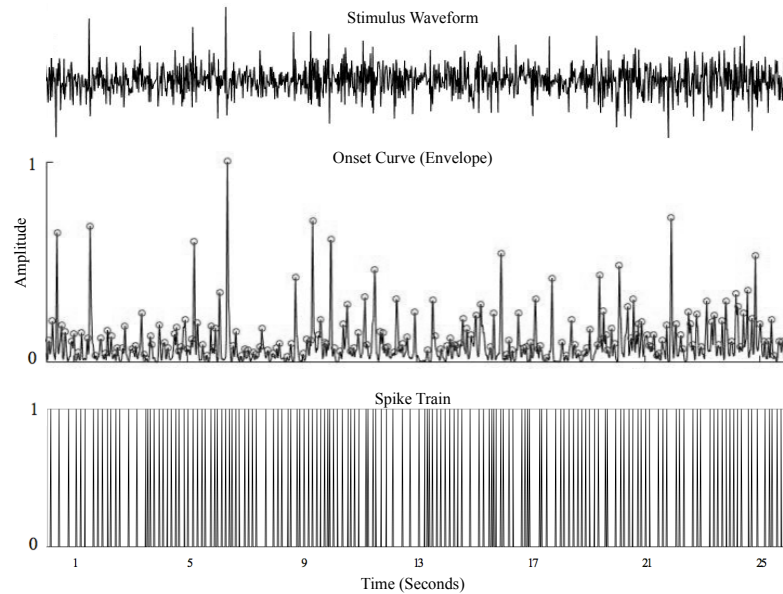


Figure 4.2. Event detection for Superstition (by Stevie Wonder). Musical events were extracted from the stimuli using the onset detection algorithm in the MIRToolbox (Lartillot & Toiviainen, 2007), which detects successive bursts of energy in a waveform and determines peaks in the resulting onset detection curve. Times of onset peaks were used to make discretized spike trains of the event series of each stimulus.

Local entrainment

Discretized radial sway had a stronger correlation to musical events of the stimuli in the high groove condition than in the low groove condition, as shown in Figure 4.3A. Correlation coefficient z scores (musicians/low groove $M=.22$, $SE=.006$, musicians/high groove $M=.27$, $SE=.008$, nonmusicians/low groove $M=.22$, $SE=.003$, nonmusicians/high groove $M=.27$, $SE=.005$) were compared using a 2 condition (low groove, high groove) \times 2 group (musicians, non-musicians) ANOVA with repeated measures. We found a main effect of condition ($F(1,19) = 131.576$, $p < .001$), with no significant group effect ($F(1,19) = .610$, $p = .444$) and no significant condition \times group interaction ($F(1,19) = .044$, $p = .835$).

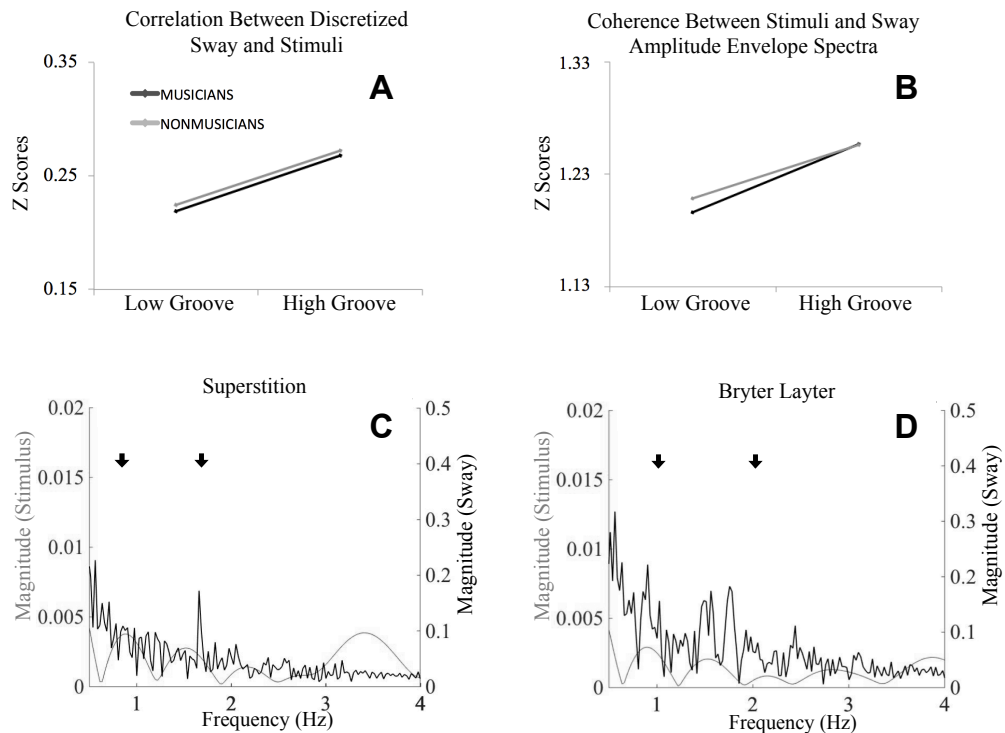


Figure 4.3. Evidence of local entrainment in postural sway at beat and meter frequencies of the musical stimuli. (A) Correlation coefficients (z transformed r scores) of the discretized sway and stimuli. (B) Spectral coherence (z transformed r scores) between amplitude envelope spectra of the stimuli and radial sway. A low-pass Butterworth filter (< 10 Hz) was used to isolate rhythm-related signal. (C) One high groove trial, with stimulus Superstition. The Superstition spectrum is plotted against the radial sway spectrum from that trial. Arrows indicate the beat and meter frequencies of Superstition, as determined from human listener judgments of the location of the beat. (D) One low groove trial, with stimulus Bryter Layter. The Bryter Layter spectrum is plotted against the radial sway spectrum from that trial. Arrows indicate the beat and meter frequencies of Bryter Layter, as determined from human listener judgments of the location of the beat.

Stimuli amplitude envelope spectra and radial sway spectra exhibit greater magnitude squared coherence in the high groove condition than in the low groove condition. As shown in Figure 4.3C and D and Figure 4.4A and B, this coherence may reflect entrainment to beat or to meter frequencies. Inter-subject variability in sway and entrainment is reflected in individual participants' sway spectra, shown in Figure 4.4. An inspection of Figure 4.4 reveals that individual trials show peaks at beat and meter frequencies. The results of the coherence analysis support individual entrainment in sway to the rhythm-related frequencies in the stimuli. Coherence estimate z scores (musicians/low groove $M=1.20$, $SE=.005$, musicians/high groove $M=1.26$, $SE=.005$, nonmusicians/low groove $M=1.21$, $SE=.005$, nonmusicians/high groove $M=1.26$, $SE=.006$) were compared using a 2 condition (low groove, high groove) \times 2 group (musicians, nonmusicians) ANOVA with repeated measures. We found a main effect of condition ($F(1,19) = 159.164$, $p < .001$), with no significant group effect ($F(1,19) = 0.796$, $p = .384$) and no significant condition \times group interaction ($F(1,19) = 1.750$, $p = .202$).

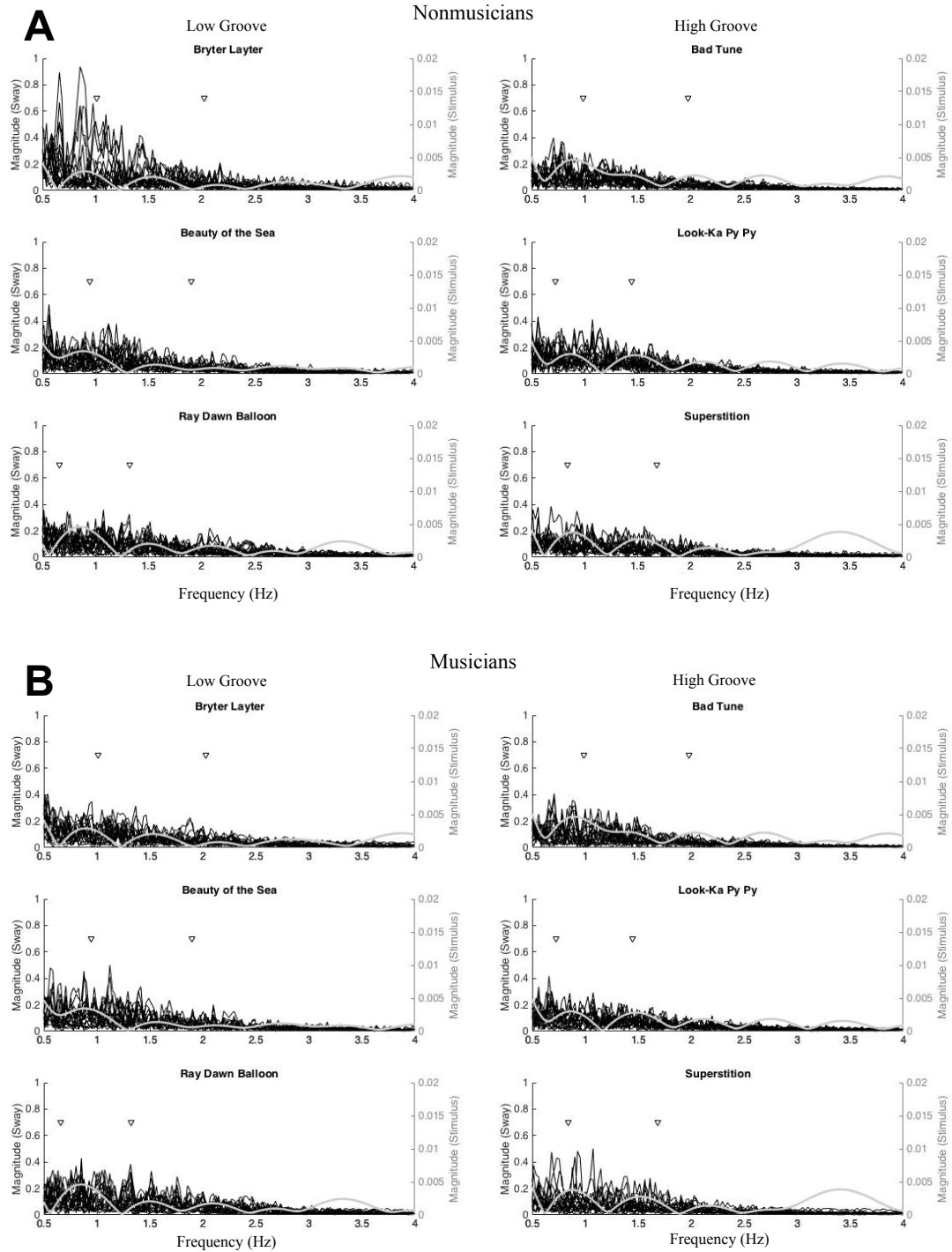


Figure 4.4. Stimuli amplitude envelope spectra plotted against radial sway spectra for nonmusicians (A) and musicians (B). Black lines indicate individual subjects averaged within trial type. Gray lines indicate stimuli amplitude envelope spectra. Arrows indicate the beat and meter frequencies of the stimuli, as determined from human listener judgments of the location of the beat.

The nPVI estimates of postural sway were compared using a 2 condition (low groove, high groove) \times 2 group (musicians, non-musicians) ANOVA with repeated measures. We found that the nPVI estimates for postural sway were smaller for musicians ($M=21.66$, $SE=.90$) relative to nonmusicians ($M=29.14$, $SE=.83$), ($F(1,19) = 5.852$, $p = .026$), suggesting that musicians have less postural sway variability from successive intervals across a trial. No other main effects or the interaction were significant, $ps > .05$ (see Figure 4.6A).

The nPVI_{difference} estimates were compared using a 2 condition (low groove, high groove) \times 2 group (musicians, nonmusicians) ANOVA with repeated measures. A significant main effect of group ($F(1,19) = 6.552$, $p = .019$) suggested there was more matching for the nonmusicians ($M=21.93$, $SE=.68$) relative to the musicians ($M=29.03$, $SE=.72$). A significant main effect of condition ($F(1,19) = 5.595$, $p = .029$) suggested there was more matching for high groove trials ($M=24.82$, $SE=.68$) relative to low groove trials ($M=26.07$, $SE=.77$). The interaction was not significant, $p > .05$ (see Figure 4.6C).

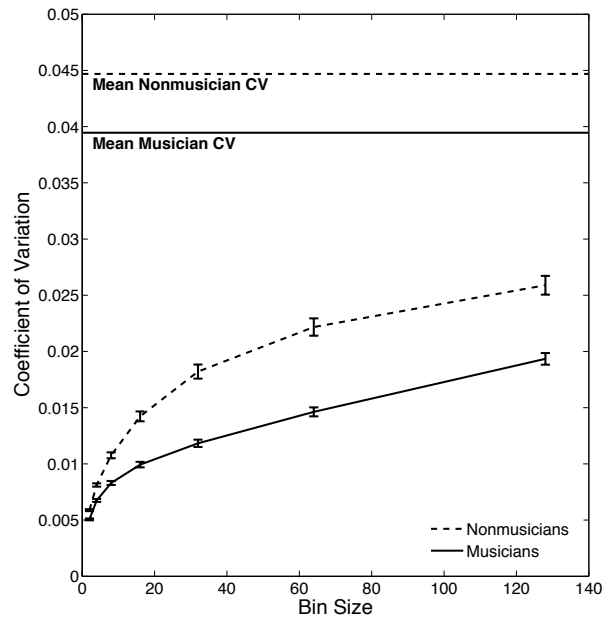


Figure 4.5. Example nMSCV profile. X-axis is the bin size. Y-axis is mean coefficient of variation. Horizontal lines indicate mean coefficient of variation for each time series. Error bars represent ± 1 standard error from the mean. nMSCV is computed by summing the mean CV function, dividing by CV, and normalizing by dividing by number of bins ($n=7$). Note the time scales for the seven bins are 40 msec, 80 msec, 160 msec, 320 msec, 640 msec, 1280 msec, and 2560 msec.

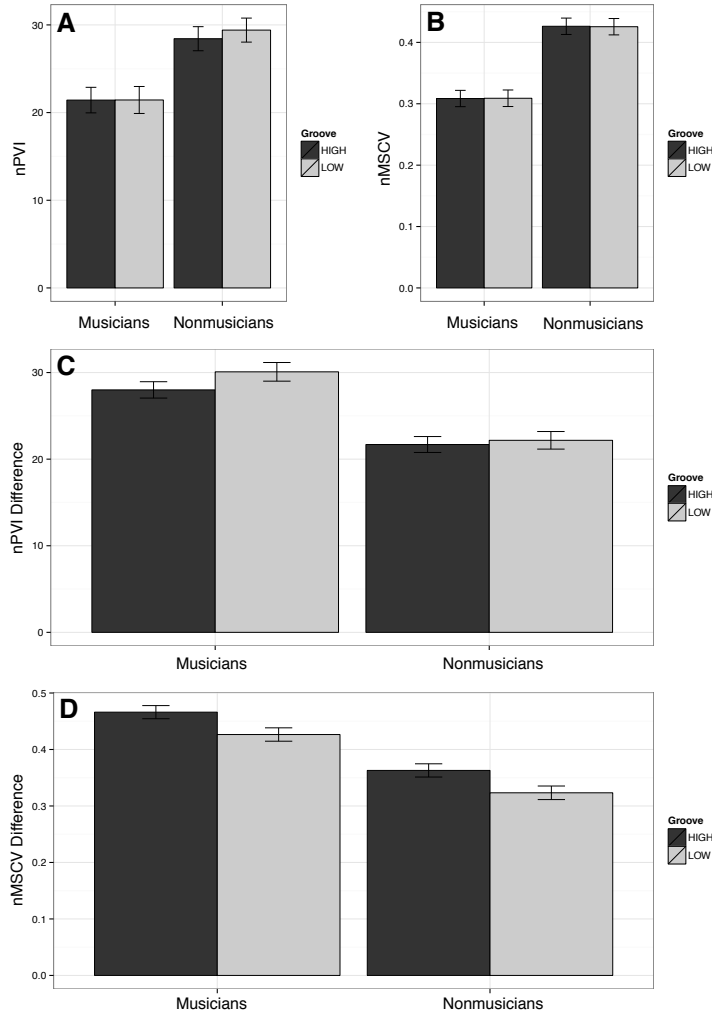


Figure 4.6. Mean postural sway nPVI (A) and nMSCV (B) estimates for group and groove factors. (C) Mean nPVI difference estimates for group and groove factors (Note that smaller estimates correspond to more matching). (D) Mean nMSCV difference estimates for group and groove factors (note that smaller estimates correspond to more matching). Error bars represent ± 1 standard error from the mean.

Global entrainment

The nMSCV estimates were compared using a 2 condition (low groove, high groove) \times 2 group (musicians, nonmusicians) ANOVA with repeated measures. We found that the nMSCV estimates for postural sway were smaller for musicians ($M=.31$, $SE=.009$) relative to nonmusicians ($M=.43$, $SE=.009$), ($F(1,19) = 8.596$, $p = .009$), suggesting that the variability of postural sway of musicians varies across multiple temporal scales of measurement more than for nonmusicians. No other main effects or the interaction were significant ($p > .05$) (see Figure 4.6B).

The nMSCV_{difference} estimates were compared using a 2 condition (low groove, high groove) \times 2 group (musicians, nonmusicians) ANOVA with repeated measures. A

significant main effect of group ($F(1,19) = 8.763, p = .008$) suggested there was more matching for the nonmusicians ($M=.34, SE=.008$) relative to the musicians ($M=.45, SE=.009$). A significant main effect of condition ($F(1,19) = 106.334, p < .001$) suggested there was more matching in the low groove trials ($M=.37, SE=.008$) relative to the high groove trials ($M=.41, SE=.008$). The interaction term was not significant ($p > .05$) (see Figure 4.6D).

Increased global matching in the low groove condition was supported by the periodicity analyzing resonator model. MPP correlation coefficient z scores (musicians/low groove $M=.85, SE=.007$, musicians/high groove $M=.77, SE=.006$, nonmusicians/low groove $M=.89, SE=.02$, nonmusicians/high groove $M=.82, SE=.02$) were compared using a 2 condition (low groove, high groove) \times 2 group (musicians, nonmusicians) ANOVA with repeated measures. We found a main effect of condition with low groove being more correlated with sway than high groove ($F(1,19) = 1799.207, p < .001$), and an effect of group, with nonmusicians' sway being more correlated to stimuli than musicians' sway ($F(1,19) = 5.668, p = .028$). There was no condition \times group interaction ($F(1,19) = 0.100, p = .755$).

Discussion

We observed reduced sway variability while listening to music relative to the silent condition, with high groove music reducing sway more than low groove music (see Figure 4.1). This supports that groove in music can influence neural mechanisms implicated in balance control, and that increasing level of groove has an increasing impact on sway variability. We expected that an increase in rhythmic regularity of sway while listening to music would result in reduced sway variability. The reduction of sway with increasing level of groove supports this hypothesis.

Furthermore, we show a stronger local correlation between musical events and postural sway in the high groove condition when compared with the low groove condition. Spectral coherence analysis supports that this is likely due to involuntary entrainment to the beat and meter frequencies in the music, and that this shorter timescale (local) entrainment is stronger with high groove than with low groove music.

Auditory features of groove

There are numerous factors that could be contributing to perception of and motor response to groove in music, including RMS energy, RMS variability, pulse clarity 'attack', spectral flux, and low frequency spectral flux (Stupacher et al., 2014). This is in line with the results of our stimuli analyses, which revealed differences in RMS, spectral flux, and low frequency spectral flux between the high and low groove music samples. Many of these individual features have been shown to influence body movement (Burger et al., 2012; Van Dyck et al., 2013), and their presence in music could also have an influence on body movement.

Other acoustic features that have been linked with perception of groove are event density (Madison et al., 2011) and structural complexity (Witek et al., 2014). We have verified that our high and low groove stimuli differ in event density and perceptually salient event density. Witek et al. (2014) showed that structural complexity in music is related to enjoyment and desire to move. They reported an inverted U-shaped relationship

between degree of syncopated drum patterns and questionnaire ratings about wanting to move and enjoyment of the music; pleasure and desire to move increased as degree of syncopation increased, until a point when pleasure and desire to move decreased with further increase in degree of syncopation (Witek et al., 2014). There seems to be an ideal level of complexity for maximal enjoyment and “grooviness”.

The question remains of what the element of groove is that influences desire and ability to entrain. Hurley et al. (2014) proposed that musical features that modulate attention contribute to groove rating, enjoyment, and entrainment. This would support that music with more attention modulating features could lead to greater local entrainment in sway. Focusing attention on posture can increase sway variability, and focusing attention on an external motor task can reduce sway variability because of an increased reliance on automatic balance control processes (McNevin & Wulf, 2002). With an increase in groove in the music, there could be an increase in attention on the music. If this is the case, then sway variability might be expected to decrease because of more reliance on automatic balance control processes when attending more to the high groove music than to the low groove music or silence.

In addition, if listening to high groove music is more cognitively demanding than listening to low groove music and silence, then sway variability might also be expected to decrease due to more reliance on automatic balance control processes (Cluff, Gharib, & Balasubramaniam, 2010). Passively listening to music is not a performance-related task, although it is possible that passive beat perception and time keeping during listening might demand attention and other cognitive resources. However, if beat perception requires sufficient attention and other cognitive resources to drive a reduction in sway, then our results would seem to suggest that beat perception while listening to high groove music requires more cognitive resources than beat perception while listening to low groove music.

Postural sway entrainment to groove

Another possible explanation is that reduced sway variability is a side effect of increased regularity in sway due to rhythmic/local entrainment. An increase in correlation between sway and stimuli, an increase in spectral coherence between sway amplitude envelope spectra and stimuli (see Figure 4.3), and similar local variability all provide supporting evidence for local entrainment. Further support can be found by the increase in sway amplitude at the stimuli beat and meter frequencies, also shown in Figure 4.3C and D and Figure 4.4A and B. Increased rhythmic regularity in postural sway following the rhythms in the music can explain the reduced overall sway variability with increasing level of groove.

