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学 位 論 文

Neural correlates of musical improvisation performance:
a magnetoencephalographic investigation

(即興演奏に伴う神経活動：脳磁計による探究)

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Abstract

The ability to improvise, or execute free associative thinking, is a powerful and useful skill for all aspects of our lives in situations where creative ideation or spontaneous responses are required. One way of training this skill is through music. Basic musical ability is intrinsic to all people regardless of age, race, or physical ability. Thus musical improvisation training has wide applicability. Paired or ensemble musical improvisation is also considered conversational, and thus training it is akin to communication training via a non-verbal auditory medium. Correspondingly, musical improvisation is a popular therapeutic tool for non-verbal auditory communication, and reports indicate its long-term therapeutic use leads to improved communicativeness, sociability, and creative expression. Long-term training of musical improvisation in healthy populations has also been reported to improve, or be significantly correlated with sociability and creativity.

To better understand these therapeutic and training-based effects, it is important to clarify the nature of brain activity associated with improvisational music performance. A fair amount of work regarding this has already been done in modalities such as magnetic resonance imaging (MRI), functional MRI, and electroencephalography (EEG). These modalities respectively offer insight into the structural, hemodynamic, and spectral neural correlates. However, how brain activity in different oscillatory frequency bands is modulated in different brain areas due to improvisational music performance has hitherto been largely unclarified. To this end, studies employing magnetoencephalography (MEG), which permits spectral-spatial analyses of brain activity, are well suited. Some MEG studies regarding music performance have been reported. However, aside from my own work, I have found no reports regarding improvisational music performance in MEG.

The primary goal of this thesis was to demonstrate the feasibility of musical improvisation performance experimentation in MEG, and produce results that would not only have practical

relevance, but also drive future studies regarding musical improvisation training/therapy and contribute neurophysiological evidence supportive of their wider implementation. To accomplish this, I designed and constructed two unique, MEG-compatible musical instruments. I also established an experimental paradigm for musical improvisation performance modeled after conversational forms of music performance used in real live performance or therapy. I then used these instruments and the musical improvisation performance paradigm in two studies. The first study targeted predominantly non-musicians (N = 13). The second study targeted improvisationally experienced musicians (N = 13). Both studies investigated spontaneous source-level brain activity associated with improvisation performance in three different frequency bands: theta (5-7 Hz), alpha (8-12 Hz) and beta (15-29 Hz). The second study furthermore investigated correlations between improvisation-associated brain activity and creative ability (N = 14).

As a result of these studies, I was able to significantly differentiate spectral-spatial brain activity associated with improvisational cognition in non-musicians, improvisationally experienced musicians, and in improvisationally experienced musicians with high creative ability. The inexperience of the non-musicians was reflected by lower alpha band and beta band activity during mental imagery of musical improvisation performance compared to copied performance in parietal brain areas, a sign of inefficient integrative processing during creative ideation. Improvisationally experienced musicians meanwhile demonstrated greater theta activity in left temporal rhythm production and communication areas, greater alpha activity in left sensorimotor and premotor areas, and less beta-activity in areas associated with inhibition control. These findings highlighted the communicative nature of the improvisational style used, and support the notion that production of novel auditory content may be facilitated by a more internally-directed, disinhibited cognitive state. Finally, compared to improvisationally experienced musicians with low creativity, those with high

creative ability inversely exhibited less theta activity for *Improvise* than *Copy* in frontal inhibition-associated areas. These results suggested that fundamental engagement of disinhibition during musical improvisation performance is a strategy employed by those with higher creative ability.

Far more than merely demonstrating the feasibility of musical improvisation performance experimentation in MEG, the present thesis has produced results that corroborate findings from other modalities, and deepen the knowledge in this field. Most importantly, the establishment of its practical paradigm provides a solid foundation for further direct neuromagnetic investigation into the effects of improvisational music training and therapy that will hopefully support its wider implementation.

Dedication

This thesis is dedicated to my daughter, Noa, who has affirmed to me the importance of improvisation in music, art, and play; who has reminded me what it is to see life with a profound sense of wonder; and who everyday inspires me to be a better person for her and for the world in which we live.

Preface and Acknowledgements

The following thesis concerns a topic that has become central to my life – improvisation. Improvisation has long been embodied in my behavior and an essential element to my favorite hobbies. However, my decision to begin embracing improvisation philosophically, and actively choosing life paths that required it (i.e. choosing the unknown over the known), was thanks to meeting Erik Christensen. Indeed, if the origin of my path to this thesis could be traced to any encounter with any one person, it would be to him. Prior to meeting Erik, although I had realized that I was in a garden, and walking down a forking path, I had never considered venturing down any path except the one whose destination was predetermined and known. Thanks to Erik, venturing down one of the unknown paths is precisely what I did, and it has led me on the most ridiculous, wayward, inexplicable, unpredictable, unconventional, fascinating adventure so vapid of idleness that I have become intractably addicted to going down them. How did Erik exert such an influence? He showed me some books, books by Ondaatje, Proust, Kafka, Saint-Exupéry, and perhaps most influentially Borges. It was equivalent to dropping in my lap a set of keys to a spaceship with unlimited fuel to travel the universe. Of course Erik too had had his own share of experience with branching out onto unknown paths. I suppose it was only inevitable and necessary that the habit would rub off on somebody else along the way. I, for one, am extremely grateful that it did, for my life has been infinitely better for it. Thank you, Erik, from the bottom of my heart.