We show evidence for global entrainment to changes in variability over time and to the complex metric structure of the music, and show that global entrainment is stronger for low groove music than for high groove music. Nonmusicians may be more susceptible to global entrainment than musicians. To our knowledge, there is no previous research on multiscale entrainment of postural sway to music. Previous work has shown that people can entrain to complex musical stimuli (Rankin & Large, 2009) and other auditory stimuli that exhibit long-range correlation properties (Hove et al., 2012; Marmelat et al., 2014; Stephen et al., 2008; Stephen & Dixon, 2012). Although the goal

of the current study was not to assess coordination with fractal auditory stimuli, we did measure the extent to which multiscale variability of postural fluctuations matched corresponding patterns in musical stimuli.

Low groove stimuli had lower salient event density than high groove stimuli and this might relate to more diffuse periodicities in low groove music. If so, this might explain why we observed greater MPP correlation coefficients during low groove trials: low groove music has more periodicities to possibly entrain to, and therefore the postural fluctuations occupied multiple periodic patterns. However, although groovy music has been described as containing multiple nested periodicities (Merker, 2014), it has not been shown that low groove has more periodicities than high groove. We expect that future analyses of groove will examine in more detail the metrical complexities and nested periodicities in music that has low or high groove ratings. Janata, Tomic, and Haberman (2012) found that the number of peaks in stimulus MPPs did not differ as a function of groove, but did observe increased peaks in MPPs when subjects freely tapped to the mid groove and low groove music relative to high groove music. Therefore, it is possible that the effect of global entrainment observed in the current study is not purely stimulus driven and reflects other factors not otherwise accounted for in the current study. The results from the nMSCV difference analyses support this explanation. Although we did not observe differences in postural sway nMSCV estimates as a function of groove, there was more global matching of postural sway with low groove musical stimuli.

Entrainment is possible with beat, meter or other more global aspects of music. As Figure 4.3 shows, the prominent beat frequency does not line up with any one peak in the low groove Bryter Layter spectrum. Instead, there is a cluster of peaks around the beat frequency and a stronger peak at the meter frequency marker. This is because the beat is not emphasized in this particular piece of music, however the meter is emphasized. Thus it is easier and more spontaneous to synchronize with the meter than the beat in this particular stimulus. In addition, the high groove musical clip, Superstition, has a clearly prominent frequency at the beat frequency, but less prominent meter. We chose to use spectral coherence to assess local entrainment because it can reveal information about whether entrainment is occurring and if this entrainment is to beat or meter frequencies.

Entrainment to different properties of musical stimuli, like beat and meter, suggest that the tendencies to entrain to music might be influenced by a collection of properties of music and experience of the listener. From numerous analyses, spanning local and global components of postural sway and musical stimuli, we found an interesting pattern of entrainment: At shorter timescales, people spontaneously entrain to high groove music, and at longer timescales, people spontaneously entrain to low groove music.

It could be that low groove music has a less defined and predictable beat structure relative to high groove music, and because of this, participants spontaneously entrain to different parts of the stimuli throughout each trial. For high groove music, with a more defined and predictable beat structure, participants spontaneously entrain more to these local rhythmic features consistently.

Previous work has shown increased spontaneous body movement while listening to high groove music, and better voluntary entrainment to high groove music when

compared with low groove music (Janata et al., 2012). Further, high groove music can influence corticospinal excitability (Stupacher et al., 2013), and there is some evidence that high groove music can influence involuntary physiological responses measured as heart rate and EEG power in multiple frequency bands (Stewart, unpublished). Our results are evidence that both high and low groove music can lead to changes in automatic balance control behavior that can be explained by local and global entrainment.

Musical Experience

We found that musical experience influenced the amount of postural variability and entrainment at local timescales. Our data support that musical experience decreases the amount of sway variability from successive intervals across a trial, and decreases the degree of nPVI matching. We also found that musical experience influenced the amount of postural variability and entrainment at global timescales. Our data support that musical experience increases the variability of sway across multiple temporal scales, but decreases nMSCV matching. Matching between postural sway periodicity and music periodicity profiles is also influenced by musical experience, with musical experience decreasing correlation between sway and stimulus. As hypothesized, nonmusicians were more susceptible than musicians to changes in postural sway and entrainment with auditory information. This can be explained with increased regularity in distributed intermittent muscular activity in the control of balance due to greater groove-induced corticospinal excitability in nonmusicians (Stupacher et al., 2013) following rhythmic regularity in musical groove.

Future directions

Now that it has been shown that groove induces both shorter and longer timescales of entrainment in postural sway, there are numerous directions that could be explored. Postural sway variability should be measured during overt modulation of attention using non-rhythmic auditory stimuli. Although we provide support that groove can lead to entrainment in sway, it is still unknown whether auditory attention-modulating stimuli can also influence sway variability.

Shorter and longer timescales of entrainment to high and low groove music could also be explored in other types of motor behaviors, such as walking and speech. The role of entrainment to auditory stimuli, such as music, could be explored in the context of motor learning and rehabilitation. Auditory environments influence movements in predictable and potentially useful ways, and groove can be used to investigate this auditory-motor interaction, even in seemingly automatic balance control processes.

Chapter 5

The EEG Mu Rhythm and Musical Beat Perception

Neural systems supporting body movement are active during music listening, even in the absence of overt movement. Covert motor activity during music processing is not well understood, but some theories propose a role in auditory timing prediction facilitated by internal motor simulation. One unanswered question is how covert motor activity during music listening relates to motor activity during overt movement. We address this question by measuring mu rhythms, 8-12 Hz cortical field phenomena associated with the somatomotor system. Mu rhythms in the scalp electroencephalogram (EEG) appear most noticeably over hand sensorimotor cortex during rest, are suppressed during and just before hand movement, and may be enhanced over hand area during and just before foot movement, possibly reflecting hand movement inhibition during movement of another effector. The behavior of mu activity during music listening without movement has yet to be determined. We recorded 32-channel EEG from eight participants in four conditions: in silence at rest and during movement of the right hand or foot, and during music listening without overt movements. As expected, right hand movement was accompanied by a bilateral decrease in mu compared to silent rest. Right foot movement was accompanied by an increase in mu over left hand somatomotor cortex, replicating previous results. Music listening was accompanied by a similar mu increase over hand somatomotor cortex, but bilaterally. This work is the first to study music-related mu modulation in the absence of overt movement and the first to source-resolve mu during music listening. Our results suggest topographically organized motor inhibition during music listening.

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Introduction

Mu rhythms in the scalp electroencephalogram (EEG) have long been associated with action and are consistently reduced in mean power during and in preparation for body movements, as most commonly studied using hand movements. This power reduction with movement, known as mu event-related desynchronization (ERD), mu suppression, or mu blocking, may arise from a decrease in synchrony of local field potential (LFP) activity in one or more areas of cortex related to cortical action processing (Yuan & He, 2014). The EEG mu rhythm is most dominant in the same 8-12 Hz frequency band as posterior alpha rhythms, but unlike posterior alpha over occipital cortex, mu activity is recorded from scalp electrode sites near sensorimotor areas. Both posterior alpha and sensorimotor mu rhythms have been associated with cortical inhibition, but of different processes (Niedermeyer, 1997); posterior alpha activity in visual cortex is suppressed during covert visual attention (Worden, Foxe, Wang, & Simpson, 2000; Foxe & Snyder, 2011), and visual working memory maintenance (Kappenman & Luck, 2011), while sensorimotor mu activity is associated with active inhibition of body movements (Niedermeyer, 1997).

The brain-computer interface literature on non-muscle mediated communication shows that mu activity is present in the idle awake state as well as during instructed abeyance of action and is suppressed during movements, action imagination and action observation (Yuan & He, 2014). Mu oscillations appear as sharp convex arc-shaped (i.e., suggestively ‘ $\mu\mu\mu$ ’-shaped) periodic waveforms that, when converted to the frequency domain, exhibit a strong fundamental in the alpha range and smaller harmonics in the beta and high-beta range. The alpha-range and first harmonic peaks are modulated in parallel during ERD and during ERS (event-related synchronization) or in a state-related mu power decrease or increase, so a decrease or increase in one band typically also occurs in the other (Yuan & He, 2014).

There is some evidence that mu activity is sensitive to motor system activity not tied to overt movements. Pfurtscheller and Neuper (1994) studied mu activity during motor cortical inhibition. They found that dorsal flexion of the right foot resulted in a transient mu power increase over both left and right sensorimotor hand areas, suggesting that excitation of the foot sensorimotor areas may have been accompanied by inhibition of other sensorimotor areas (e.g., hands in their hand/foot movement paradigm). Importantly, this study shows that rather than simply representing an ‘idling’ (passive resting) state or instructed abeyance of action, willful movement inhibition of an effector may produce enhanced mu rhythms, e.g. in response to instructed movements of other effectors.

An open question is whether mu activity is also sensitive to brain motor system activations that are known to occur during musical rhythm perception. Music listening appears to be tightly bound to the motor system. To move to music is so compelling that it often occurs without intention and appears to reinforce positive affect during music listening (Janata, Tomic, & Haberman, 2012). This music-movement relationship is strong enough to be used for optimizing body movement, as in the case of atypical gait (Sejdić, Fu, Pak, Fairley, & Chau, 2012; Hunt, McGrath, & Stergiou, 2014). Music has measurable impacts on distributed muscle activity, activating our entire motor systems (Ross, Warlaumont, Abney, Rigoli, & Balasubramaniam, 2015). The connection is strong enough that even when we are not overtly moving, motor structures in the brain and corticospinal pathways are in use when we listen to rhythmically patterned sounds such as in music, as shown with functional brain imaging (Grahn & Brett, 2007; Chen, Penhune, & Zatorre, 2008; Bengtsson et al., 2009; Burunat, Tsatsishvili, Brattico, & Toiviainen, 2017), magnetoencephalography (MEG; Iversen, Repp, & Patel, 2009), transcranial magnetic stimulation (TMS; Stupacher, Hove, Novembre, Schütz-Bosbach, & Keller, 2013), and electromyography (EMG; D’Ausilio, Altenmuller, Olivetti Belardinelli, & Lotze, 2006).

Although an intimate music-movement relationship is apparent, it is unknown what role this so easily recruited motor activity has in rhythm perception *per se*. Patel and Iversen, in their Action Simulation for Auditory Prediction (ASAP) hypothesis, suggest that internal motor simulation has a necessary role in the predictive aspect of auditory rhythm perception (Patel & Iversen, 2014; Iversen, Repp, & Patel, 2009; see Ross, Iversen, & Balasubramaniam, 2016 for a review on this topic). However, this debate is missing some foundational knowledge about how covert motor activity during music listening relates to motor activity during overt movement. Understanding the relationship

between covert music-induced motor system activity and motor system activity tied to overt movement is needed to better define internal motor simulation in this context. Because mu rhythms can be used to address questions of motor activity and inhibition without overt movement, they can be used to examine covert motor processes including those that occur during music listening.

The relevance of mu activity to action and action planning is backed by an extensive literature, but previous examinations of mu activity during music listening are scarce. Li *et al.* (2011) reported mu suppression during music listening, but the sound stimuli they used were produced by people playing a game that made noise when the player performed certain key presses. Though these stimuli might have sounded musical to some extent, they were not musical compositions with predictable rhythms and beat structure, and were in any case confounded by motor actions. The stimuli were presented to subjects who had played the game previously and therefore had associations between the sounds and the movements that would have produced the sounds. Although Li *et al.*'s results cannot be extended to understanding mu during musical rhythm perception, their study shows that motor imagery induced by sounds can be associated with changes in mu power (Li, Hong, Gao, Wang, & Gao, 2011). Mercadié, Caballe, Aucouturier, and Bigand (2014), and a presentation by Wu, Lim, Hamm, & Kirk (2012), reported mu suppression during music listening, but whether or not the subjects were asked to sit still while listening was not stated.

Much of the work on mu during movement has used a hand or finger as the movement effector. It is not yet agreed whether mu activity in these experiments originates specifically in hand sensorimotor areas, or if the cortical mu source area is less focal (Srinivasan, Winter, & Nunez, 2006). Although the results described in Pfurtscheller and Neuper (1994) may be interpreted to imply that the sources of mu activity have a topographical organization in accord with the well-known somatomotor homunculus, this topographical organization of mu source activity has otherwise been incidentally assumed because sensorimotor cortical activity is generally topographically organized in both primary motor and facing somatosensory cortices. However, some more recent fMRI evidence supports this topographical organization of mu source activity (Yuan & He, 2014).

Here, in the first source-resolved mu examination during music listening, we use mean mu rhythm power changes to study movement planning and simulation, both of overt movements of different effectors and during music listening without overt movements. In the experiment reported here, we observed mu activity during movement of the right hand or right foot, and during sitting still without moving in silence and during music listening. We hypothesized that mu activity would be relatively strong during quiet sitting, and weakest during hand movements. We expected to replicate the findings of Pfurtscheller and Neuper (1994) of mu power increase during foot movements. We also expected to observe modulation of mu activity during music listening because of its concomitant motor system activation but were unsure whether to expect an increase or decrease in mu power based on the limited existing reports on mu rhythms during music listening.

Based on existing evidence (Yuan & He, 2014; Pfurtscheller & Neuper, 1994), we did expect that mu power modulations would be bilateral. However, our predictions for

right hemisphere mu activity ipsilateral to the right hand and foot movements were less confident since those movements might decrease mu activity in (left) somatomotor cortex controlling right hand movements and not in the ipsilateral (right) hemisphere.

To our knowledge, this is the first study to examine mu activity systematically during musical listening as well as during motor action and silent inaction.

Methods

Participants

Eight healthy adults (6F, 2M) between the ages of 20 and 26 (mean age = 23.625 \pm 2.62 years) were recruited from the University of California, Merced student population. All subjects were right-hand dominant. Four subjects had three or more years of musical training or experience and four subjects had none. All subjects were screened for hearing impairment, amusia, neurological or movement conditions and recent injury to arms or legs. The experimental protocol was carried out in accordance with the Declaration of Helsinki and all participants gave informed consent prior to testing.

Experimental protocol

Participants were asked to remain seated without moving while maintaining eyes-open fixation on a cross in front of them during the experimental trials. The experiment was controlled using Paradigm software (ver. 2.5.0.68). There were four conditions, each comprised of 36 ten-second long trials. In the silent condition, subjects were instructed to sit motionless in silence. In the finger-tapping condition, subjects were instructed to tap freely at an approximate rate of two taps per second with the index finger of their right hand. In the foot-tapping condition, subjects were instructed to tap freely, also at an approximate rate of two taps per second, with their right foot. In the music listening condition, subjects were instructed to listen to clips of music while sitting motionless.

Musical stimuli were created from the twelve instrumental musical excerpts used in the Beat Alignment Test, Version 2 (Iversen & Patel, 2008). Musical excerpts were presented without an overlying metronome beep (in contrast to their use in the BAT). These excerpts were taken from several genres (jazz, rock, orchestral), were each 11 seconds in length with an amplitude ramp up at the beginning of the stimulus and an amplitude ramp down at the end of the stimulus (up and down ramps were both over a 500 ms length of time), digitized at 44.1 kHz (mono). The musical excerpts were normalized to the mean, minimum and maximum volume.

EEG was collected during all trials using an ANT Neuro Waveguard 32-channel 10-20 EEG system with sintered Ag/AgCl electrodes, an Asalab amplifier and Asalab software. Data were sampled at 1024 Hz. At the beginning of each trial, an event was sent from Paradigm to Asalab to mark the start of a new trial in the EEG recording. Tap times were not recorded. Segments of EEG were extracted for each trial, starting at the recorded trial onset and lasting 10 seconds. This protocol was reviewed and approved by the UC Merced Institutional Review Board.

Analyses

All EEG preprocessing and analyses were performed in MATLAB using the EEGLAB toolbox (Delorme & Makeig, 2004), following “Makoto’s Preprocessing

Pipeline” (https://sccn.ucsd.edu/wiki/Makoto's_preprocessing_pipeline). EEG data were down sampled to 256 Hz, then 1-Hz high-pass and 50-Hz low-pass filters were applied (basic FIR; Winkler, Debener, Muller, & Tangermann, 2015). Minimal data cleaning (*pop_cleanline*), channel rejection and noise removal (*clean_rawdata*) were applied. Data were re-referenced to the sample-by-sample all-channels average. Data were epoched (from trial onset to 10 seconds) and aberrant epochs were rejected based on conservative guidelines (Delorme, Terrence, & Makeig, 2007), by applying an amplitude threshold of $\pm 500 \mu\text{v}$. Additionally, we applied a data improbability test. This method of excluding artifacts computes the statistical probability of observing a value in the observed distribution, and we used a 6 standard-deviation threshold for single-channel and a 2 standard-deviation data rejection threshold for all-channels activity level, as recommended by Delorme, Terrence, and Makeig (2007).

Extended infomax independent component analysis (ICA) decomposition was performed separately on each subject’s preprocessed data after applying principal component analysis (PCA) to reduce the data dimension by 1, as necessary for ICA decomposition following average referencing. Single (or rarely, dual-symmetric) equivalent dipole model fitting (using *dipfit2*) was performed for brain-based independent component (IC) processes (defined as ICs having a brain-centered equivalent dipole model with scalp map residual variance, after regressing out the dipole model scalp projection, below 15%). Dipole fitting used a head model based on a standard MNI MR head image. Thereafter, across-subjects IC cluster analysis was performed (as described in more detail below) based on similarities in component dipole locations and activity patterns.

ICA decomposition is a data-driven signal analysis technique for blind source separation (Bell & Sejnowski, 1995). ICA separates a signal into maximally temporally independent components (ICs) and can be used to interpret scalp EEG recorded during experimental tasks as the sum of localizable brain processes (Burunat, Tsatsishvili, Brattico, & Toiviainen, 2017; Makeig, Bell, Jung, & Sejnowski, 1996; Makeig et al., 2002, Makeig et al., 2004b). Scalp data accounted for by any IC can be back-projected into the electrode montage by multiplying the IC activation time course by the IC scalp map representing the topographic distribution of its projection to the scalp channels (Makeig, Jung, Bell, Ghahremani, & Sejnowski, 1997, Makeig, Debener, Onton, & Delorme, 2004a). In the current study, the locations of the equivalent dipole models for the brain-based ICs, as well as their spectra and other signal properties, were used to determine which ICs were mu-related (Pfurtscheller & McFarland, 2012). This allowed analysis of mu-related maximally-independent EEG signal sources in individual subjects for the four conditions.

Visual inspection of the raw data revealed that mu activity was clearly present in every subject. We studied the IC topographic (scalp) maps and frequency profiles to determine which were mu-related, using criteria set out in Pfurtscheller & McFarland (2012). We looked for a bilateral projection, typically with opposite signs dominating, and stronger to central than to occipital scalp. Further, mu IC source activity spectra should have near-harmonically related peaks in the alpha and beta bands. All the mu-related ICs’ equivalent dipoles were compatible with the source being generated in or

near primary somatomotor areas (Arroyo, Lesser, Gordon, Uematsu, Jackson, & Webber, 1993).

To compare spectral power in mu across conditions and subjects, a k-means IC clustering method was used (Onton & Makeig, 2006). IC clustering is needed to group ICs from different data sets that are most likely generated in the same cortical area and also have similar activity (spectral, time/frequency, and/or ERP) parameters. K-means clustering groups ICs based on a distance measure built from the selected spatial and activity measures. We then calculated cluster centroids, points in the template head model that minimize the total clustering distance from the respective cluster centroids to the cluster ICs (Onton & Makeig, 2006). Cluster-mean scalp maps and activity spectra were used to define which clusters were mu-related using the same criteria as for individual ICs. Visual inspection confirmed that all the individual ICs in each mu-related cluster appeared mu-like.

A one-way repeated measures ANOVA was used to compare mean power in the (8-12 Hz) mu range between the four conditions in each mu-related cluster (Pfurtscheller & Neuper, 1994; Pfurtscheller & McFarland, 2012). Another one-way repeated measures ANOVA was used to compare mean power in the (16-24 Hz) beta band range including the first mu harmonic across the four conditions for each mu-related cluster (Pfurtscheller & Neuper, 1994; Pfurtscheller & McFarland, 2012). These ANOVAs were followed by pairwise comparisons to assess how source-resolved mu activity differed between the four conditions. Degrees of freedom were adjusted using the conservative Greenhouse-Geisser correction for violation of the sphericity assumption (Mauchly's, $p < .001$).

Results

Two clusters met the topographic and spectral criteria and were thereby determined to account for mu-related brain activity. One cluster centroid was localized by equivalent dipole analysis to the left hemisphere (see Figure 5.1 below) and the other to the right hemisphere (Figure 5.2).

Left hemisphere cluster

The left hemisphere IC cluster was a group of twelve ICs that included one or two ICs from all eight subjects. The centroid was at Talairach coordinate (-59, 5, 31). Using MRIcon (v2.1.38-0), we determined this to be in or near left premotor cortex, with centroid just anterior to primary motor cortex in Brodmann area 6. See Figure 5.1 for the cluster component and centroid equivalent dipoles, mean and individual IC scalp maps, and cluster centroid mean spectra in the four conditions. In each condition, the cluster activity spectrum exhibited both sharper mu and broader beta band peaks that included the first harmonic of the mu rhythm maximum.

The left mu cluster exhibited 8-12 Hz mu band spectral power differences between conditions $F(1.693, 59.258) = 67.487, p < .001$ (Figure 5.1C and 5.3A). There were also differences in 16-24 Hz beta band spectral power between conditions $F(2.596, 184.350) = 644.823, p < .001$ (Mauchly's, $p = .004$; Figure 5.1C and 5.3B).

Pairwise comparisons revealed the following: During right hand finger tapping, mean beta band power was lower than in the resting condition ($p < .001$), consistent with this cluster being localized in or near the (right hand-area) left motor cortex. During right

foot tapping, mean peak power was larger than in the resting condition in both mu ($p < .001$) and beta ranges ($p < .001$). These results are consistent with the ERS during foot tapping and topographical organization of mu sources in cortex found by Pfurtscheller and Neuper (1994). While we might have expected to find mu activity and condition mu activity sources compatible with sources in midline foot-related somatomotor cortex, we did not find such foot-related mu activity sources there.

Music listening while sitting motionless produced mu-source spectra that looked similar to right foot tapping, with a power increase (ERS) in both hand area mu clusters compared to rest in both the mu ($p < .001$) and beta ($p < .001$) ranges. In both the mu ($p < .001$) and the beta ($p < .001$) ranges, mu power during music listening was higher than during right hand movement. Mu power did not differ between music listening and right foot movement ($p = .797$, n.s.). In both the mu ($p < .001$) and beta ($p < .001$) ranges, mu power during right foot movement was higher than during right hand movements. Figure 5.3A and 5.3B depicts condition differences from the rest condition.

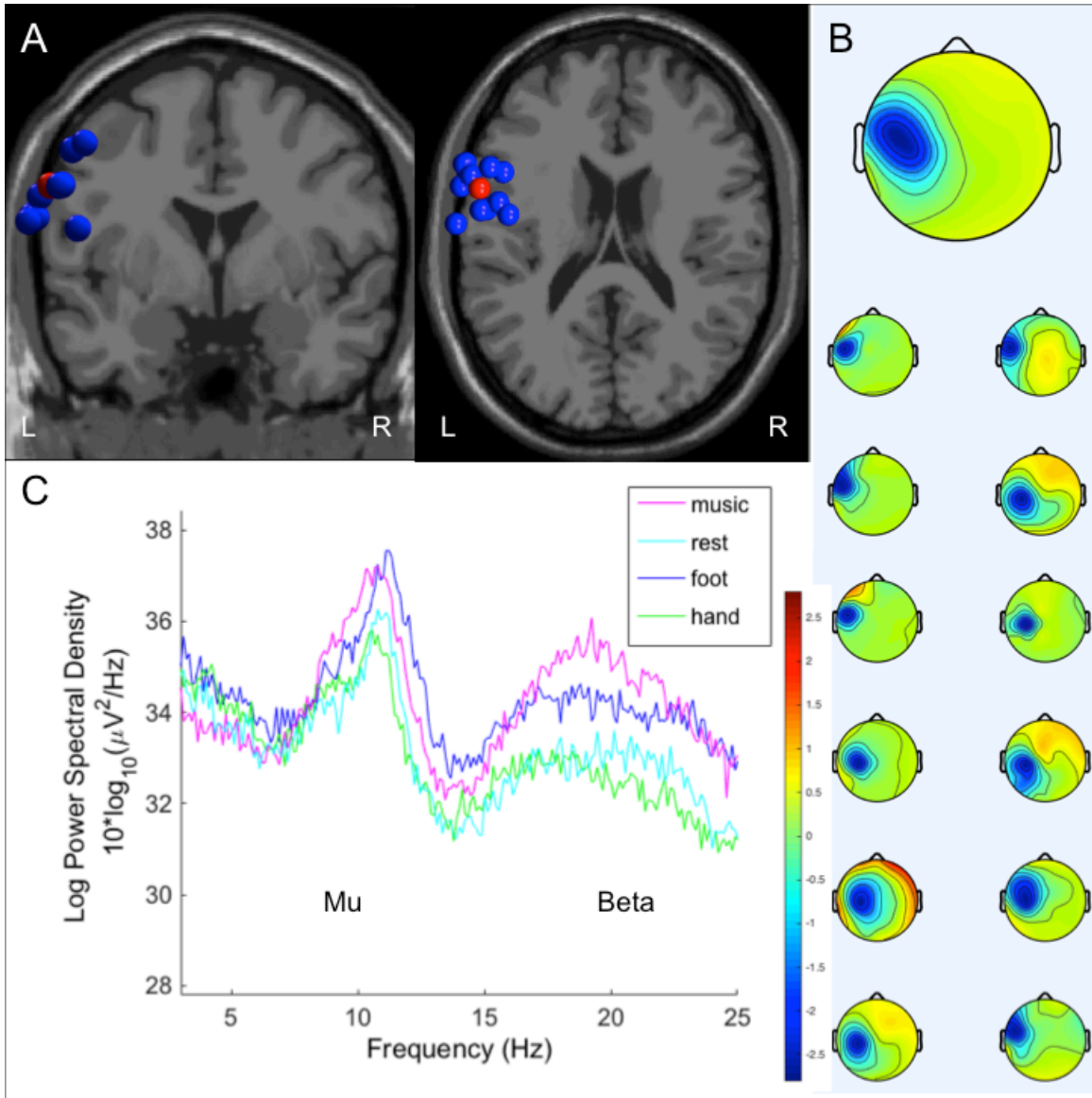


Figure 5.1. Left hemisphere mu rhythm cluster (12 independent components from all 8 participants). (A) Cluster component equivalent dipoles in blue, and dipole centroid in red. Centroid localized to Talairach (-59, 5, 31), left BA6 in or near right hand somatomotor cortex (B) Cluster mean (top) and individual IC scalp maps (below). + [red]; 0 [green]; - [blue] (C) Cluster mean log power spectra in the four experimental conditions. The broad 16-24 Hz beta band peak comprises mu-harmonic and other beta band activity.

Right hemisphere cluster

The right hemisphere cluster included six ICs from five of the 8 subjects. The cluster centroid was at Talairach (47, 1, 44). MRIcon (v2.1.38-0) lists this as being in or near right premotor cortex, again just anterior to primary motor in Brodmann area 6. See Figure 5.2 for the cluster component and centroid equivalent dipole positions, mean and

individual IC scalp maps, and cluster centroid mean spectra in the four conditions. Each condition again exhibited mu and beta range peaks. In each condition, the mean spectra gave evidence for two mu peaks at about 9 Hz and 11 Hz.

There were differences between conditions in both mean 8-12 Hz mu band spectral power $F(1.644, 57.552) = 16.910, p < .001$ (Mauchly's, $p < .001$, Figures 5.2C and 3C) and mean 16-24 Hz beta band spectral power $F(2.178, 154.604) = 52.258, p < .001$ (Mauchly's, $p < .001$; Figure 5.2C and 5.3D). Pairwise comparisons revealed that right hand finger tapping produced less mean beta power than in the resting condition ($p < .001$). Right foot tapping also produced less beta power than at rest ($p < .001$). In the mu frequency range, mean power during right finger tapping ($p = .490$) and right foot tapping ($p = 1.000$) did not differ from the resting condition. In both the mu ($p < .001$) and beta ($p < .001$) ranges music listening while sitting was associated with higher mean mu activity than the other conditions. Music listening produced more power than during right hand movements in both the mu ($p < .001$) and beta ($p < .001$) ranges, and more power than during right foot movements, again in both the mu ($p < .001$) and beta ($p < .001$) ranges. Neither mu ($p = .479$) nor beta ($p = 1.000$) mean power differed between right hand and right foot movement conditions. See Figure 5.3C and 5.3D for plots of mean mu power in all four conditions in relation to rest.

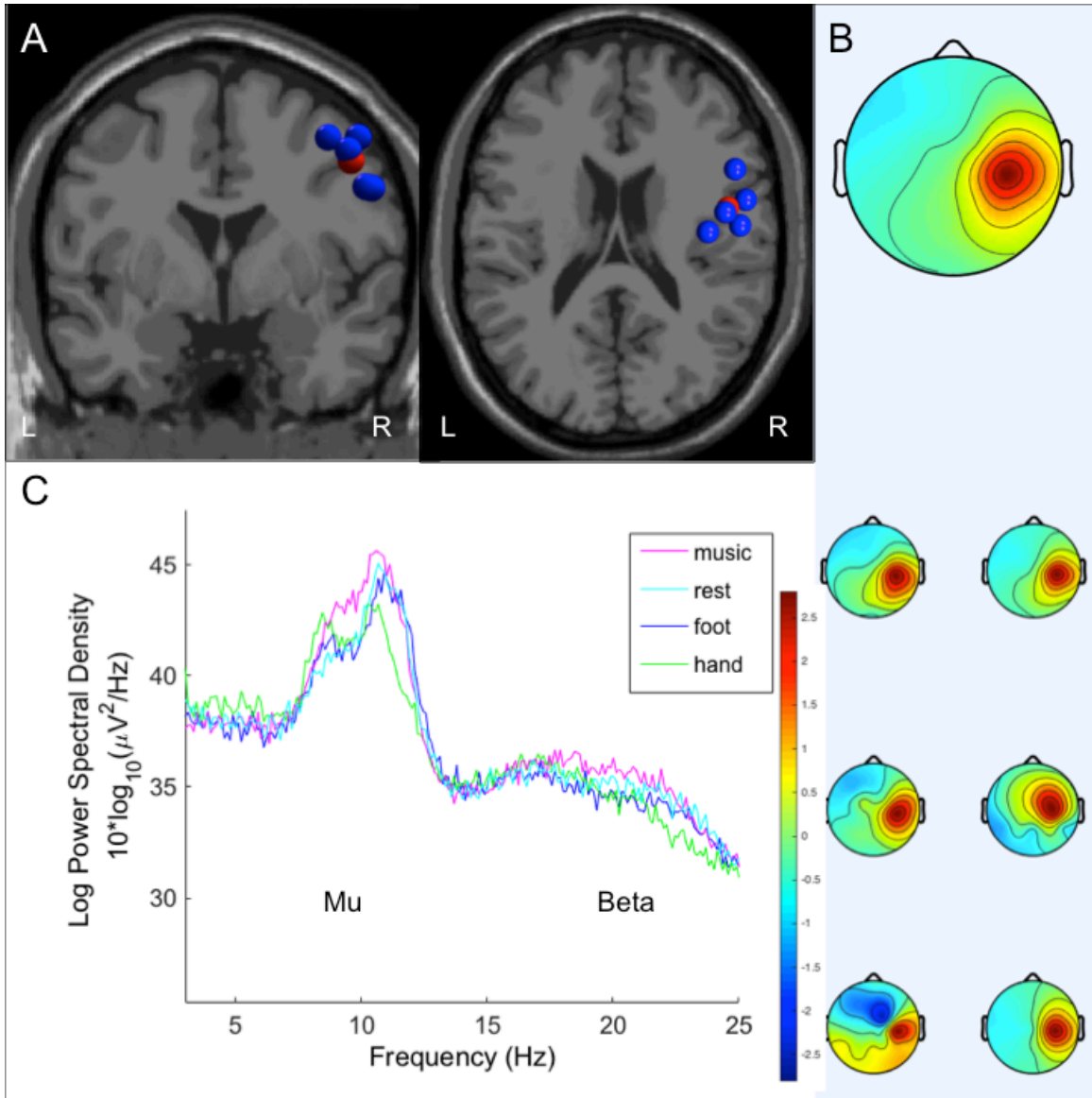


Figure 5.2. Right hemisphere mu rhythm cluster (6 independent components from 5 of the 8 participants). (A) Cluster component equivalent dipoles in blue and dipole centroid in red. Centroid localized to Talairach (47, 1, 44), right BA6 near left hand somatomotor cortex. (B) Cluster mean (top) and individual IC scalp maps (below). + [red]; 0 [green]; - [blue] (C) Mean log power spectra in the four experimental conditions. Note evidence for two mu peaks in each condition (near 9 Hz and 11 Hz), and the broad, shallow beta band peak with some suggestion of inflection points near mu first harmonics (18 Hz, 22 Hz).

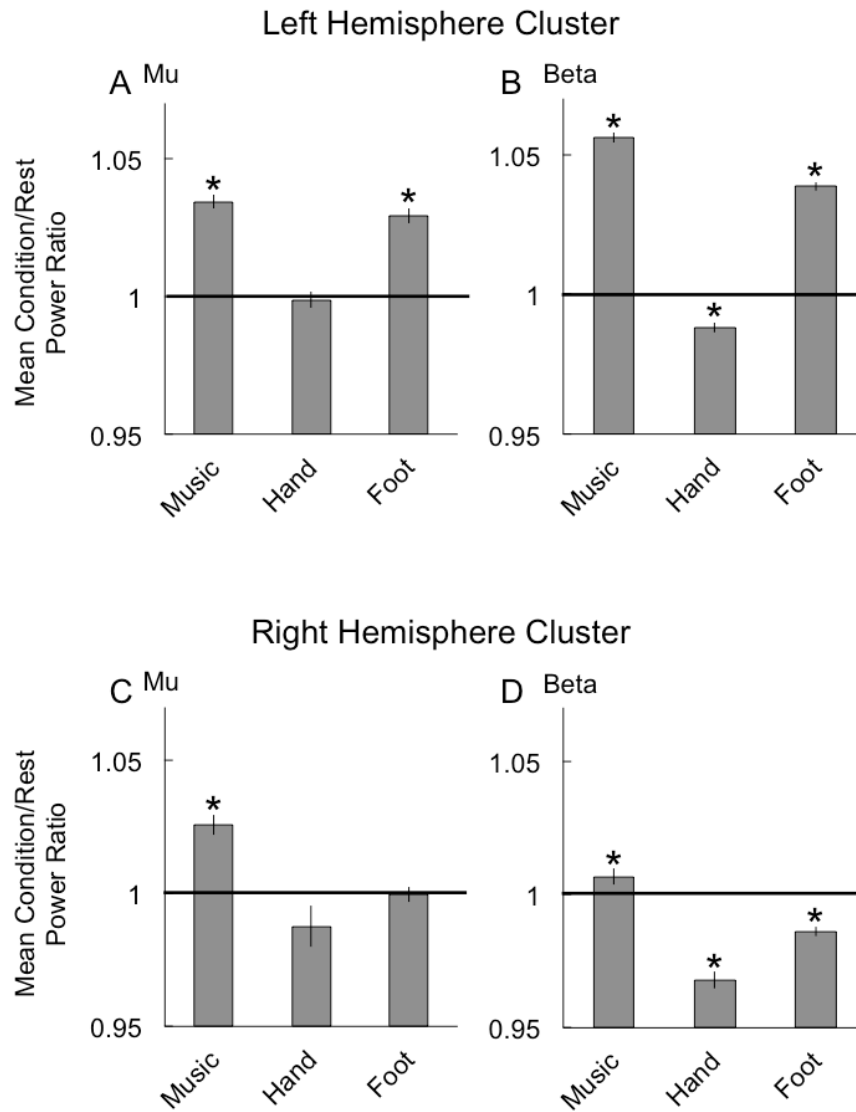


Figure 5.3. Ratios of mean power during music listening, hand movement, and foot movement conditions to mean power in the rest condition (ERD, this ratio < 1; ERS, this ratio > 1). Asterisks mark conditions significantly different from the rest condition. Left hemisphere mu rhythm cluster spectral power change from rest in mu (A) and beta (B) ranges. Additionally, in the left hemisphere music listening produced more power than right hand movement in both mu and beta ranges, but no difference in mu power from right foot movement. In the left hemisphere, right foot movement produced more power than right hand movements in both mu and beta ranges. (C) Mu and (D) beta right hemisphere source cluster spectral power changes during music listening compared to rest. In right hemisphere sources, music listening produced more power than right hand movements, and more power than during right foot movements. In right hemisphere sources there were no differences in mean mu or beta band power between right hand and foot movement conditions.

Discussion

We measured source-resolved mu activity in the 8-12 Hz range, as well as in a broader beta band peak in the 16-24 Hz range (Pfurtscheller & McFarland, 2012; Pfurtscheller & Neuper, 1994) during four conditions: movement of the (1) right hand or (2) right foot, and during sitting still without moving (3) in silence and (4) during music listening. Our findings during hand and foot movement conditions are consistent with past work showing suppression of mu over hand somatomotor cortex during hand movement, and increased mu over hand somatomotor cortex during foot movement, which might support active movement inhibition of the right hand during directed foot movements. Right foot movement was accompanied by a mean mu power increase in only left somatomotor cortex. While we did not observe a corresponding mu increase in the right hemisphere, in contrast with Pfurtscheller and Neuper (1994), our partial replication supports their interpretation that mu rhythm activity is associated with movement inhibition.

We expected that while sitting still listening to music the level of mu activity might differ from its level in the ‘silent still’ condition, related to concomitant covert music-related motor cortical activity supporting music listening, but we were unsure whether to expect a mean power increase or decrease based on the limited reports on mu rhythms during music listening. Here, sitting still while listening to music was, in fact, accompanied by bilateral mu power increases in or near primary somatomotor hand areas. Following the literature on motor cortical inhibition (Pfurtscheller & Neuper, 1994), the results of our music listening condition are consistent with active hand movement inhibition during music listening. The relative mu increase in hand areas during still music listening was similar to that observed in the left-hemisphere hand mu cluster during right foot movements (without music). However, during still music listening hand-mu cluster mu activity increased bilaterally.

Our results support the hypothesis that increased mu activity during music listening may reflect active suppression of the urge to move. As work on musical ‘groove’ sensations shows, sensorimotor coupling is pleasurable and listening to music can lead to an urge to move in time with the rhythms in the music (Janata, Tomic, & Haberman, 2012). Motor systems are active when we listen to rhythms (Grahn & Brett, 2007; Chen, Penhune, & Zatorre, 2008; Iversen, Repp, & Patel, 2009) and suppression of overt body movement is natural during restful listening or as required in social settings inappropriate for music-related movement and in experimental paradigms in which the participant is asked to sit still, such as in the task reported here. The nature of and particular role of music listening-related internal motor-related simulation without overt movement is unknown, but there is mounting evidence that it is necessary to support auditory timing predictions (Grube, Cooper, Chinnery, & Griffiths, 2010a; Grube, Lee, Griffiths, Barker, & Woodruff, 2010b; Grahn & Brett, 2009; Ross, Iversen, & Balasubramaniam, 2018), however active suppression of overt movement may be a necessary during this covert motor activity. As our task included the instructions to remain still during music listening, our EEG results may be evidence for active motor inhibition during the music listening condition.

A number of forms of beta activity are known to exist, including frontal beta, rolandic beta, and high beta (Spitzer & Haegens, 2017). This diversity strongly suggests that beta band activity may encompass several different phenomena, as reported by Onton & Makeig (2009), including mu-related activity (Spitzer & Haegens, 2017). Here, we analyzed mu and beta band activities separately to clearly show that the EEG effective source activities we isolated using ICA decomposition exhibited known mu activity characteristics.

In both hand mu clusters we observed a second, broader beta band peak. Broad beta band activity has widely been shown to be involved in timing and anticipation, independent of mu (Iversen, Repp, & Patel, 2009; Fujioka, Ross, & Trainor, 2015), though how mu-harmonic activity is related to other beta activity that has been reported during music listening or other motor tasks is not known. Evidence in support of activity in the two reported mu-activity source clusters being typical mu activity includes its stereotypical scalp distribution, frequency peak in the 8-12 Hz range, a beta band activity peak including twice the frequency of the first peak, and stronger suppression during contralateral hand movement (Pfurtscheller & McFarland, 2012). Further, condition differences in beta band power in the mu-related clusters generally followed the mu band power differences.

The mu activity sources localized in our data to left and right motor or premotor cortex exhibited spectral power differences between hand and foot movement conditions, supporting previous proposals concerning topographical organization of mu source activity in primary somatomotor cortex.

Here, both left and right hemisphere sources were localized to in or near premotor cortex just anterior to primary motor cortex. Although rostral divisions of premotor cortex do not project directly to primary motor, there is some evidence of somatotopy in caudal premotor areas just anterior to primary motor (Graziano, 2006) from research using microstimulation (Godschalk, Mitz, van Duin, & van der Burg, 1995; Chouinard & Paus, 2006) and histological tracers (Muakkassa & Strick, 1979) in non-human primates and single pulse transcranial magnetic stimulation (TMS) in humans (Groppa, Werner-Petroll, Münchau, Deuschl, Ruschworth, & Siebner, 2012). At present, however, we cannot make strong anatomical claims about these localizations given the limitations of our data, e.g. our lack of individual electrode position measurements and our use of template rather than individual head models using standard rather than individualized estimates of skull conductance (Acar, Acar, & Makeig, 2016). Magnetoencephalographic (MEG) studies have localized hand-movement related mu activity to small areas in primary somatomotor cortex in or close to the hand projection area (Tihonen, Kajola, & Hari, 1989; Jones, Kerr, Wan, Pritchett, Hämäläinen, & Moore, 2010).

This work is the first to study music listening-related mu modulation in the absence of overt movement and is also the first to source-resolve mu during music listening, reinforcing confidence that mu source activity is topographically organized in somatomotor cortex, something previously assumed from scalp projection patterns but not clearly demonstrated at the effective source level.

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Chapter 6

The Role of Posterior Parietal Cortex in Beat-Based Timing Perception: A Continuous Theta Burst Stimulation Study

There is growing interest in how the brain's motor systems contribute to the perception of musical rhythms. The Action Simulation for Auditory Prediction (ASAP) hypothesis proposes that the dorsal auditory stream is involved in bidirectional interchange between auditory perception and beat-based prediction in motor planning structures via parietal cortex (Patel & Iversen, 2014). We used a transcranial magnetic stimulation protocol, continuous theta burst stimulation (cTBS), that is known to down-regulate cortical activity for up to 60 minutes following stimulation, to test for causal contributions to beat-based timing perception. cTBS target areas included left posterior parietal cortex (lPPC), which is part of the dorsal auditory stream, and left supplementary motor area (lSMA). We hypothesized that down-regulating lPPC would interfere with accurate beat-based perception by disrupting the dorsal auditory stream. We hypothesized that we would induce no interference to absolute timing ability. We predicted that down-regulating lSMA, which is not part of the dorsal auditory stream but has been implicated in internally timed movements, would also interfere with accurate beat-based timing perception. We show (N=25) that cTBS down-regulation of lPPC does interfere with beat-based timing ability, but only the ability to detect shifts in beat phase, not changes in tempo. Down-regulation of lSMA, in contrast, did not interfere with beat-based timing. As expected, absolute interval timing ability was not impacted by the down-regulation of lPPC or lSMA. These results support that the dorsal auditory stream plays an essential role in accurate phase perception in beat-based timing. We find no evidence of an essential role of parietal cortex or supplementary motor area in interval timing.

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Introduction

When listening to musical rhythms, we actively engage with the auditory streams by making timing predictions about underlying periodicities. It has been argued that we experience rhythmic events in relation to an internal scaffolding of temporal predictions (Iversen & Balasubramaniam, 2016; Repp, 2005b; Repp & Su, 2013). Periodic timing predictions are central to beat-based time perception, in a manner that is distinct from the mechanisms of absolute interval timing (Ross, Iversen, & Balasubramaniam, 2016; Iversen & Balasubramaniam, 2016; Patel & Iversen, 2014; Teki, Grube, Kumar, & Griffiths, 2011; Teki, Grube, & Griffiths, 2012).

Making beat-based timing predictions, relies, of course, on the auditory system but has also been shown to reliably activate motor structures, including premotor cortex (Chen, Penhune, & Zatorre, 2009), even in the absence of overt movement (Grahn & Brett, 2007; Teki et al., 2012). A key outstanding question is *what is the role of motor*

systems in beat-perception (Zatorre, Chen, & Penhune, 2007). Is activity in motor planning areas of the brain during rhythm perception merely a passive byproduct of unexecuted motor acts or does it play some more active role in shaping auditory perception? There is mounting evidence for the later possibility, that making and maintaining beat-based timing predictions *requires* interaction between auditory and motor systems (Zatorre et al., 2007; reviewed in Ross et al., 2016).

It has long been suggested that beat-based timing utilizes an *internal predictive model*, meaning that we make timing predictions that are adjusted based on error between the predictions and the experienced auditory feedback (Iversen & Balasubramaniam, 2016; Repp, 2005b; Repp & Su, 2013). The theory that perception of rhythmic timing incorporates prediction and adjustment based on sensory feedback is supported by the following four observations. First, negative mean asynchrony in synchronized finger-tapping tasks can be explained by inaccurate predictions of when the beat should be and error correction suggests that we adjust for these inaccuracies (Miyake, 1902; Repp, 2005b; Woodrow, 1932). Second, rhythm perception is tempo flexible, meaning that we adjust for changes in timing, perhaps based on inaccurate predictions and using error correction mechanisms (Hanson, Case, Buck, & Buck, 1971; London, 2004; McAuley, Jones, Holub, Johnston, & Miller, 2006; Patel & Iversen, 2014; van Noorden & Moelants, 1999). Further evidence for top-down influence, such as described by internal predictive models, on rhythm perception has been demonstrated by showing perceptual susceptibility to willful control (Iversen, Repp, & Patel, 2009) and improved perceptual acuity of events that occur on the beat (Su & Pöppel, 2012). See Ross, Iversen & Balasubramaniam, 2016 for a more detailed review of these four pieces of evidence supporting that rhythm perception involves prediction and correction. This process of prediction and error correction is similar to the process described for internal predictive models for body movement planning and execution.

The notion of a predictive model does not necessarily imply motor system involvement, but there is growing evidence that timing predictions are made using the motor system (Arnal, 2012; Morillon & Baillet, 2017; Teki, Grube, Kumar, & Griffiths, 2011; Teki et al., 2012) and are adjusted continuously based on the perceived auditory stream information (Repp, 2005b). These predictive models also critically influence ongoing auditory perceptual processing, conceptually requiring bidirectionality in auditory-motor interactions (Iversen et al., 2009; Manning & Schutz, 2013; Phillips-Silver & Trainor, 2005; Phillips-Silver & Trainor, 2007). Bidirectional interchange between auditory and motor processes is supported by neuroanatomical and behavioral evidence (Blecher, Tal, & Ben-Shachar, 2016; Kotz, Brown, & Schwartz, 2016; Grahn & Brett, 2007), beta band modulation in EEG studies of rhythm perception (Fujioka, Trainor, Large, & Ross, 2012; Iversen et al., 2009), and perceptual data of patients with motor and premotor lesions (Grahn & Brett, 2009; Grube, Cooper, Chinnery, & Griffiths, 2010).

Cerebellum, premotor areas, supplementary motor area, and the basal ganglia have frequently been implicated in imaging studies of beat-based perception and synchronization (Zatorre et al., 2007; Grahn & Brett, 2007; Grahn & Brett, 2009). Chen and Penhune (2007) suggested that higher-level timing control involves basal ganglia, dorsal premotor cortex, and supplementary motor area and that the cerebellum is

involved in more fine-grained timing correction. It is thought that functionally segregated timing networks exist for absolute timing of intervals and beat-based timing (Grube, Cooper, Chinnery, & Griffiths, 2010; Grube, Lee, Griffiths, Barker, & Woodruff, 2010), which involves prediction (Iversen & Balasubramaniam, 2016; Patel & Iversen, 2014), but these timing networks have not been mapped. Grube, Cooper, Chinnery and Griffiths (2010) showed detriments in interval timing perception with chronic cerebellar dysfunction, but no effect on beat-based timing. Grube, Lee, Griffiths, Barker and Woodruff (2010) used a causal design with transcranial magnetic stimulation (TMS) to show that down-regulation of medial cerebellum results in detriments in interval timing perception, but not in their test of beat-based timing. These studies suggest that cerebellum is actively involved in absolute timing and that there might be functionally distinct networks for interval timing and beat-based timing (Grube, Cooper, Chinnery, & Griffiths, 2010; Grube, Lee, Griffiths, Barker, & Woodruff, 2010; Teki et al., 2011; Teki et al., 2012).

The basal ganglia, premotor areas, and supplementary motor area (SMA), are connected via a basal ganglia-thalamo-premotor loop (Alexander, Crutcher, & DeLong, 1990; Schell & Strick, 1984). Patients with Parkinson's disease, which is characterized by cell death of dopamine producing cells in the substantia nigra of the basal ganglia, exhibit underactivity in structures that receive basal ganglia output, such as SMA and pre-SMA (Haslinger et al., 2001; Jahanshahi et al., 1995; Rascol et al., 1994). Dopamine therapies have been shown to modulate activity in some patients in basal ganglia, SMA and pre-SMA (Haslinger et al., 2001; Rascol et al., 1994). Grahn and Brett (2009) showed that patients with Parkinson's disease can exhibit impairments in beat-based timing discrimination, but it is unclear whether this impairment is due to lesions in basal ganglia or underactivity in SMA or pre-SMA (Grahn & Brett, 2009). It is also unknown how the basal ganglia, SMA and pre-SMA are involved in beat-based timing, but Grahn and Brett (2009) suggest they may be involved in detecting the underlying beat.

The dorsal auditory pathway, connecting auditory and mid to dorsal premotor cortices via parietal regions, has been proposed as a substrate for motor-auditory interactions critical for beat-based time perception in the Action Simulation for Auditory Prediction (ASAP) hypothesis (Patel & Iversen, 2014). ASAP makes two specific claims: that the motor planning system is *necessary* for beat-based perception and that auditory and motor planning cortices interact using bidirectional projections through parietal cortex. Parietal cortex is thus predicted by ASAP to be a critical link in beat-based timing. Although parietal cortex has been less often associated with timing than motor and premotor cortices, it has been implicated in some studies (Pollok et al., 2017; Pollok, Gross, Müller, Aschersleben, & Schnitzler, 2005; Coull & Nobre, 2008; Coull, Cotti & Vidal, 2016) as well as playing a role in music cognition (Zatorre, Halpern, & Bouffard, 2010; Foster, Halpern, & Zatorre, 2013).

One region that is not explicitly included in the dorsal auditory pathway proposed by the ASAP hypothesis is the supplementary motor area (SMA). This is surprising because SMA is commonly and consistently implicated in studies of beat-based timing, typically associated with internally-guided movements (Grahn & Brett, 2007; Grahn & Brett, 2009; Chen et al., 2009; Chauvigné, Gitau, & Brown, 2014), including continuation timing (Rao, et al., 1997). Given this role in internally generated periodicity

it is reasonable to expect that SMA would also play a role in beat perception (Teki et al., 2012).

In the current study, we focus on these two regions, posterior parietal cortex and supplementary motor area, one predicted to be involved in beat-based time perception by the ASAP hypothesis, and one not, with the aim of resolving the relationship of these regions to beat perception, and possibly refining the ASAP hypothesis. While most previous studies have used functional activity measures to point to regions involved in beat perception, such studies cannot directly probe the causal role of such regions. Ultimately, causal manipulation is the only way of directly proving that auditory-motor interactions are bidirectional, and the only way of directly testing the central claim of ASAP that motor regions are causally involved in beat perception. There has been a scarcity of such causal studies attempting to map out a beat-based timing network, which the current study aims to remedy.

Using a causal design complementary to that used by Grube et al. (2010), we tested the active role of supplementary motor area and posterior parietal cortex in beat-based timing perception. We used a continuous transcranial magnetic theta burst stimulation (cTBS, Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005) applied over left posterior parietal cortex (IPPC), left supplementary motor area (ISMA), and a sham stimulation condition. Although both right and left hemispheres may be involved in beat-based timing, we focused on the left hemisphere in this study for a number of reasons. Pollok and colleagues have shown a strong left hemisphere role for motor timing (Pollok, Rothkegel, Schnitzler, Paulus, & Lang, 2008). There is some evidence for predictive movement control being lateralized to the dominant hemisphere and muscle stiffness regulation or exploratory motor behavior being lateralized more to the non-dominant hemisphere (Yadav & Sainburg, 2014; Kaulmann, Hermsdörfer, & Johannsen, 2017). Our participants were all right hand dominant, so we decided to focus on left hemisphere targets, although we are planning studies to compare hemispheric differences in beat-perception. We measured interval and beat-based timing before and after stimulation. We predicted, based on the arguments presented above, that beat-based timing perception thresholds would increase, indicating decreases in perceptual acuity, with cTBS-induced cortical down-regulation in both IPPC and ISMA. We expected no change in interval timing perception thresholds in any of the conditions, supporting the possibility of functionally distinct timing networks for interval and beat-based timing.

Methods

Participants

Participants were 25 healthy adults (12 male, 13 female), ages 18-23 years (mean age = 19.8 years, SD = 1.62 years), recruited from the University of California, Merced student population and the Merced, CA local population. All participants were dominantly right-handed, and screened for atypical hearing, amusia, and contraindications for TMS including increased risk for seizure, unstable medical problems, metal in the body other than dental fillings, neurological or psychiatric illness, history of syncope, and head or spinal cord surgery or abnormalities (Huang et al., 2005). Participants were asked to remove all metal jewelry prior to TMS. 14 participants reported no musical training or experience. 7 participants reported 5 or more years of

musical training or experience (15 years of violin/10 years of guitar, 10 years of piano and guitar, 9 years (4 of guitar and 5 of vocal training), 9 years of piano and clarinet, 7 years (5 of piano and 2 of violin), 6 years (3 of guitar, 1 of piano, and 2 of choir), and 5 years (2 in choir and 3 in band)). The other four participants reported 2 years of violin, less than 1 year of trumpet, 1 year of guitar, and 1 year of piano. Music listening preferences included a wide range of genres spanning pop, hip-hop, rap, alternative/rock, country, classical, R&B, punk, metal, j-pop, jazz, electronic, reggae, and blues. The experimental protocol was carried out in accordance with the Declaration of Helsinki, reviewed by the UC Merced IRB, and all participants gave informed consent prior to testing.

Procedures

Psychoacoustic Testing

When testing for deficits in beat-based perception, it is critical to test if these are merely a consequence of lower-level absolute timing deficits, or are truly deficits in relative, beat-based timing. Consequently, in addition to beat timing tests (described below), an adaptive test of absolute interval timing was used to determine a psychoacoustic threshold for detecting differences in timing between two auditory stimuli. This was a single interval duration discrimination test, similar to that used by Grube et al. (2010) and implemented in Mathworks' MATLAB using custom designed functions and the Psychophysics Toolbox, Version 3. This perceptual threshold from the interval timing task was used to represent perceptual acuity for interval discrimination. An increase in threshold can be interpreted as a decrease in perceptual acuity. Specifically, this threshold indicates the minimum interval duration difference that cannot be correctly identified as different. Interfering with normal activity in timing networks involved in this timing task would be expected to raise the perceptual threshold determined by this test. Stimulus beeps were created using MATLAB and were 200 Hz pure tones that lasted 0.1 seconds each. This test was selected because it is a test of duration-based timing. Each participant performed the test before and immediately after application of cTBS to the selected cortical site.

In this single interval duration discrimination test, participants were instructed to make a "same" or "different" judgment between a reference interval of variable duration, presented first, and a target interval, presented second, for 50 trials. Intervals refer to the duration of silence between pairs of tones; reference intervals were 300, 360, 420, 480, 560, and 600 ms presented in a randomized order. The initial target interval duration was 90% of the reference interval, and it was adaptively decreased by 6% or increased by 12% after every two consecutive correct or one incorrect response, respectively. Discrimination thresholds were calculated as the mean of the absolute value of the difference between the target and reference interval of the last 6 incorrect trials, which roughly estimates a correct point of the psychometrical function. The adaptive method we used was a combined transformed and weighted method. It used the 1-up 2-down method (Levitt, 1971) with asymmetric step sizes (Kaernbach, 1991) $S_{up} = 2S_{down}$. We propose the equilibrium point is described by $S_{down}P(DOWN) = S_{up}[1-P(DOWN)]$, where $P(DOWN) = [P(X_p)]^2$ as in (Levitt, 1971). Solving for the convergence point $P(X_p)$

gives $\sqrt{2/3} = 0.816$, meaning this procedure estimates the interval length for which a correct discrimination would be given 81.6% of the time.

Beat Alignment Test (BAT), Adaptive Version (A-BAT)

Two tests of relative, beat-based timing using musical stimuli were used that adapted in difficulty based on participant performance and determined beat-based timing thresholds for inter-beat interval changes and phase shifts. These tests were based on the adaptive procedure used by Grube et al. (2010), but instead tested musical timing error detection instead of timing discrimination with non-complex sounds. Beat-based timing thresholds from these timing tasks were used to represent perceptual acuity for changes in inter-beat intervals and phase shifts with musical stimuli. An increase in threshold can be interpreted as a decrease in perceptual acuity for detecting these timing changes. Specifically, these thresholds indicate the minimum timing difference that could not be correctly identified as different. See Grube et al. (2010) for more details about the adaptive procedure. Interfering with normal activity in timing networks involved in these timing tasks would be expected to raise perceptual thresholds determined by these tests. These tests were implemented in Mathworks' MATLAB using custom designed functions, the Psychophysics Toolbox, Version 3 and stimuli from the Beat Alignment Test (BAT), Version 2 (Iversen & Patel, 2008). Each participant performed the tests before and after application of cTBS to the selected cortical site.

The Beat Alignment Test (Iversen & Patel, 2008) was designed to test beat perception in a purely perceptual manner that does not require rhythmic movement usually used to assess beat perception. Musical excerpts are presented with an added metronome beep that is either on-beat, with beeps corresponding to the beat, or perturbed in one of two ways, with a tempo manipulation (IBI [Inter Beat Interval] condition) or an asynchrony, or phase, manipulation (PHA condition). Twelve musical excerpts were taken from several genres (jazz, rock, orchestral). Each is 11 seconds in length, 44.1 KHz (mono), and the amplitude ramps up over 500 ms. The musical excerpts were normalized to control for mean, minimum and maximum amplitude. The beeps were 1 KHz pure tones, 100 ms in length, and start 5 seconds after the music starts. The timing of the on-beat beeps were based on taps made by one author (JRI), averaged across 6 trials to get mean inter-tap intervals for each interval in each excerpt (BAT version 2; Iversen & Patel, 2008). Participants were instructed to discriminate between correct and altered IBIs (Phases) in 26 trials each in the IBI (Phase) subtest by responding after hearing the musical excerpt by button press in a forced choice task (response alternatives: on-beat or off-beat). Trials 1 and 2 were always on-beat. Trial 3 had an IBI (Phase) that was altered by 10% (30%). For each trial after trial 3, an incorrect response resulted in moving back in a progression of difficulty and 2 correct responses in a row resulted in moving forward in a progression of difficulty. A correct response followed by an incorrect response resulted in the next trial using the same level of difficulty.

A-BAT, IBI: In the progression of difficulty, lengthened and shortened IBIs were alternated. The progression of difficulty started at a 10% or -10% IBI, followed by 9% or -9% IBI, 8% or -8% IBI, 7% or -7% IBI, an on-beat trial, and then 2 each of a mixture of positive and negative 6%, 5%, 4%, 3%, 2%, and 1% IBI, with on-beat trials inserted after

the first $\pm 4\%$ trial and after the second $\pm 3\%$ trial. The final trials were always on-beat trials, but were not used to calculate the threshold. IBI discrimination thresholds were calculated as in our single interval duration discrimination test, mirroring the method used by Grube et al. (2010) as the mean of the absolute value of the IBI deviation amount of the last 6 incorrect off-beat trials.

A-BAT, PHA: In the A-BAT, phase subtest, the superimposed beeps always had the correct tempo, but were shifted slightly earlier or later than the on-beat trials. The structure of the test was identical to the IBI test, but with an initial phase shift of $\pm 30\%$, followed by a 20% or -20% phase shift, 15% or -15% phase shift, 10% or -10% phase shift, 9% or -9% phase shift, an on-beat trial, and then a mixture of both positive and negative 8%, 7%, 6%, 5%, 4%, and 3% phase shifts, with on-beat trials inserted after the $\pm 6\%$ trial and after the $\pm 4\%$ trial, and then both a positive and negative 2% phase shift and both a positive and negative 1% phase shift.

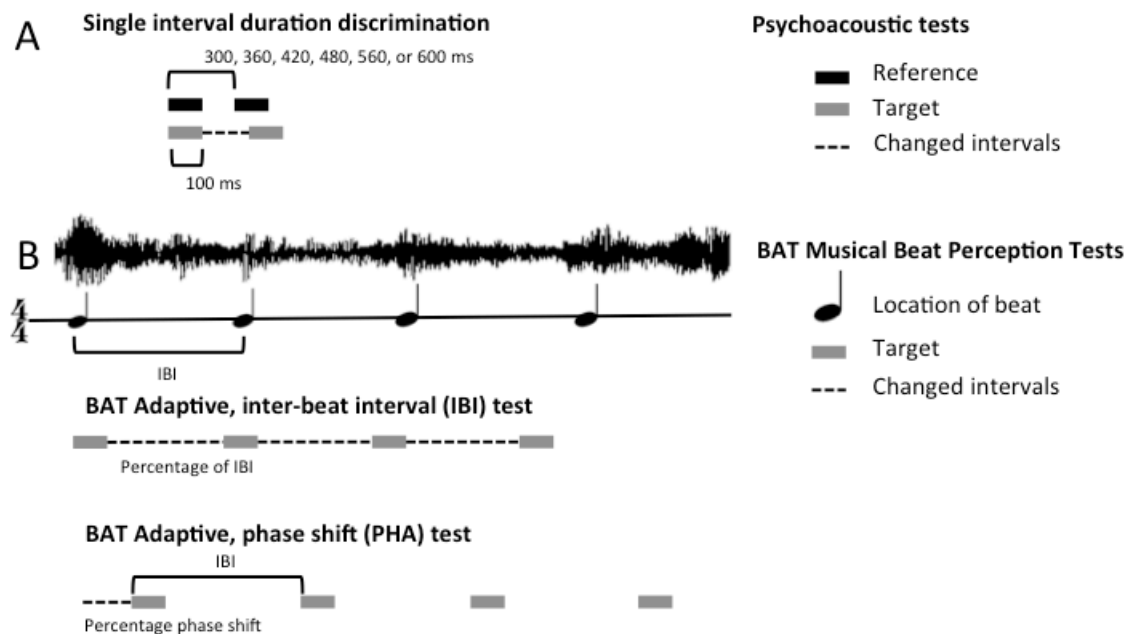


Figure 6.1. Adaptive timing tasks used for finding perceptual thresholds. (A) Single interval duration discrimination test. (B) Tests of relative timing using musical stimuli (A-BAT). This is the adaptive version of the Beat Alignment Test, Version 2 (Iversen & Patel, 2008) and is used to determine perceptual thresholds for detecting changes in inter-beat interval (lengthening or shortening) and in shifts in phase (forward or backward).

Transcranial Magnetic Stimulation

We used a continuous theta burst stimulation paradigm (cTBS), as described by Huang et al. (2005) to down-regulate cortical activity at target locations. The protocol used was a 40 second train of 3 pulses at 50 Hz, repeated at 200 ms intervals, for a total of 600 pulses. This cTBS protocol was applied at 80% of the participant's active motor

threshold (AMT). AMT was determined for each participant as the lowest stimulator intensity sufficient to produce a visible twitch with single pulse TMS to left motor cortex in 5 of 10 trials in the first dorsal interosseous muscle (FDI) of the right hand during isometric contraction. High concordance has been shown between using threshold estimations determined with electromyography (EMG) and visual twitch (Pridmore et al., 1998; Stokes et al., 2005), and visual twitch is often used to determine AMT (Sandrini, Umiltà, & Rusconi, 2011; Göbel et al., 2001; Göbel et al., 2006), as we have done. Although visible twitch was used to determine AMT, the best location in left motor cortex for right FDI activation was determined by comparing motor evoked potentials' (MEPs') size and consistency. MEPs were recorded when at rest, with Ag/AgCl sintered electrodes placed over the belly of the FDI muscle with a ground electrode placed over bone near the right elbow. For single pulse TMS to primary motor cortex, the figure of eight coil (Magstim, D70² double 70mm coil) was placed tangential to the head at an angle of ~45° from the anterior-posterior midline.

After AMT was determined, cTBS was applied to left posterior parietal cortex (IPPC), left supplementary motor area (ISMA), or left M1 with the coil facing away from the participant's head in a sham stimulation condition. Participants received all three stimulation conditions, in a randomized order, with a minimum of 7 days between each condition. Magstim Visor 2 3D motion capture guided neuro-navigation was used to scale each individual participant's brain model to the Talairach brain using head size and shape and to guide stimulation of IPPC and ISMA. We used 3D coordinates determined from previous literature for IPPC and ISMA as target stimulation sites. Our IPPC target was at Talairach -40, -50, 51, following the example of Krause et al., 2012. These coordinates are consistent with other studies and produced measurable behavioral effects when stimulated with TMS (Krause et al., 2012). Our ISMA target was at Talairach -6, -12, 54, reported by Chauvigue, Gitau, & Brown (2014) and determined using an activation likelihood (ALE) meta-analysis of 43 imaging studies. See Figure 6.2 for coil placement.

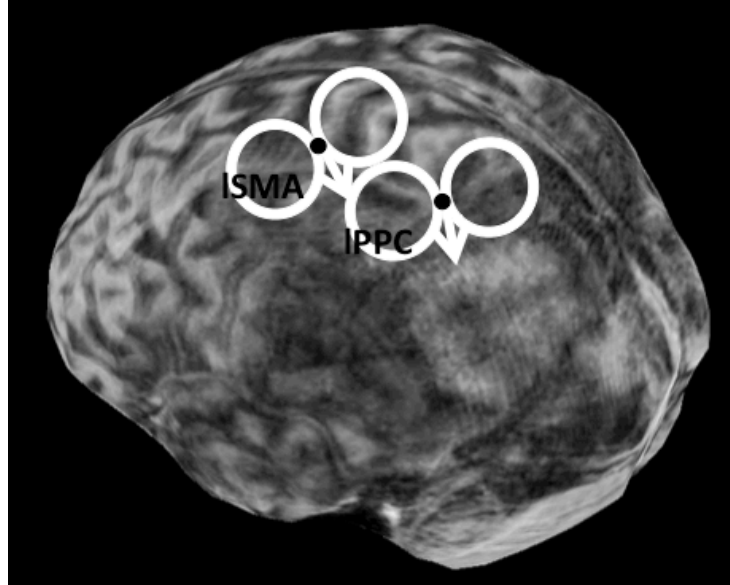


Figure 6.2. Stimulation sites and coil orientations for ISMA and IPPC conditions. Center of coil was placed at Talairach -6, -12, 54 for ISMA and -40, -50, 51 for IPPC, with the coil facing anteriorly at $\sim 45^\circ$ from the anterior-posterior midline (Janssen, Oostendorp, & Stegeman, 2015).

Results

The effect of cTBS to IPPC, ISMA and with sham stimulation was measured for interval timing and detection of deviations in inter-beat interval and phase relative to the beat of music. Thresholds were compared before (pre) and after (post) stimulation with paired samples t-tests, adjusted for multiple comparisons using the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995), and Wilcoxon signed rank tests (Figure 6.3). Pre and post thresholds were also modeled across condition for each test using linear mixed effects models, with a fixed effect for pre- vs. post-stimulation and random effects for condition and for participant (which assumes a different baseline or mean threshold for each participant and accounts for inter-subject variability). P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question (Winter, 2013). Change in threshold was calculated as the difference of post- to pre-stimulation thresholds for each test and each condition, with a greater difference indicating worsening of performance after stimulation (Figure 6.4).

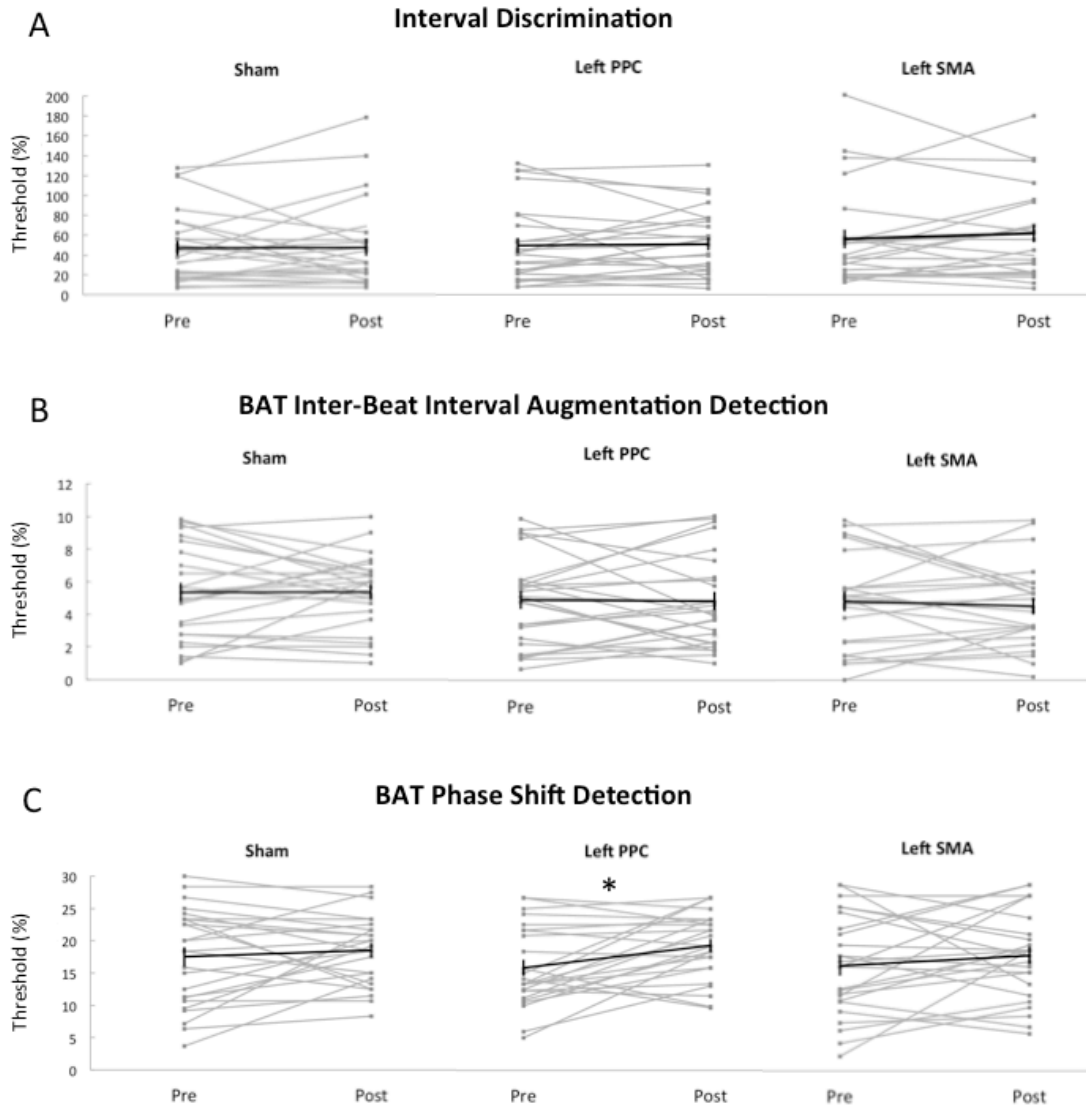


Figure 6.3. Individual (grey) and mean (black) pre- and post-cTBS thresholds for the three timing tasks in the two stimulation conditions and sham stimulation. Error bars represent ± 1 standard error from the mean. (A) Single interval duration discrimination (B) Inter-beat interval deviation detection with musical stimuli (A-BAT, IBI) (C) Phase shift detection with musical stimuli (A-BAT, Phase). There was an increase in detection thresholds pre- to post-stimulation in phase shift detection with musical stimuli with cTBS to left PPC ($t(24) = -2.998$, $p = .006$; Cohen's $d_z = .600$, Hedge's $g_{av} = .592$; $Z = -2.501$, $p = .012$), marked with an asterisk. This effect remained statistically significant after controlling for the 3 multiple comparisons (Benjamini & Hochberg, 1995).

Single interval duration discrimination

Participant thresholds for pre-tests ($47.24\% \pm 5.42$) and post-tests ($50.39\% \pm 6.17$) were within the expected range based on thresholds reported in Grube et al. (2010),

although our average is somewhat higher than the average reported by Grube et al. (2010). See Figure 6.3A for individual participants' and mean thresholds. As expected, there were no significant changes pre- to post-stimulation in single interval duration discrimination in the sham condition ($t(24) = .418, p = .680; Z = -.874, p = .382$) or with cTBS to ISMA ($t(24) = .926, p = .364; Z = -.901, p = .367$) or IPPC ($t(24) = .751, p = .321; Z = -.659, p = .510$). The linear mixed effects model supports no change from pre- to post-stimulation across the three conditions ($\chi^2(1) = .621, p = .431$). These results indicate that cTBS did not cause deficits in single interval perception.

A-BAT, inter-beat interval deviation detection

Participant thresholds for pre-tests ($5.00\% \pm .17$) and post-tests ($4.89\% \pm .25$) were within the expected range. See Figure 6.3B for individual participants' and mean thresholds. There were no significant changes pre- to post-stimulation in inter-beat interval deviation detection with musical stimuli in the sham condition ($t(24) = -.063, p = .951; Z = .000, p = 1.000$) or with cTBS to ISMA ($t(24) = .650, p = .522; Z = -.296, p = .767$) or IPPC ($t(24) = .132, p = .896; Z = -.054, p = .957$). The linear mixed effects model supports no change from pre- to post-stimulation across the three conditions ($\chi^2(1) = .139, p = .709$). These results indicate that cTBS did not cause deficits in altered inter-beat interval detection with music stimuli.

A-BAT, phase shift detection

Participant thresholds for pre-tests ($16.47\% \text{ shift} \pm .53$) and post-tests ($18.47\% \text{ shift} \pm .51$) indicate that our participants were generally worse at detecting click-track phase shifts than they were at detecting inter-beat interval deviations. See Figure 6.3C for individual participants' and mean thresholds. There was an increase in phase shift detection thresholds pre- to post-stimulation following cTBS to IPPC ($t(24) = -2.998, p = .006$; Cohen's $d_z = .600$, Hedge's $g_{av} = .592; Z = -2.501, p = .012$). Effect size was calculated following Lakens (2013). This effect remained statistically significant after controlling for multiplicity (3 multiple comparisons) with a false discovery rate of 0.05, following the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995). In contrast, there were no changes in phase shift detection following the sham cTBS condition ($t(24) = -.818, p = .421; Z = -.602, p = .547$) or with cTBS to ISMA ($t(24) = -1.063, p = .298; Z = -1.072, p = .284$). The linear mixed effects model supports a significant change from pre- to post-stimulation across the three conditions ($\chi^2(1) = 5.837, p = .016$).

The threshold increase after cTBS to IPPC translates to an average 21.9% increase in phase shift needed to detect that the metronome was off-beat ($(\text{post-cTBS} - \text{pre-cTBS}) / \text{pre-cTBS}$). Interestingly, there was considerable inter-subject variability in baseline performance on this A-BAT phase shift test, and the appearance of a bimodal distribution, leading to the impression of two groups that were differentially effected by IPPC down-regulation: Only those participants with relatively good baseline performance suffered after cTBS. Figure 6.3C shows individual participants' thresholds. 16 of the 25 participants had pre-cTBS thresholds of below 16%, which we consider as good performance on this task. These participants' performance was most influenced by the application of cTBS to IPPC, bringing their thresholds up into the range of the poor

performing participants. For these 16 participants with good baseline sensitivity to phase shift, there was a 49.1% increase in phase shift needed to detect that the metronome was off-beat after cTBS to IPPC. The remaining 9 of 25 participants performed similarly poorly post-cTBS. A regression analysis of baseline performance and performance decrement after cTBS revealed a relationship between increasing threshold and decreasing TMS-induced change in threshold ($r = -0.637$, $p = .001$). Interestingly, it does not appear that musical training was related to performance in the task because both poor performing and good performing groups had members with musical training and members without musical training. See Figure 6.4B for good and poor performers' thresholds.

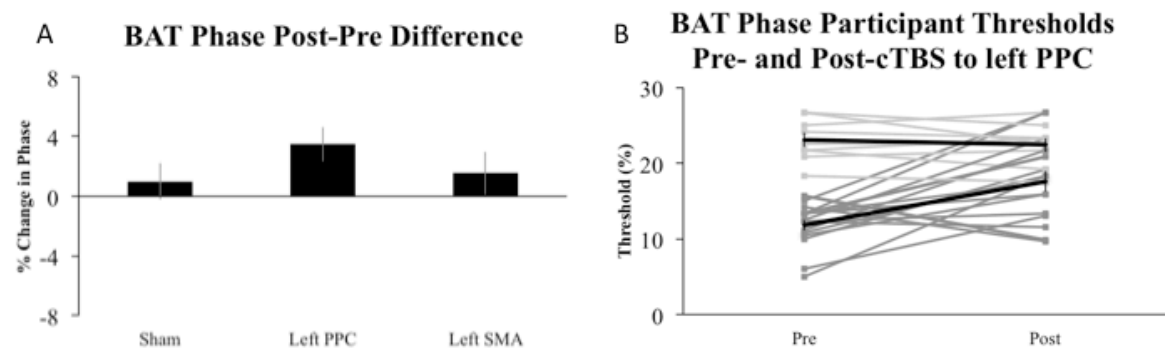


Figure 6.4. (A) Threshold differences pre- to post-stimulation for the A-BAT phase shift detection task in the two stimulation conditions and sham stimulation. Differences are post-pre. Error bars represent ± 1 standard error from the mean. (B) Individual participant thresholds from the A-BAT, phase shift detection subtest showing good performers (dark grey) and poor performers (light grey) and mean thresholds for the two groups (black). Error bars represent ± 1 standard error from the mean.

Discussion

Using focal down-regulation of cortex with cTBS, the present experiment tested the roles of ISMA and IPPC in a range of timing tasks: absolute interval timing perception and in detection of altered inter-beat intervals and phase shifts in musical timing. We found a significant effect of cTBS to IPPC on phase shift detection in the musical timing task (Figure 6.3C), and no other effects were found. Performance was worse for detecting timing delay/advance (phase shift) relative to the musical beat as indicated by an increased detection threshold. This indicates a decrease in perceptual acuity in judging stimulus timing relative to a musical beat. These findings demonstrate that IPPC plays a causal role in accurate beat-based timing, directly supporting the 'ASAP hypothesis' prediction that the auditory dorsal stream (which includes PPC) plays a causal role in auditory beat perception. IPPC is suggested to play an active role in beat-based timing by virtue of its gateway role in the dorsal auditory pathway, with bidirectional projections between auditory and motor planning cortices. Interestingly, IPPC seems to be involved primarily in participants with better pre-cTBS phase shift detection performance, suggesting it may have a role in making fine distinctions in beat phase.

Given past results showing the involvement of SMA in beat-based perception and synchronization (Grahn & Brett, 2009; Grahn & Brett, 2007; Chen et al., 2009; Chauvigné et al., 2014), it is surprising that our tests of beat-based timing were not negatively affected by cTBS down-regulation of ISMA. These results, considered together, suggest that the basal ganglia-thalamo-premotor loop and the dorsal auditory stream may be involved in different aspects of beat-based timing. They suggest that SMA and pre-SMA implications in beat-based timing could represent down-stream effects of activity in the basal ganglia and not causal roles of SMA and pre-SMA for this type of timing perception. Coull and Nobre (2008) propose that cortical circuits connecting premotor to parietal regions are recruited for temporal expectation. They also propose that absolute timing relies more heavily on basal ganglia circuits, with SMA co-activation being context dependent. However, it is not clear from their work as to which contexts are necessary for co-activation. The present results suggest that SMA might not have a direct and active role in beat perception. The exact role of SMA in these networks needs careful examination through both imaging and causal investigations.

The present findings also support past work arguing for functionally segregated timing networks for absolute and relative timing (Grube et al., 2010; Teki et al., 2012). We did not find any effects of cTBS to ISMA or IPPC in a test of absolute timing. This test of absolute timing was modeled after the test used in Grube et al. (2010) with which participants showed poorer performance after cTBS to medial cerebellum. Grube et al. (2010) demonstrated a specific cerebellar contribution to absolute timing and we found no evidence for causal contributions of IPPC or ISMA to absolute timing. However, although our test of absolute timing was similar to the test used by Grube et al. (2010), the adaptive method was not exactly the same and targeted a slightly different target threshold and, therefore, cannot provide a perfect dissociation.

We demonstrate a specific parietal contribution to relative timing on a musical phase detection test. Although parietal cortex has been implicated in imaging studies of beat perception (Pollok et al., 2005), and the dorsal auditory stream connects auditory and premotor areas by way of parietal cortex and has been proposed to be involved in beat perception (Patel & Iversen, 2014), the mechanisms that involve PPC are undetermined. Zatorre et al. (2007) discussed ventral and dorsal pathways projecting from primary auditory cortex and the possible functional roles of these pathways. One suggestion is that ventral and dorsal auditory projections parallel ventral and dorsal visual streams (Rauschecker & Tian, 2000). In this model, ventral pathways support time-independent object processing and dorsal pathways support spatial processing and tracking time-varying events (Warren, Wise, & Warren, 2005; Belin & Zatorre, 2000; Zatorre & Belin, 2005), which Zatorre et al. (2007) suggest is most likely to connect with motor areas because body movements exist in time and space.

The suggestion that PPC is involved in predictive mechanisms involving motor networks is not without precedent: PPC has been suggested to play a role in exploratory or anticipatory movements in the control of balance (Kaulmann, Hermsdörfer, & Johannsen, 2017), along with prefrontal and primary motor cortices (Mihara et al., 2012). Kaulmann, Hermsdörfer and Johannsen (2017) show that cTBS to right PPC reduces variability in postural sway movements, and suggest that this could support that parietal cortex is involved in exploratory or anticipatory movements.

Some insight into what this difference is might be found in the work of Zatorre and colleagues. In a series of fMRI studies, PPC is implicated for temporal manipulation of musical sounds (Zatorre, Halpern, & Bouffard, 2010; Foster, Halpern, & Zatorre, 2013). In these studies, participants were asked to imagine a familiar tune, listen to a sequence of notes, and decide whether the sequence of notes was the familiar tune played in reverse. The task required participants to imagine a manipulated (time-reversed) version of the melody. Unlike other imaging studies of auditory imagery, which implicate secondary auditory cortex, SMA and inferior frontal areas (see Zatorre & Halpern, 2005 for a review), this study required temporal manipulation of auditory imagery. Parietal cortex, as well as right auditory, ventrolateral and dorsolateral frontal cortices were active during the mental manipulations (Zatorre et al., 2010; Foster et al., 2013). This suggests that parietal cortex is involved in active engagement with or temporal manipulation of music. Left parietal cortex has also been suggested to play a role in temporal attention (Coull & Nobre, 1998), temporal expectation (Coull & Nobre, 2008), and temporal predictability (Coull, Cotti, & Vidal, 2016), as well as auditory motor synchronization (Pollok et al., 2017).

If PPC is required for beat-based timing *in general*, then it is surprising that our results do not show negative effects of down-regulation of IPPC on detection of changes in inter-beat intervals in the A-BAT, IBI test. Some aspect of the A-BAT, Phase shift detection appears to use IPPC in a way that the A-BAT, IBI detection does not. Although accurate beat perception requires both tempo and phase perception, the two may be supported by separate cognitive processes, evidenced by the differences in error correction in the sensorimotor synchronization work of Bruno Repp and colleagues. Repp (2005b) suggests that the two processes rely on distinct cognitive control mechanisms and possibly different brain circuits. Correction can be based on temporal reference points (such as a metronome or a tap) or on temporal intervals, created by the difference between a metronome and a tap. The A-BAT, IBI tests for detection of changes in tempo, but changes in tempo also result in misalignments in phase. We suggest that participants might be using temporal references in the A-BAT, IBI and asynchronies in the A-BAT, Phase. The IBI and phase subtests of the A-BAT target different aspects of beat-based timing, and so it is not surprising that they are differentially affected by IPPC stimulation. However, the question remains of how specifically IPPC contributes to phase shift detection.

Research using causal designs should be continued with a goal of mapping out causal interactions in absolute and relative timing networks, and to specifically test hypotheses, such as ASAP, which propose beat-perception networks. Further investigations are needed to understand the involvement of the basal ganglia-thalamo-premotor loop and the dorsal auditory stream in absolute and predictive time perception. These results encourage mechanistic proposals of predictive beat perception that involve parietal cortex, and mechanistic proposals should incorporate the underlying electrophysiology of the dorsal stream through left and right PPC.

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Chapter 7

Dorsal Premotor Contributions to Auditory Rhythm Perception: Causal Transcranial Magnetic Stimulation Studies of Interval, Tempo, and Phase

It has been suggested that movement planning networks are critical for time perception. The Action Simulation for Auditory Prediction (ASAP) hypothesis proposes that the dorsal auditory stream is involved in predictive beat-based timing through bidirectional interchange between auditory perception and dorsal premotor (dPMC) prediction via parietal regions, as has been supported by brain imaging and transcranial magnetic stimulation (TMS). However, causal impact of dPMC on time perception has not been tested directly. We used a TMS protocol that down-regulates cortical activity, continuous theta burst stimulation (cTBS), to test for causal contributions of left dPMC to time perception. Three experiments measured (1) discrete interval timing perception, and relative beat-based musical timing for (2) tempo perception and (3) phase perception. Perceptual acuity was tested pre- and post-cTBS using a test of sub-second interval discrimination and the Adaptive Beat Alignment Test (A-BAT). We show (N = 30) that cTBS down-regulation of left dPMC interferes with interval timing perception and the ability to detect differences in musical tempo, but not phase. Our data support causal involvement of premotor networks in perceptual timing, supporting a causal role of the left dPMC in accurate interval and musical tempo perception, possibly via dorsal stream interactions with auditory cortex.

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Introduction

Perception of musical beat is a predictive form of time perception, distinct from absolute interval timing (Iversen & Balasubramaniam, 2016; Ross, Iversen, & Balasubramaniam, 2016; Patel & Iversen, 2014; Teki, Grube, & Griffiths, 2012; Teki, Grube, Kumar, & Griffiths, 2011). In absolute timing, intervals are perceived and encoded discretely, but in relative, beat-based timing, intervals are interpreted relative to a perceived and ongoing beat structure (Teki, Grube, Kumar, & Griffiths, 2011). Beat perception entails predictions about tempo (beat period) and about phase (beat onset times). The mechanisms involved with making beat-based timing predictions are of interest for a number of reasons. One reason is that beat perception seems to be a human ability, with only minimal analogues in some non-human species. Beat perception is also a defined test case for the study of sensorimotor interactions, with a rich literature on prediction and error correction in finger-tapping synchronization to auditory rhythms (Repp & Su, 2013; Repp, 2005b). Recent evidence suggests that in some scenarios the motor system might actively shape the perception of sound (Ross, Iversen, & Balasubramaniam, 2016; Patel & Iversen, 2014; Morillon & Baillet, 2017).

The dorsal premotor cortex (dPMC) is involved with movement planning, including for sound guided motor synchronization (Chen, Penhune, & Zatorre, 2009; Giovannelli et al., 2014). Additionally, dPMC is active during purely perceptual timing tasks, in the absence of overt movement (Bengtsson et al., 2009; Grahn & Brett, 2007). However, it remains unknown if such 'purely perceptual' activity in dPMC is necessary to perceptual processing of the beat, or if it is an epiphenomenal consequence of planning for unexpressed overt movement (Leaver, van Lare, Zielinski, Halpern, & Rauschecker, 2009). A number of accounts have hypothesized an active motor role in perception (Ross, Iversen, & Balasubramaniam, 2016; Morillon & Baillet, 2017). One, which predicts a specific role for dPMC, is the ASAP hypothesis, which proposes that motor planning regions are involved in making beat-based timing predictions that are causally necessary for beat perception (Patel & Iversen, 2016). Further, the dorsal auditory pathway is hypothesized to be where auditory and motor networks interact to compare timing predictions in motor cortex with incoming sounds (Patel & Iversen, 2016). The dorsal auditory pathway connects caudal auditory regions, such as posterior superior temporal gyrus, with dorsal frontal premotor regions, such as dorsal premotor cortex, via parietal regions such as the angular gyrus, and this pathway is bi-directional (Rauschecker & Tian, 2000). dPMC is part of the dorsal auditory stream, so finding its involvement in beat-based timing would support the ASAP hypothesis.

ASAP posits that beat-based timing relies on internal predictive models that are continuously updated (Iversen & Balasubramaniam, 2016; Repp & Su, 2013; Repp, 2005b), and describes how some aspects of beat perception support that an internal predictive model is being used (Patel & Iversen, 2014). These aspects include negative mean asynchrony which is thought to demonstrate timing prediction (Repp, 2005b; Miyake, 1902; Woodrow, 1932; Aschersleben, Gehrke, & Prinz, 2001), tempo flexibility in the perception of rhythmic structure (van Noorden & Moelants, 1999; Hanson, Case, Buck, & Buck, 1971; London, 2004; McAuley, Jones, Holub, Johnston, & Miller, 2006), the susceptibility of beat perception to willful control, and improved perceptual acuity of events that occur on the beat (Iversen, Repp, & Patel, 2009), which all support that top-down predictions can influence auditory perception. In addition to this evidence, beat perception has been shown to be directly influenced by body movement (Manning & Schutz, 2013; Phillips-Silver & Trainor, 2005; Phillips-Silver & Trainor, 2007; Su & Pöppel, 2012; Su, 2012; Su & Jonikaitis, 2011), which supports that motor behavior or planning may also influence auditory perception (Ross, Iversen, & Balasubramaniam, 2016; Patel & Iversen, 2014). In support of the proposal that beat perception uses the dorsal auditory stream, we show in previous work that TMS-induced down-regulation of posterior parietal cortex, a critical link between premotor and auditory regions in this pathway, interferes with phase aspects of beat perception (Ross, Iversen, & Balasubramaniam, 2018).

The dorsal auditory pathway, also referred to as the dorsal stream, is associated with localization of sounds in space, phonological processing and sensorimotor integration and control of speech (Rauschecker & Tian, 2000; Rauschecker, 2011; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009). The dorsal stream includes both afferent and efferent tracts, enabling bidirectional communication between auditory and premotor cortex. There is some evidence that the dorsal stream is involved in auditory

temporal processing (Foster, Halpern, & Zatorre, 2013), with a suggested role in musical processing: in imagined time-reversed musical melodies (Foster et al., 2013; Zatorre, Halpern, & Bouffard, 2010) and in musical phase perception (Ross, Iversen, & Balasubramaniam, 2018).

However, a central question that has not yet been directly tested is if dPMC has a causal role in timing and beat perception. One method to directly assess causal contributions is through transient modulation of cortical function using transcranial magnetic stimulation (TMS). Specifically, TMS can be used to determine causal contributions to perceptual tasks of different brain areas by functionally modulating cortical excitability and observing changes in perception. Continuous theta burst stimulation (cTBS), a TMS protocol, down-regulates focal cortical excitability through hyperpolarization of cell bodies, which can be measured behaviorally (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005).

Two prior studies have used brain stimulation to probe brain mechanisms for different aspects of timing behavior. Grube, Lee, Griffiths, Barker, & Woodruff (2010) used cTBS to demonstrate causal involvement of motor networks in absolute interval timing perception and Pollok, Overhagen, Keitel, & Krause (2017) used a related technique, tDCS, to demonstrate causal contributions of dorsal premotor regions to rhythm reproduction using an auditory-motor synchronization and continuation tapping paradigm (Pollok et al., 2017). In previous work using cTBS, we show that down-regulation of left PPC interferes with accurate perception of beat phase timing in music but not beat tempo timing or single absolute interval discrimination (Ross, Iversen, & Balasubramaniam, 2018). Notably, this work examined changes in timing perception using tasks that did not require explicit motor synchronization. As PPC is an intermediary node in the dorsal auditory stream, mediating between auditory and premotor cortices, this provided support for the ASAP hypothesis. The current study tests the next link in the chain as, to our knowledge, brain stimulation techniques have not been used previously to observe changes in timing perception without motor synchronization with down-regulation of dPMC.

To explore specific causal contributions of dPMC to timing, we present three targeted studies to address the following questions: (1) Is dPMC causally involved in absolute interval timing perception? (2) Is dPMC causally involved in musical beat tempo timing perception? (3) Is dPMC causally involved in musical beat phase timing perception? For this work, we targeted left dPMC (Figure 7.1, Talairach -32, -12, 62; coordinates taken from Chauvigné, Gitau, & Brown, 2014) and tested timing perception performance before and after cTBS. We contrasted this with timing perception performance before and after a sham cTBS stimulation, in which participants believed they were receiving brain stimulation but were not. Based on Pollok et al. (2017), we might have expected dPMC to be involved in both absolute and relative timing, but because they used a continuation tapping task, we were unsure whether this role of dPMC for internally generated rhythm would be sufficient to support predictions about absolute interval timing perception, and therefore were unsure whether to expect cTBS down-regulation of left dPMC to disrupt accurate interval timing perception. Based on the proposals set forth by the ASAP hypothesis (Patel & Iversen, 2014), we expected to find evidence that dPMC is causally involved in both tempo and phase timing.

Methods

Participants

Participants were thirty healthy adults (20 female, 10 male), ages 18-34 years (mean = 20.0, SD = 2.92), recruited from the University of California, Merced, student population. All participants were dominantly right-handed and screened for atypical hearing, amusia, and contraindications for TMS including increased seizure risk, unstable medical conditions, metal implants in the body other than dental fillings, neurological or psychiatric illness, history of syncope, and head or spinal cord surgery or abnormalities (Huang et al., 2005). Participants were asked to remove all metal jewelry before the TMS treatment. Seven participants reported three or more years of musical training or experience, with an average length of training or experience in this group 11.1 years (SD = 7.86). One participant reported 1 year of musical training or experience. The other twenty-two participants reported no musical training or experience. There were not enough participants with musical training or experience to test whether musical experience modulates the effects of cTBS on left dPMC. The experimental protocol was carried out in accordance with the Declaration of Helsinki, reviewed and approved by the University of California, Merced, Institutional Review Board, and all participants gave informed consent prior to testing.

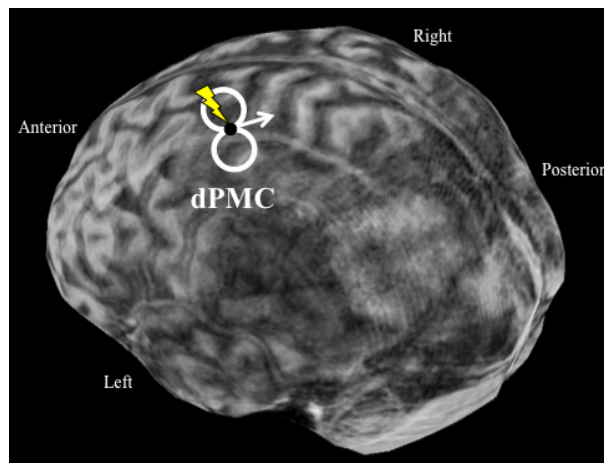


Figure 7.1. Left dorsal premotor cortex stimulation target and coil orientation. Center of coil was placed at Talairach -32, -12, 62 (Chauvigné et al., 2014), with the coil facing anteriorly to induce an anterior to posterior flow of current (indicated here with an arrow; Janssen, Oostendorp, & Stegeman, 2015).

Interval Timing Discrimination test

An adaptive test of absolute interval timing was used to determine a psychoacoustic threshold for detecting differences in timing between two auditory stimuli. This was a single-interval duration discrimination test, similar to that used by Grube et al. (2010) and implemented in MathWorks' MATLAB (Natick, MA) using custom-designed functions and the Psychophysics Toolbox, Version 3. Perceptual threshold from the interval timing perception task was used to represent perceptual acuity for sub-second interval discrimination. An increase in threshold can be interpreted as a

decrease in perceptual acuity. Specifically, this threshold indicates the minimum interval duration difference that cannot be correctly identified as different. Interfering with normal activity in timing networks involved in this timing task would be expected to raise the perceptual threshold determined by this test. Stimulus beeps were created using MATLAB and were 200 Hz pure tones that lasted 0.1 sec each. Each participant performed the test before and immediately after application of cTBS. In this single-interval duration discrimination test, participants were instructed to make a “same” or “different” judgment between a reference interval of variable duration, presented first, and a target interval, presented second, for 50 trials. Intervals refer to the duration of silence between pairs of tones; reference intervals were 300, 360, 420, 480, 560, and 600 milliseconds presented in a randomized order. The initial target interval duration was 90% of the reference interval, and was adaptively decreased by 6% or increased by 12% after every two consecutive correct or one incorrect response, respectively.

Discrimination thresholds (as a percentage) were calculated as the mean of the absolute value of the difference between the target and reference interval of the last six incorrect trials. The adaptive method we used was a combined transformed and weighted method, using the 1-up 2-down method (Levitt, 1971) with asymmetric step sizes (London, 2004) $S_{up} = 2S_{down}$. We propose the equilibrium point is described by $S_{down}P(DOWN) = S_{up}[1-P(DOWN)]$, where $P(DOWN) = [P(X_p)]^2$ as in Levitt (1971). Solving for the convergence point $P(X_p)$ gives $\sqrt{2/3} = 0.816$, meaning this procedure estimates the interval length for which a correct discrimination would be given 81.6% of the time. See Ross, Iversen, & Balasubramaniam (2018) for more details about the stimuli and adaptive procedure on this test.

Beat-Based Timing Test

The Beat Alignment Test, version 2 (BAT; Iversen & Patel, 2008) was designed to test beat perception in a purely perceptual manner that does not require rhythmic movement usually used to assess beat perception. Musical excerpts are presented with an added beep track that is either on-beat, with beeps corresponding to the beat, or perturbed with a tempo or phase manipulation. Each participant performed an adaptive version of each of the BAT subtests (A-BAT IBI and A-BAT PHA, described below) before and after application of cTBS. An increase in threshold on these subtests can be interpreted as a decrease in perceptual acuity for detecting timing differences between music and the beep track. Specifically, these thresholds indicate the minimum tempo or phase differences that cannot be correctly identified as different. Interfering with normal activity in timing networks involved in tempo timing or phase timing would be expected to raise perceptual thresholds determined by these tests.

Tempo Timing Perception test

The A-BAT IBI (Ross, Iversen, & Balasubramaniam, 2018; Iversen & Patel, 2008) is an adaptive version of the inter-beat interval (IBI) subtest of the BAT (Iversen & Patel, 2008). It is a test of tempo timing perception with musical stimuli that adapts in difficulty based on participant performance and determines beat-based timing thresholds for inter-beat interval changes. Musical excerpts are presented with a beep track that is either on-beat, with beeps corresponding to the beat, or perturbed with a tempo

manipulation. Participants were instructed to discriminate between correct and altered IBIs in 26 trials by responding after hearing the musical excerpt by button press in a forced-choice task (response alternatives: on-beat or off-beat). See Ross, Iversen, & Balasubramaniam (2018) for more details about the stimuli and adaptive procedures.

Phase Timing Perception test

The A-BAT PHA (Ross, Iversen, & Balasubramaniam, 2018; Iversen & Patel, 2008) is an adaptive version of the phase (PHA) subtest of the BAT (Iversen & Patel, 2008). It is a test of phase timing perception with musical stimuli that adapts in difficulty based on participant performance and determines beat-based timing thresholds for detecting shifts in phase. Musical excerpts are presented with an added beep track that is either on-beat, with beeps corresponding to the beat, or perturbed with a phase shift manipulation. Participants were instructed to discriminate between correct and altered phase in 26 trials by responding after hearing the musical excerpt by button press in a forced-choice task (response alternatives: on-beat or off-beat). See Ross, Iversen, & Balasubramaniam (2018) for more details about the stimuli and adaptive procedures.

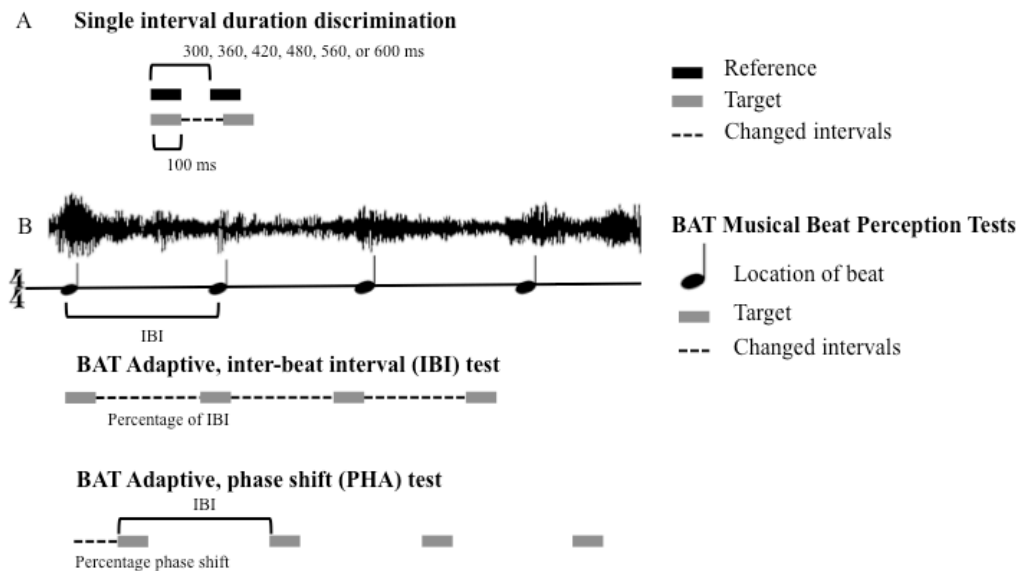


Figure 7.2. Adaptive auditory timing tests used for determining perceptual thresholds. (A) Experiment 1: Single-interval duration discrimination test (Ross, Iversen, & Balasubramaniam, 2018; Grube et al., 2010) (B) Experiment 2/3: Tests of musical timing perception (A-BAT; Ross, Iversen, & Balasubramaniam, 2018; Iversen & Patel, 2008), used to determine perceptual thresholds for detecting musical tempo (experiment 2) and phase alignment (experiment 3).

TMS

cTBS (described by Huang et al., 2005), was applied to down-regulate cortical activity at left dPMC or in a sham stimulation condition. The protocol used was a 40-sec train of three pulses at 50 Hz, repeated at 200-millisecond intervals, for a total of 600 pulses (Huang et al., 2005). This cTBS protocol was applied at 80% of the participant's

active motor threshold (AMT), while adhering to safety guidelines for participants and the equipment. If a participant's 80% of AMT was a greater intensity than can safely be administered with our system, we stimulated at the maximum intensity that was safe. AMT was determined for each participant as the lowest stimulator intensity sufficient to produce a visible twitch with single pulse TMS to left motor cortex in 5 of 10 trials in the first dorsal interosseous (FDI) muscle of the right hand during isometric contraction. Although visible twitch was used to determine AMT, the best location in left motor cortex for right FDI activation was determined by comparing motor-evoked potentials' size and consistency. Motor-evoked potentials were recorded when at rest, with Ag/AgCl sintered electrodes placed over the belly of the FDI muscle with a ground electrode placed over bone near the right elbow. For single-pulse TMS to primary motor cortex, the figure of eight coil (Magstim, D702 double 70 mm coil, Carmarthenshire, United Kingdom) was placed tangential to the head at an angle of $\sim 45^\circ$ from the anterior–posterior midline (Janssen, Oostendorp, & Stegeman, 2015). After AMT was determined, cTBS was applied to left dPMC (experimental condition) or left M1 with the coil facing away from the participant's head (sham stimulation condition). All participants received both stimulation conditions, in a randomized order, with a minimum of 7 days between each condition.

Neuronavigation

Brain stimulation was guided using the Magstim Visor 2 3-D motion capture neuronavigation system. The system enabled scaling the Talairach brain using individual participant's head size and shape. We used 3-D coordinates determined from previous literature for the left dPMC target site, determined using an activation likelihood meta-analysis of 43 imaging studies, reported by Chauvigne, Gitau, & Brown (2014). See Figure 7.1 for coil placement and orientation (Janssen et al., 2015).

Data analysis

All perceptual thresholds were determined using the above described adaptive perceptual tests.

Statistics

Changes pre- to post-cTBS in perceptual acuity (i.e. perceptual threshold) were analyzed with IBM© SPSS© Statistics, Version 20, using paired samples t-tests for each of the stimulation conditions (dPMC and sham). Additionally, we used linear mixed effects models created in R 3.3.2 (R Core Team, 2016), using the *lmer* function from the *lme4* package (version 1.1.13) with a fixed effect for pre- versus post-cTBS and random effects for condition and for participant. P values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question (Winter, 2013).

Results

Analysis of pre- to post-cTBS changes in perceptual acuity was completed for each timing experiment (See Materials and Methods below and Figure 7.2 for more details on the perceptual tests), with N=30 completing all three tests, using paired

samples t-tests. Additionally, to support t-tests and probe robustness of the findings, pre- to post-cTBS changes were compared across sham and left dPMC stimulation conditions using linear mixed effects models, with a fixed effect for pre- versus post-cTBS and random effects for condition and for participant. P values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question (Winter, 2013).

Interval Timing Discrimination

T-test comparison of interval discrimination thresholds pre- to post-cTBS was significant, with a 22.87% higher threshold after the treatment (interval difference threshold: pre = $48.22 \pm 6.88\%$, post = $59.25 \pm 8.56\%$; $t(29) = -2.083$, $p = .046$, Cohen's $d = 0.38$). This higher threshold after down-regulation of left dPMC indicates a decrease in perceptual acuity for differentiating single interval durations. As a control, we found no pre- to post-cTBS difference with sham stimulation (interval difference threshold: pre = $35.39 \pm 5.00\%$, post = $37.84 \pm 4.57\%$; $t(29) = -0.606$, $p = .549$, Cohen's $d = 0.11$; See Figure 7.2A for more on the interval timing test; See Figure 7.3A for interval thresholds). A linear mixed effects model revealed no significant changes across sham and dPMC conditions for pre- to post-cTBS down-regulation ($\chi^2(1) = 2.3116$, $p = .1284$), meaning this model does not support an effect of stimulation site on the pre- to post-cTBS threshold change.

Tempo Timing Perception

T-test comparison of tempo detection thresholds pre- to post-cTBS was significant, with a 19.93% higher threshold after the treatment (tempo deviation threshold: pre = $4.41 \pm .52\%$, post = $5.29 \pm .57\%$; $t(29) = -2.318$, $p = .028$, Cohen's $d = .42$). This higher threshold after down-regulation of left dPMC indicates a decrease in perceptual acuity for detecting differences in tempo. As a control, we found no pre- to post-cTBS difference with sham stimulation (tempo deviation threshold: pre = $4.59 \pm .54\%$, post = $5.06 \pm .48\%$; $t(29) = -.857$, $p = .399$, Cohen's $d = 0.16$; See Figure 7.2B for more on the tempo timing test; See Figure 7.3B for tempo detection thresholds). A linear mixed effects model revealed no significant changes across conditions for pre- to post-cTBS down-regulation ($\chi^2(1) = 3.3225$, $p = .0683$), meaning this model does not support an effect of stimulation site on the pre- to post-cTBS threshold change.

Phase Timing Perception

T-test comparison of phase detection thresholds pre- to post-cTBS was not significant (phase shift threshold: pre = $15.81 \pm 1.55\%$, post = $17.07 \pm 1.59\%$; $t(29) = -1.265$, $p = .216$, Cohen's $d = .23$), thus the data do not support a change in perceptual acuity for detecting changes in phase. We also found no pre- to post-cTBS difference with sham stimulation (phase shift threshold: pre = $15.36 \pm 1.33\%$, post = $16.98 \pm 1.36\%$; $t(29) = -1.375$, $p = .180$, Cohen's $d = 0.25$; See Figure 7.2B for more on the phase timing test; See Figure 7.3C for phase detection thresholds). A linear mixed effects model revealed no significant changes across conditions for pre- to post-cTBS down-regulation ($\chi^2(1) = 3.2291$, $p = .0723$), meaning this model does not support an effect of stimulation site on the pre- to post-cTBS threshold change.

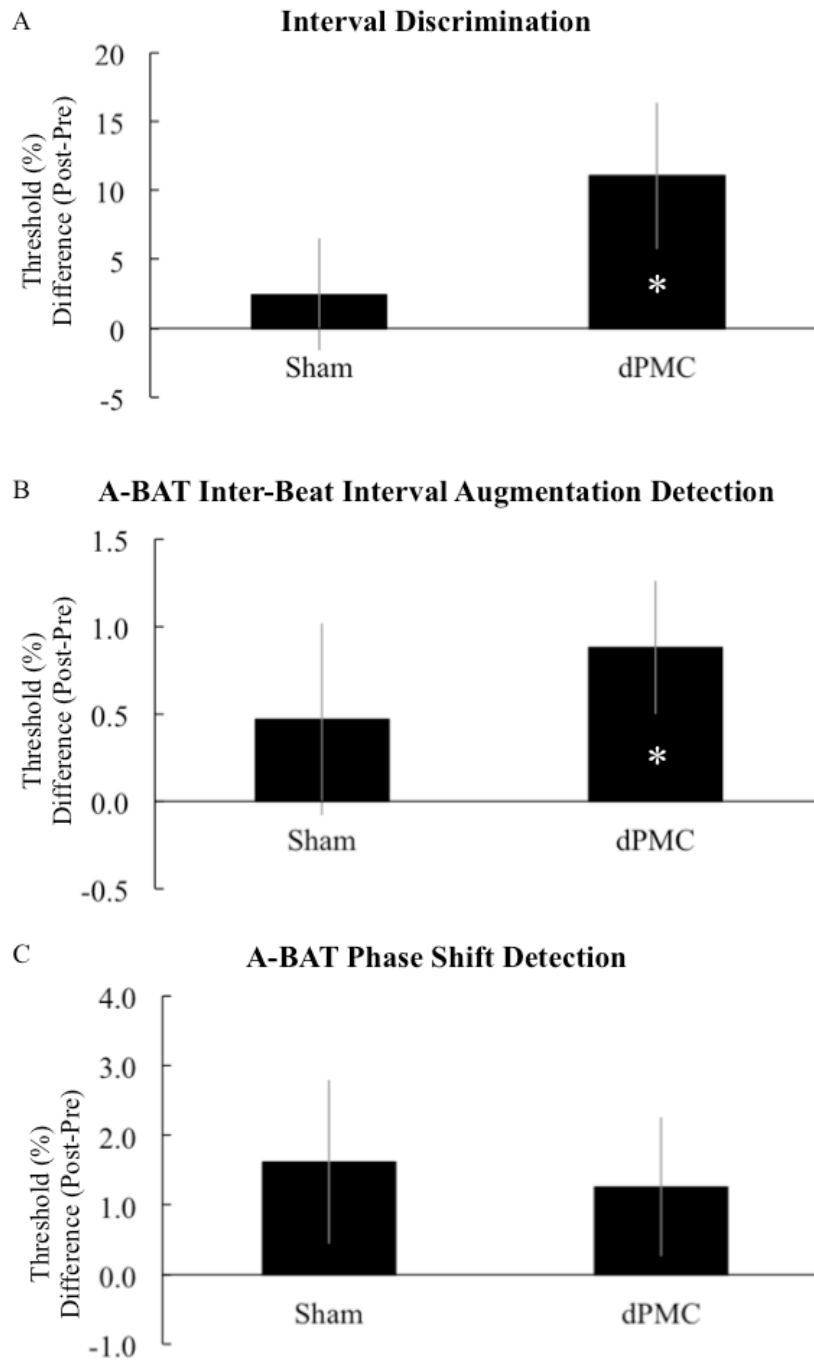


Figure 7.3. Mean post-cTBS minus pre-cTBS threshold differences for the three timing perception experiments in the left dorsal premotor stimulation condition and sham stimulation. Error bars represent ± 1 standard error from the mean. Asterisks indicate significance at $p < .05$ (A) Experiment 1: Single-interval duration discrimination (Ross, Iversen, & Balasubramaniam, 2018; Grube et al., 2010) (B) Experiment 2: Musical tempo detection (A-BAT IBI; Ross, Iversen, & Balasubramaniam, 2018; Iversen & Patel, 2008) (C) Experiment 3: Musical phase detection (A-BAT Phase; Ross, Iversen, &

Balasubramaniam, 2018; Iversen & Patel, 2008). There was an increase in detection thresholds pre- to post-cTBS in experiment 1 ($t(29) = -2.083$, $p = .046$, Cohen's $d = 0.38$) and experiment 2 ($t(29) = -2.318$, $p = .028$, Cohen's $d = .42$) with left dPMC down-regulation.

Discussion

Using focal down-regulation of left dPMC with cTBS brain stimulation, the present series of experiments tested for specific causal roles of left dPMC in different aspects of timing perception. These experiments were designed to observe interval timing perception (Figure 7.2A; Ross, Iversen, & Balasubramaniam, 2018; Grube et al., 2010), musical tempo perception and musical phase perception (Figure 7.2B; Ross, Iversen, & Balasubramaniam, 2018). We found ($N = 30$) that cTBS down-regulation of left dPMC interferes with two aspects of timing perception: interval timing perception acuity (Figure 7.3A) and the ability to detect changes in musical tempo (Figure 7.3B).

In a design similar to the one presented here, Grube et al. (2010) used cTBS to demonstrate causal involvement of motor networks in timing perception. In their work, cTBS to medial cerebellum raised perceptual thresholds on a test of absolute interval timing perception, but not on a beat-based timing test. Their work supports that networks used for absolute interval timing and for relative, beat-based timing are distinct. The work presented here also supports that absolute interval timing perception may rely on different networks than some forms of beat-based timing (here phase timing perception), but perhaps not on others (here tempo perception). We show that aspects of beat perception appear to be separable, but also that interval timing perception and beat-based timing may have points of overlap.

Interestingly, and contrary to our hypothesis, while our past cTBS study found that PPC down-regulation affected phase perception, with the dPMC target we did not find any evidence of disruption of musical phase timing (Figure 7.3C). Our initial hypotheses were based on the, possibly simplistic, notion that the entire dorsal stream would be equally involved in all aspects of beat timing, such that disruption of any node in the stream would lead to both tempo and phase timing effects. However, the pattern of results across our two studies suggest that tempo and phase timing might reflect distinct timing mechanisms sub-served by different nodes or networks (Repp & Su, 2013; Repp, 2005b) or different motor network hubs (Pollok et al., 2017). Numerous prior behavioral studies have suggested that in sensorimotor synchronization, tempo and phase may be supported by distinct processes, evidenced, for example, by the differences in tempo and phase error correction in sensorimotor synchronization (Repp & Su, 2013; Repp, 2005b). Repp (2005b) suggested that the two processes rely on distinct cognitive control mechanisms and possibly different brain circuits.

Pollok et al. (2017) used tDCS approaches to test for causal contributions of dorsolateral premotor cortex to an auditory-motor synchronization and continuation tapping task. Although differences in intensity, depth, focality, and mechanism of stimulation between TMS and tDCS lead us to only cautiously compare the two brain stimulation techniques, both techniques have protocols that down- and up-regulate cortex, and similar perceptual and behavioral effects might be expected to some degree. Pollok et al. (2017) show that both down-regulation and up-regulation to a dorsal premotor target

leads to worsening of accuracy in tapping continuation post-metronome, but no change in accuracy during auditory-motor synchronization, suggesting causal involvement of dorsal premotor cortex in precise internal timing of isochronous sequences but not in sensory-guided timing. Specifically, Pollok et al. (2017) show that down-regulation leads to a hastening of tapping with smaller inter-tap intervals, and up-regulation leads to a slowing of tapping with larger inter-tap intervals.

The mechanisms of premotor cortical contributions to timing accuracy for tempo are uncertain, as is how tempo timing relates to predictive beat-based timing in the case of complex rhythms. However, Pollok et al. (2017) show that tDCS down-regulation of dPMC seems to increase, instead of decrease, tendency for negative mean asynchrony, a hallmark of predictive timing, while up-regulation of the area seems to decrease negative mean asynchrony. This is somewhat surprising based on theories of premotor timing prediction, and indicates that the specific mechanisms of dPMC for timing prediction are not yet clear. Pollok et al. (2017) suggest that different cortical areas within motor control networks have distinctive roles in sub-second timing. In support of this hypothesis is dissociation between left posterior parietal cortex (Ross, Iversen, & Balasubramaniam, 2018; Krause, Weber, & Pollok, 2014; Krause et al., 2012) and left dPMC in specific timing task interference (Pollok et al., 2017), and the work presented here.

Pollok et al. (2017) used an auditory-motor synchronization and continuation tapping paradigm. We uniquely show here evidence for causal contributions of premotor networks to auditory timing perception in the absence of a motor task, which supports the predictions outlined in the ASAP hypothesis (Patel & Iversen, 2014), although it also reveals the need for a more nuanced expansion. Future studies are needed to reveal specifically which premotor networks are involved in different aspects of auditory timing perception.

One limitation of the current design is that our three experiments used adaptive thresholding tests of timing perception acuity that have not been verified to estimate the same perceptual thresholds across tests. That is, the interval discrimination test and the musical tempo and phase subtests of the A-BAT have not yet been shown to be comparable in difficulty and therefore we cannot yet conclude that task ease or difficulty do not contribute to a null result. It is thus not possible to compare the thresholds across the three studies. This concern does not impact positive results. Thus, while our data show evidence for a causal role of dPMC in musical tempo perception, but not in phase perception, this cannot be considered a dissociation between tempo and phase timing perception at this time. We can, however, compare like tests across our two studies (Ross, Iversen, & Balasubramaniam, 2018) and unambiguously state that we observed phase effects with left PPC down-regulation but not with left dPMC down-regulation, and conversely tempo effects with left dPMC down-regulation but not with left PPC down-regulation. Further work, with explicitly matched difficulty across perceptual tests will be needed to dissociate between different types of timing perception.

Another limitation of the current approach is that individual differences in perceptual thresholds on these tests combined with known individual differences in response to cTBS protocols (Hamada, Murase, Hasan, Balaratnam, & Rothwell, 2012) results in considerable variability in the perceptual threshold data. This variability might explain why the linear mixed effects models comparing pre- to post-cTBS change across

stimulation condition (sham vs. left dPMC) were not significant, while pre- to post-cTBS threshold means clearly increased after dPMC stimulation, but not sham.

Conclusion

Findings from the present studies suggest causal involvement of left dPMC in interval timing and musical tempo timing perception, and thus support hypotheses that the motor system plays an active role in timing and beat perception. We found no evidence for causal involvement of the left dPMC in musical phase timing perception. Our studies also demonstrate that tempo, phase, and absolute interval timing might recruit different distributed networks in the brain.

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Chapter 8

Discussion and Conclusions

Sound Informs Movement Control

We present evidence that the sounds we hear can affect balance and play into balance control mechanisms. This is an example of how audition can directly inform action, even without intentional entrainment. Little is known about how sounds influence postural sway, and about how different types of sounds influence sway in different ways. I have focused on the influence of unstructured sound in the form of white noise and structured sound in the form of music.

Although we present some plausible explanations for why sound and music reduce postural sway variability, and support for these explanations, further investigations are needed to dissect the causes and mechanisms underlying these effects. For example, stochastic resonance is an important topic of discussion for the effect of noise on balance variability that has clinical implications and follows from previous work on balance control (see Priplata et al., 2002; Priplata et al. 2003; Priplata et al., 2006), but any level of detail pertaining to the specifics of this auditory-motor interaction is not known. In addition, the critical components of stochastic resonance are thought to be noise and some type of sub-threshold signal in a threshold based system, but it is unknown how critical it is that the noise is random or that the signal is sub-threshold. However, regardless of the shortcomings, this work adds to the accumulating literature supporting that perception (in this case auditory perception) informs movement control by demonstrating that sounds can influence subtle movements involved with balance maintenance.

It should be noted that the literature on postural sway is backed by densely sampled movement tracking of continuously evolving sway. This paradigm produces rich time series datasets that are conducive to nonlinear dynamical and multiscale analyses. This approach can be contrasted with the causal methods we present using TMS to observe specific perceptual changes with focal cortical disruption. Our beat perception work relies heavily on mechanistic theory-driven hypotheses and explanations and on largely reductionist methods, including psychoacoustics. However, both approaches here resulted in support of the perspective that perception and action are closely tied, influencing each other bi-directionally, with perception informing action and action planning informing perception. Every methodology used in the brain sciences makes assumptions and has weaknesses, but underlying truths about the nervous system should be apparent across paradigms.

One way, going forward, to bridge the gap between the two paradigms, and to avoid fallacies of interpretation due to methodological weaknesses, is to pair continuous time series methods (such as movement tracking and EEG) with mechanistic theory-driven causal experimental designs. Technological advances, such as TMS compatible EEG systems and mobile EEG systems, are strengthening the potential for experimental designs that are sympathetic to ecological frameworks, robust to single-method pitfalls, and that result in clear cause and effect conclusions about brain function. Another way to bridge the gap between the two paradigms is to design causal studies based on theories that contextualize brain processes within body-environment systems. Motor simulation

theories are a good place to start, and can thus provide some mechanistic and ecological explanations for perception-action interactions, such as in musical beat perception.

Movement Planning Networks Inform Sound Perception: Motor Simulation Theories of Musical Beat Perception

How we move to music has become a systematic field of inquiry that focuses on body synchronization with musical rhythms (Iversen & Balasubramaniam, 2016; Janata, Tomic, & Haberman, 2012; Repp, 2005a; Repp, 2005b; Ross, Warlaumont, Abney, Rigoli, & Balasubramaniam, 2016). Many have marveled at the ubiquity of the skill across cultures (Madison, 2006; Madison, Gouyon, Ullén, & Hörnström, 2011; Janata et al., 2012) and that it has neural signatures that are present early in infant development (Kuhl, Ramirez, Bosseler, Lin, & Imada, 2014). Musicality and musical auditory-motor entrainment may have a place in our evolutionary history, perhaps as a predecessor to language or through gene-culture co-evolution (Patel, 2018; Patel, Iversen, Bregman, & Schulz, 2009), or to support complex auditory sequencing as proposed by the gradual audiomotor evolution hypothesis (Merchant & Honing, 2014). Music impels us to move in time with a perceived pulse or beat, which suggests there is a forward connection between auditory and motor systems that enables sound to guide movement (Stephan, Heckel, Song, & Cohen, 2015), and this relationship has been explored for movement rehabilitation in patients with Parkinson's disease (Ventura, Barnes, Ross, Lanni, Sigvardt, & Disbrow, 2016; Nombela, Hughes, Owen, & Grahn, 2013; Thaut et al., 1996) and during recovery after stroke (Altenmüller & Schlaug, 2013).

An interesting and largely unexplained phenomenon is that motor planning networks are active when we merely listen to music with a beat without moving at all (Chen, Penhune, & Zatorre, 2008; Bengtsson, et al., 2009; Grahn & Brett, 2007; Grahn & Brett, 2009; Stupacher, et al., 2013; Iversen, Repp, & Patel, 2009). An open question is: Is the motor system necessary for musical beat perception, or is this motor activity in the brain a consequence of unexecuted, or covert, movement during beat perception (Ross, Iversen, & Balasubramaniam, 2016)? The former view may be surprising at first consideration, but is consonant with the idea that perception and action are intimately coupled in a continuously interacting bidirectional perception-action relationship (Gibson, 1966). In this view, perception informs motor planning and the motor system influences active perceptual processes. This bi-directionality between action and perception is present in many models and theories of musical beat perception, which we describe here. While there is a long history of study in how sensory systems inform action, there is mounting evidence for more bi-directionality between the systems—that internal forward models make predictions about sensory consequences of motor acts and the proposed outcome is that those predictions help guide action and scaffold perception (Prinz, 1997; Wolpert & Flanagan, 2009). An important task for music neuroscience, using studies of rhythm and timing, is to explore to what extent this bi-directionality exists between motor planning and auditory perception.

Here we describe theories that posit the role of the motor system as either (1) “shadowing” or “mirroring” the auditory system or (2) that suggest a more causal or predictive role without which human musical beat perception would be impaired. These theories come from observations of entrainment, studies that use brain imaging, lesion

studies, and internal model paradigms. We then contrast these theories with other motor theories, including those of mirror neurons and those of speech perception, and propose that brain stimulation is a necessary experimental step going forward in defining the causal role of the motor system in auditory rhythm perception.

Entrainment and Beat Perception

Many empirical studies have inferred from entrainment data that beat perception is anticipatory in nature (Miyake, 1902; Repp, 2005b; Woodrow, 1932). When people are asked to tap a finger in time with an auditory rhythm, precise timing analyses show that taps often temporally precede the beat, which is an effect that has been coined *negative mean asynchrony* (Miyake, 1902). The explanation is that humans spontaneously generate expectations of the timing of rhythmic components (Aschersleben, Gehrke, & Prinz, 2001; Drewing, Hennings, & Aschersleben, 2001), and this is reflected in anticipatory timing errors when trying to entrain.

Another aspect of beat-based timing that we learn from entrainment paradigms is that rhythm perception is tempo flexible. Rhythms can speed up or slow down and, despite these temporal fluctuations, people perceive an underlying rhythmic structure. In contrast to the rare cases of synchronous vocal production in non-human species, which is not demonstrably flexible, humans can entrain movements to a range of tempi between 94 and 176 beats per minute (Hanson, Case, Buck, & Buck, 1971; London, 2004; McAuley, Jones, Holub, Johnston, & Miller, 2006; Patel & Iversen, 2014; van Noorden & Moelants, 1999).

Both of these traits of beat perception in humans reflect that musical beat is a perceptual construct instead of a stimulus property, influenced by but not uniquely determined by rhythms. Musical beat is susceptible to conscious control and active metrical interpretation on the part of the listener (Iversen, Repp, & Patel, 2009), and the sense of beat actively shapes the perception of rhythm. Iversen and colleagues (2009) describe a study in which people were asked to impose different metrical interpretations onto a rhythmically ambiguous phrase. Magnetoencephalography (MEG) recordings reflected these imagined metrical structures despite physical stimulus invariance. A person's metrical interpretation influences early evoked neural responses in the beta range of oscillatory MEG, with a stronger response on the imagined beat. What is even more convincing is that these early evoked neural responses resemble those of non-imagined physical accents (Iversen et al., 2009). Negative mean asynchrony, tempo flexibility, and sense of beat that is separate from physical stimulus properties all can be explained by top-down influences on auditory timing perception. It is logical to surmise that motor system activity might play a role in these top-down contributors to beat perception.

To explore whether motor activity contributes to top-down aspects of musical beat, it must first be shown that beat perception is subject to influence by motor behavior. What is known is that overt body movement can improve perception of timing (Manning & Schutz, 2013) and influence perceptual interpretation of ambiguous rhythms (Phillips-Silver & Trainor, 2005; Phillips-Silver & Trainor, 2007). Overt and covert motor activities are associated with changes to perceptual acuity. Recent studies have shown improvements in beat perception and finger tapping entrainment to music when subjects

were instructed to search for the pulse by moving their bodies (Su & Pöppel, 2012). In other words, when we move to music, we understand the rhythmic elements better. Further research has shown that demonstrations of accelerating motion lead to faster perceived tempo of musical excerpts (Su, 2012; Su & Jonikaitis, 2011). Taken together, these results provide evidence that beat and meter perception is shaped by motor activity. However, it does not reveal what the role is of the motor system in beat perception when no overt movement is involved.

Imaging

One way neural mechanisms can be observed without overt behavior is with brain imaging technologies, such as fMRI, MEG and EEG. These approaches have repeatedly shown that parts of the motor planning system are active during rhythm perception, even in the absence of overt movement, particularly for rhythms that evoke a strong sense of beat. In particular, beat perception engages dorsal premotor cortex, supplementary motor area (SMA), pre-SMA, basal ganglia, and lateral cerebellum (Bengtsson et al., 2009; Chen, Penhune, & Zatorre, 2008; Grahn & Brett, 2007; Stupacher, Hove, Novembre, Schütz-Bosbach, & Keller, 2013). Although these activations are distributed across multiple regions, they are all areas of the brain that are associated with motor preparation. This large body of neuroimaging evidence allows us to confidently deduce that beat perception engages both motor and secondary motor structures consistently and robustly. Unfortunately, the glaring limitation of this work is that it also does not answer the causal question of the role of motor activity during music listening with or without body movement.

A parsimonious interpretation of this co-activation of motor regions while listening to rhythm, and a commonly referenced one, is that this activity is related to anticipatory movement preparation. Consistent with this “mere” motor-preparation view, corticospinal excitability is modulated by listening to music with a strong beat. Stupacher et al. (2013) measured motor excitability during passive listening using transcranial magnetic stimulation (TMS) and demonstrated that excitability was time locked to the beat, and the degree of excitability reflected the participants’ level of auditory–motor training. Further, motor excitability in amateur pianists while listening to a piano piece increases after learning to play that piece of music on the piano (D’Ausilio, Altenmüller, Belardinelli, & Lotze, 2006), and motor excitability is sensitive to differences in rhythmic properties between musical excerpts (Stupacher et al., 2013).

Additional support for motor planning involvement in auditory perception can be found in MEG and EEG studies of beta band neural oscillations, as mentioned in the above section (Iversen et al., 2009). Auditory beta-band modulation is influenced by top–down processes: voluntary metrical interpretation of rhythms modulates beta-band responses to sound (Iversen et al., 2009). Such modulation is suggested to reflect ongoing motor planning processes. Beta band modulation is thought to be related to anticipatory processing; beta activity decreases just after tone onset but its rebound may reflect sequence tempo (Fujioka, Trainor, Large, & Ross, 2012). The same study found co-activation of auditory and motor cortical areas, even without a motor response, although causality could not be addressed.

Lesion Studies

Traditionally in the brain sciences, causality has been determined using studies of damaged or lesioned brains. We can observe cases where dysfunction of motor regions impairs rhythm perception. Currently limited but accumulating evidence in this area suggests that motor system activation while listening to rhythms may not merely be an epiphenomenon of suppressed movement, but may also play a causal role in shaping rhythm perception.

Patients with impaired basal ganglia function due to Parkinson's disease (PD) show impairments in a rhythm discrimination task compared with age-similar control subjects (Grahn & Brett, 2009). In the abovementioned study, both PD and healthy participants were presented with a discrimination task using beat-based rhythms or non-beat-based rhythms. While there was no difference in discrimination ability between the groups for non-beat-based rhythms, discrimination of beat-based rhythms was reduced in the PD group suggesting that the basal ganglia are important for perception of musical beat (Grahn & Brett, 2009), perhaps for generating an internal beat structure (Grahn & Rowe, 2013). Although further research is needed to determine how direct and causal the basal ganglia's involvement is in beat perception, Kotz, Brown, and Schwartze (2016) suggest that the basal ganglia's role in beat perception might stem from some aspect of motor preparation or planning.

Internal Models

Discourse in another area that might shed some light onto the role of the motor system in beat perception is that of *internal motor models*. From the perspective of this work, putative internal models used for auditory expectation could be understood as either forward or inverse. Forward internal models, such as efference copies, are used to predict sensory outcomes resulting from motor behavior. Inverse internal models are used to plan motor behavior based on desired sensory outcomes (Miall, 2003; Pfordresher, 2011; Tian & Poeppel, 2010).

These models and their roles in coordinating action and perception can be illustrated with studies of singing. Studies of internal models involved in singing have looked at how altered perceptual feedback perturbs ongoing production, presumably through a mismatch with an existing forward internal model and disrupted inverse internal model creation. This has been shown with internal models for vocal pitch production (Pfordresher, 2011), volume production, known as the Lombard effect (Lombard, 1911; Zollinger & Brumm, 2011), and fingertip force production (Therrien, Lyons, & Balasubramaniam, 2012). Disruption of the process involving inverse internal models is thought to be the reason some people consistently sing pitches that are too high or low when trying to match pitch (Pfordresher, 2011). This phenomenon is referred to as poor-pitch singing, and has been shown to not be attributable to perceptual deficits in pitch perception, motor deficits, or pitch memory deficits (arguably, as outlined in Hutchins & Peretz, 2012). The majority of the general population can carry a tune with pitch and timing proficiency, but a small percentage cannot reliably match pitch even if they show no impairment in pitch discrimination tasks (Dalla Bella, Giguère, & Peretz, 2007). Pfordresher's (2011) explanation for poor-pitch singing is that it is a deficit in creating an inverse internal model from perception of a pitch that can then be used for

pitch production. This vocal imitation weakness has also been demonstrated in intonational speech (Pfordresher & Mantell, 2009).

Accurate predictions about internal and external sensory effects of action are needed for skilled movement (Wolpert & Flanagan, 2009), including those underlying the articulatory processes in singing. One key aspect of internal models is that predictions cannot be static but instead allow for online updating; discrepancies between predictions and sensory consequences are continuously translated into changes to the internal model (Wolpert & Flanagan, 2015; Wolpert & Flanagan, 2009; Wolpert & Kawato, 1998; Yang, Wolpert, & Lengyel, 2016). Mere shadowing does not support this informative and flexible interchange between action and perceptual consequences via error-based modification to the internal model. There are clear advantages to having a bi-directional predictive relationship between auditory and motor systems.

Specific Theoretical Proposals

Some domain-general frameworks have been developed, including ideomotor theories (Shin, Proctor, & Capaldi, 2010) and common-coding. Common-coding approaches present perception and action as having common representation in the brain (Prinz, 1997), thus making claims about the predictive nature of the relationship between the auditory and motor system. According to the common-coding accounts, actions are coded as the perceived effects of those actions (*action effects*). Thus viewing another person moving activates these action-perception representations, allowing for perceptual prediction generation. The theory is supported by evidence showing shared neural substrate for perceived and actualized movements, and by interference when the two try to access this representation simultaneously (Prinz, 1997), reminiscent of Gibson's (1966) account of perception being in service of generating opportunities for action, and vice versa.

In a recent article, Press and Cook (2015) argued that domain general motor contributions to perception undermine the theory that motor activation while watching human movement is for action simulation: that it is only shadowing. They describe a number of domain-general motor contributions to perception, including recognition of simple movement parameters (direction, position, velocity), timing, inference about human motion in masked point-light displays, mental rotation, and visual search. The authors classify these as domain general because they are not necessarily related to complex motor actions such as grasping; these contributions could be understood as generically relating to movement. However, this evidence does not negate that these contributions are used to form sensory predictions.

Contrary to the common-coding and shadowing accounts, the idea that the motor system may influence auditory cognition has been present in the literature for some time (Bolton, 1894), and has recently been discussed by a number of authors (Arnal, 2012; Jeannerod, 2001; Prinz, 1997; Rauschecker, 2011; Repp, 2005b; Schubotz, Friederici, & von Cramon, 2000; Sperry, 1952; Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009; Zatorre, Chen, & Penhune, 2007). Recent accounts of sensory gain during movement support top-down motor influences on sensory state (Niell & Stryker, 2010; Nozaradan, Schönwiesner, Caron-Desrochers, & Lehmann, 2016; Wekselblatt & Niell, 2015). Simulations developed by Karl Friston and colleagues show that there could be

shared representation encoding both motor intentions and motor behavior, and that this might allow for active inference, which can be understood as action-oriented predictive processing (Friston, Mattout, & Kilner, 2011). Based on these mathematical models, Andy Clark proposed a predictive coding model that describes motor behavior as a way of selecting sensory input (Clark, 2015). In this framework, information flow is driven by top-down sensory predictions about proprioception and other sensory effects, and the only bottom up information is in the form of prediction errors. This active inference is in the form of downward connections from motor cortex (as from sensory cortex) that carry predictions of sensory effects that are only met with bottom up prediction errors. This framework puts forth a forward model that is corrected when confronted by unexpected sensory consequences. It bypasses the need for inverse models and efference copies in favor of error modulated corollary discharge (i.e. encoded sensory predictions), and is a low cost strategy with minimal computational demands (Clark, 2015). In a recent variation on predictive coding, perception of rhythmic incongruity is modeled with an additional bottom up component: precision (Vuust, Dietz, Witek, & Kringelbach, 2018). In this “predictive coding of rhythmic incongruity model” (PCRI), predictions are adjusted based on prediction error that is *precision-weighted*. Precision, in this model, describes the weighting of error based on the statistical probability of error occurring. If precision is low, this means there is a high uncertainty about what the meter is, and if precision is high, this means the meter is very predictable. This predictability of rhythmic structure effectively up- or down-regulates the influence of sensory error on updating timing predictions (Vuust et al., 2018).

Another theory, the Action Simulation for Auditory Prediction (ASAP) hypothesis of Patel and Iversen (2014) makes a strong claim for a necessary predictive role of the motor system: activity in the motor planning system is necessary for beat-based perception, and fundamentally shapes our perception of events via connections in the dorsal auditory pathway enabling premotor, parietal and temporal cortices to interact. The ASAP hypothesis suggests that the motor planning system uses the same neural machinery involved in simulation of body movement (e.g., periodic movement patterns) to generate or entrain its neural activity patterns to the beat period, and that these patterns are communicated from motor planning regions to auditory regions where they serve as a predictive signal for the timing of upcoming beats and shape the perceptual interpretation of rhythms. This hypothesis expands on an earlier suggestion by Iversen et al. (2009) that in beat perception the motor system affects the auditory system by injecting precisely-timed beat related modulations, which itself was based on an earlier psychological suggestion that the beat may involve “covert action” (Repp, 2005b). In contrast to “mirroring” theories, and to the motor theory of speech perception (discussed below), under ASAP the putative motor planning timing signals may, but need not, be related to imagery of movements of the type that would be required to create the perceptual input. Instead, they may be purely abstract timing, possibly, but not necessarily coupled to specific actions.

The central neuroscientific claim of the ASAP hypothesis is that beat perception involves temporally precise two-way communication between auditory regions and motor planning regions. This is related to the concept of reentry, “a process of temporally ongoing parallel signaling between separate maps along ordered anatomical connections”

(Edelman, 1989). According to ASAP, (1) neural signals from auditory to motor planning regions provide information about the timing of auditory events; (2) these signals influence the timing of periodic motor planning signals in motor regions, and (3) these planning signals flow from motor regions back to auditory regions to provide a signal that predicts upcoming beat times. In forward models such as predictive coding, primary information processing operates on predictions of sensory consequences, but in simulation-based models such as ASAP, top-down (anticipatory) and bottom-up (reactive) processes work in parallel, continuously influencing each other.

Another extant model of beat perception that posits top-down influence on auditory processing is the dynamic attending theory (DAT), which proposes that attention is modulated with temporal event structure (Jones, 1976). DAT relates motor influence on auditory processing to active suppression during vocalization (Arnal, 2012). Nonlinear oscillator models suggest that one way this might be achieved is by entrainment of neural oscillations with rhythmic auditory events, with reciprocal interactions among several layers of the network required to predict the beat (Large, Herrera, & Velasco, 2015; Large & Jones, 1999; Large & Snyder, 2009).

Other Related Motor Theories

Although there is considerable evidence for (Rizzolatti & Craighero, 2004) and controversies surrounding mirror neuron theories (Hickok, 2009), it has been argued that mirror neurons might play an important role in generating inverse and forward internal models (Miall, 2003). Mirror neurons are best known for their activity during visual observation, but can also become active when hearing an action without seeing the action (Kohler et al., 2002). Although there are obvious parallels between the theories of motor simulation and mirror neurons (Koelsch, 2012), the mirror neurons associated with ventral premotor area do not appear to be related directly to more dorsal premotor areas that are associated with beat perception.

There is a long history of discussing motor involvement in speech perception, and we might turn to it for comparison and contrast. Much as there is motor activation when listening to rhythms, numerous studies show neuroimaging evidence of motor activation while participants listen to speech (Skipper, Nusbaum, & Small, 2005; Wilson, Saygin, Sereno, & Iacoboni, 2004). In addition, there is a range of evidence to suggest that speech effector muscles show facilitation when listening to speech (Fadiga, Craighero, Buccino, & Rizzolatti, 2002). MEG analysis of infants between the ages of 7 and 11 months supports that motor activation while listening to speech is present in infants that are just learning to make pre-speech sounds (Kuhl et al., 2014). It would appear that this multisensory and multimodal relationship is present very early in speech development, and that it is likely an integral part of speech perception. Some accounts of speech perception, such as the Motor Theory of Speech Perception (Galantucci, Fowler, & Turvey, 2006; Liberman & Mattingly, 1985) and Analysis by Synthesis (Stevens & Halle, 1967), propose that speech perception relies on motor estimation or expectation.

The Motor Theory of Speech Perception was proposed to address the problem of perceptual invariance (Liberman & Mattingly, 1985), which makes its motivation quite distinct from motor simulation theories of rhythm perception. Invariance is the observation that a speech signal can have considerable acoustic variation due to context,

the speaker's gender and vocal qualities, and noise but listeners are still able to group speech sounds into meaningful categories such as phonemes. Liberman and colleagues proposed that speech sound categories are derived by inferring the neural representation of the gestures that produced the sounds (Liberman & Mattingly, 1985).

The Motor Theory of Speech Perception has been criticized for a number of reasons including its relation to theories of speech modularity and lack of specification about how acoustic signals are mapped to gestures (Sussman, 1989). Another criticism of the Motor Theory of Speech Perception and motor theories in general is that patients with damage to the motor system can exhibit normal action recognition (Stasenko, Garcea, & Mahon, 2013), and normal phonemic discrimination, although explicit labeling of speech sounds is impaired (Stasenko et al., 2015). Stasenko et al. (2015) posit a more nuanced view that motor representations may be called upon when other language cues are not present, such as semantics or context.

Although there are similarities between motor theories for speech perception and motor theories for beat perception, there are also many clear differences. Perhaps foremost, in motor theories of speech, sounds are mapped to motor representations the perceiver would use to produce the same sounds. In complex music, at least for non-musicians, such a direct mirroring is inconceivable. Second, speech perception relies on linguistic context in a way that beat perception does not. Third, as mentioned above, the motivations behind the theories are distinct. Motor activity in speech perception was proposed as a mechanism for creating speaker invariance of speech perception, whereas motor involvement in rhythm perception is proposed as a source of temporally precise signals to modulate rhythmic expectation and grouping, as well as implement the observed willful endogenous influences on rhythm perception. Fourth, the neural circuits implicated in motor theories of speech are distinct from those proposed by motor simulation theories of beat perception. Speech listening has been shown to be accompanied by bilateral activations in superior ventral premotor cortex, which are associated with speech motor production, and in primary motor cortex (Wilson et al., 2004). Although there is activation during passive speech listening in motor areas (Wilson, Molnar-Szakacs, & Iacoboni, 2008; Wilson et al., 2004), this does not provide support for bidirectional predictive auditory–motor processes. In addition, the temporal regularity of rhythmic contexts could enable prediction in a way that naturalistic speech might not. Beats have a more predictable structure in a way that speech, with all its irregularities, does not. For this reason, beat perception might allow for more motor simulation than speech perception, and beat perception paradigms might be more ideal for investigations of perceptually relevant motor recruitment.

The Way Forward: Brain Stimulation

The evidence reviewed above can be organized into two perspectives: motor system activation while listening to rhythms is (1) only shadowing or (2) has a predictive and causal role in beat perception. Much of the evidence is suggestive of a predictive and causal role, but many questions remain that need to be answered to move forward with this work. How might we make further progress on these questions? We would like to make experimental suggestions for causal studies needed to test the validity of these perspectives. We remark on other motor theories of perception and how they do and do

not contribute to advancing support of either of these perspectives. In addition, further work is required to clearly elucidate how the dorsal auditory stream might help distinguish between music and acoustic stimuli such as speech (Hickok, Buchsbaum, Humphries, & Muftuler, 2003).

Transcranial magnetic stimulation (TMS) is a technique that uses magnetic field pulses applied to the surface of the scalp to cause functional changes in the electrical neural activity in superficial cortical regions (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005). TMS protocols use parameters such as magnetic field power and pulse frequency to induce temporary excitement or disruption to target cortical regions, and therefore can be used to change cortical activity during or before asking participants to do behavioral experiments to see if changing cortical activation leads to changes in behavior (Huang et al., 2005). Functionally, these protocols can be thought of as inducing safe and temporary brain lesions in order to observe any changes in the person's perception or behavior.

TMS protocols have been used to explore motor theories of speech. TMS-induced disruption of premotor cortex has been shown to disrupt speech perception (Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007), but Stassenko and colleagues (2015) argue that the spread of TMS-induced changes might lead to disruption of sensory regions in addition to premotor targets. Figure eight TMS coil designs advertise focal stimulation, but the spread of activation in nearby cortex or through network connections is not well understood. However, even in studies of clinical lesions we see support of motor theories.

There is some existing work with TMS showing, using causal designs, the neural substrate involved with timing abilities. Low-frequency repetitive TMS applied over left dorsolateral premotor cortex (dPMC) can interfere with accuracy on a finger tapping synchronization task to an auditory metronome, and this disruption in accuracy occurs whether the participant is tapping with their right or left hand (Pollok, Rothkegel, Schnitzler, Paulus, & Lang, 2008). Because synchronization employs beat-based predictive timing mechanisms, it may be concluded that left dPMC is involved in beat-based timing. Continuous theta burst stimulation (cTBS), a TMS protocol that down-regulates cortical activity at the focal target location (Huang et al., 2005), interferes with interval-based timing when applied over medial cerebellum, but does not interfere with beat-based timing (Grube, Lee, Griffiths, Barker, & Woodruff, 2010). This supports a functional dissociation between interval and beat-based timing, and suggests that cerebellum is involved in interval, but not beat-based, timing. In the work presented here, we show that cTBS to parts of the dorsal auditory stream can selectively interfere with interval timing, tempo perception, or musical phase perception (Chapters 6-7).

Although there is a scarcity of causal work on neural contributors to beat-based timing, the weight of these studies is considerable due to the strengths of causal designs. Additional causal work is needed to explore the current motor theories of beat perception, and to ground these theories to their neural underpinnings. TMS protocols provide powerful causal methodology that can temporarily alter cortical activity in focal motor and premotor regions, either by exciting or suppressing activity (Huang et al., 2005), and this can be used to test theories that claim that the role of the motor system is obligatory for beat-based timing (Ross, Iversen, & Balasubramaniam, in prep; Ross, Iversen, & Balasubramaniam, 2018). For example, disruption of the internal model/simulation

mechanisms for beat perception should lead to declines in accurate rhythm perception and auditory–motor synchronization. Thus, manipulating motor planning activity and internal model generation in a rhythm task should lead to changes in accurate rhythm perception and production.

Summary

The theories related to speech perception suggest that motor activation during speech listening could be mirroring/shadowing and also used for auditory processing. The long history of motor theories of speech provide beat perception theories with frameworks in which to operate, but do not meet the standard of proof for theories that propose that motor activation during music listening reflects predictive processes. Beat-perception and entrainment paradigms, internal model frameworks, and demonstrations of functional connectivity are contributing to mounting evidence for predictive simulations in motor networks. However, these methodologies can only provide suggestive evidence. Extending these paradigms using causal methodology is needed in order to conclusively show that motor networks not only shadow speech and music but also provide predictive models that can be actively updated and maintained. Direct tests of a causal role of the motor system in beat perception are needed that perturb the motor system, either through dual task paradigms or through direct neurostimulation. Motor theories of perception, such as predictive coding and the ASAP hypothesis, propose that motor simulation is likely integral to auditory beat-based timing. Beat perception studies have been used to demonstrate the strong relationship between motor activation and listening to repetitive sounds, and this relationship has possible implications for understanding evolutionary origins of music and its relation to language. Tests of the theories of motor involvement for speech perception provide support for robustness of the link between motor system activation and auditory processing, and with evidence from beat perception and internal model paradigms, provide suggestive evidence for predictive simulation. Further research should implement causal studies to directly test for predictive motor models in beat perception. TMS is a technique that can be used non-invasively to investigate the causal relationship between motor simulation and beat-based timing, and more generally to help explore beat perception as a specific example of an action-based perceptual system, providing an example of how the study of music and brain can address general mechanisms of brain function.

Conclusions

The chapters presented in this dissertation demonstrate the strong relationship sound perception has with our body movements. Chapter 2 shows that unstructured auditory noise can reduce variability in anticipatory and feedback-based balance movements when we are standing upright, and we suggest that this might be explained by a feature of our nervous system called Stochastic Resonance (Ross & Balasubramaniam, 2015). Chapter 3 suggests that this effect has the potential to be used to address the problem of falls in typically aging adults (Ross, Will, McGann, & Balasubramaniam, 2016). Chapter 4 shows that rhythmically predictable sound, in the form of “Groovy” music, also reduces variability in balance movements, but in this case by inducing sub-attentional motor entrainment in the distributed muscles used for balance maintenance (Ross, Warlaumont, Abney, Rigoli, & Balasubramaniam, 2015). Chapter 5 shows that

music listening is accompanied by neural activity consistent with movement inhibition of the hands (Ross, Iversen, Makeig, & Balasubramaniam, in prep). Chapter 6 shows that interfering with activity in left parietal cortex using TMS brain stimulation disrupts time perception used for judgments of musical phase alignment, and we suggest this might be due to dorsal auditory stream disturbance (Ross, Iversen, & Balasubramaniam, 2018). Chapter 7 shows that interfering with activity in the left dorsal premotor cortex disrupts time perception used for judgments of duration and mismatches in musical tempo (Ross, Iversen, & Balasubramaniam, in prep). Together, Chapters 6 and 7 support the controversial claim that networks known to be involved in movement planning are critically recruited for auditory timing perception by showing that interference of these movement planning networks disrupts accurate timing perception. This work supports that the dorsal auditory stream is where premotor and auditory cortices interact to contribute bi-directionally to musical rhythm perception, as proposed by the Action Simulation for Auditory Prediction Hypothesis of Patel and Iversen (2014).

Collectively, this work explores the interaction between auditory and motor systems in humans with three main objectives. (1) To show that our auditory environment has clear and measurable impacts on subcortical and cortical movement control and planning, and on neural signatures of movement control. (2) To show that music can be used to explore predictive, reactionary (i.e. feedback-based), and inhibitory aspects of movement control. (3) To investigate the validity of claims that network activity used for movement control and planning can causally contribute to auditory perception. Demonstrated specifically in Chapter 3 but discussed throughout all chapters is the message that the robust synergy between human audition and action has enormous potential for clinical applications, which I would like to explore further as a more mature academic. However, the overarching significance of the work presented, I believe, is to show that action and perception are codependent processes with continuously updating bidirectional interactions, and viewing them as such reveals a sum that is greater than its constituent parts. I have accomplished this by focusing on the auditory system in lieu of all perceptual modalities, but recognize that the nature of this approach is contradictory to the goal. As shown by the research of Dr. Lawrence Rosenblum, and others, sensory perception is inherently multimodal, with motor interactions within and across all sensory modalities. In future work as a postdoctoral researcher, I will explore multimodal interactions between sensory perception and movement control. The largest shortcoming of the work presented here, however, is in functional and mechanistic explanations, grounded in neural substrate, of causal roles of motor planning on perception. Why do we use motor systems during perceptual activities? The discussion presents some theories that might help explain the role of motor planning networks in musical beat perception, but ultimately I must acknowledge that there are more open questions than explanations on this topic at the present time. Now is an exciting time for motor control enthusiasts, and I hope that my measly doctoral student contributions add something valuable to the puzzle of action for perception.

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To: Marjorie S. Zatz, Dean of Graduate Education
From: Jessica Marie Ross, PhD Candidate, Cognitive & Information Sciences
Date: May 3, 2018
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Thank you for your time.

Sincerely,
Jessica Ross



Jessica Marie Ross, Doctoral Candidate
Cognitive & Information Sciences, UC Merced



Professor Ramesh Balasubramaniam, Ph.D.
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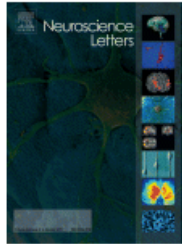


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Best regards,

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