Thank you to Clay Lewis for teaching me the true meaning of the phrase, “It hurts so good.” Through your coaching and guidance, I not only learned that the most arduous and difficult roads lead to the best destinations, but I also learned to endure, overcome, and most importantly, enjoy all the challenges along the way. Thanks to you and this knowledge, completing my doctoral degree never seemed insurmountable or oppressive. Rather, it seemed inevitable. All the stress, sleeplessness, and pain I have encountered along the way

have been like sore muscles after good hearty workouts. And of course every workout and every bout of sore muscles only leads to you running faster and jumping higher, progressively improving with every step towards your goal, and oh it really does hurt so good.

Thank you to John and Elizabeth Harper, Ron and Nancy Kuzdak, and John Coleman, your friendships were lights in the darkness, and your homes islands of respite during my first major foray into the unknown. To John Coleman in particular, thank you for teaching me that one can simultaneously be a scientist, a Cape Cod fisherman, a drinker of good whiskey, and a hockey player who is not afraid to remove his false teeth when someone tries to push him around. Thank you all for your trust, your love, and your generosity throughout some of the most challenging and eventful periods of my life. That I have come this far in no small part thanks to the positive influence of your friendship and care. Thank you so much.

Thank you to my big brother, Daniel Schoenbrod, for traveling 340 miles every other week to teach me your knowledge and skills, for seeing in me more than I could see myself, for giving me the opportunity to teach, to lead, and to grow. Training Wing Tsun with you cemented my interest and passion for improvisation, and the confidence and insight I have gained through your tutelage and friendship have served me in every facet of my life, including the pursuance of this degree. Thank you. Thank you too to David Ko, Jason Wood, Josh Palideni, Tim Reißmann, Kai-Michael Pitzen, and all the other members of our school.

To my dear friends, Tomoyuki & Mikiko Endo, your kindness and friendship prompted me to embark down one of the most extraordinary paths I have ever taken. Indeed, I hold you both personally responsible for me learning Japanese, finding a wife, moving to Japan, building a family, and ultimately pursuing my doctoral degree at Hokkaido University. You and your whole family are precious to me, and I am forever in your debt.

To Ron McPherson, I could not have asked for a better scientific mentor. By working with you I learned how to write, how to think, how to argue. I learned what it means to accomplish more by 8:00AM than most people accomplish by 5:00PM. I learned how to make really strong coffee, and negotiate good deals on guitars. I learned that you can never know how much you do not know. Most importantly, through General Tso's chicken take-out, music jam sessions, an occasional pint at lunch, and daily banter between a cubicle wall, that science is just as much about the inquiry as it is about the relationships we build with our colleagues. Thank you so much for all you have taught me, and your continued support over all these years.

To Christine Gleason, Richard Kopke, Anthony Horner, and Sandra Juul, thank you so much for giving me a place in your laboratories, and permitting me to gain scientific experience and skills that have become invaluable for completing this thesis. To Sunny in particular, thank you not only for your professional support, but your kindness and compassion for me personally and for my music.

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Hwang, thank you so much for inspiring me and guiding me towards pursuance of my doctorate. Who would have thought it was possible to just walk into one of the best universities in Japan and study whatever I wanted?! I certainly would not have if it had not been for you. Thank you so much to you and your whole family. I hope I can pay forward the extraordinary blessings of your kindness and generosity.

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List of Abbreviations

MEG: Magnetoencephalography
PSP: Postsynaptic potential
EEG: Electroencephalography
MRI: Magnetic resonance imaging
fMRI: Functional magnetic resonance imaging
SQUID: Superconducting quantum interference device
HPI: Head position indicator
ICA: Independent component analysis
SNR: Signal to noise ratio
MNE: Minimum norm estimation
ROI: Region of interest
DMN: Default mode network
DLPFC: Dorsal lateral prefrontal cortex
IFC: Inferior frontal cortex
POP: Pars opercularis
POB: Pars orbitalis
PTG: Pars triangularis
RMF: Rostral middle frontal cortex
PrCG: Precentral gyrus
MIDI: Musical instrument digital interface
RM ANOVA: Repeated measures analysis of variance
HC: High creativity
LC: Low creativity
SPM Plus: Raven's Standard Progressive Matrices Plus test
STS: Superior temporal sulcus
CUN: Cuneus cortex
ICC: Isthmus cingulate cortex
PEC: Pericalcarine cortex
PCu: Precuneus cortex
SPC: Superior parietal cortex

CAC: Caudal anterior cingulate

FFG: Fusiform gyrus

ITG: Inferior temporal gyrus

LOC: Lateral occipital cortex

LNG: Lingual gyrus

PCL: Paracentral Lobule

PoCG: Postcentral gyrus

STG: Superior temporal gyrus

MTG: Middle temporal gyrus

FFG: Fusiform gyrus

PHG: Parahippocampal gyrus

SMG: Supramarginal gyrus

PCC: Posterior cingulate cortex

1 Introduction

Improvisation is the art or act of doing anything spontaneously without previous preparation. All of us engage in it in some form or another, in varying degrees, throughout our daily lives. Every social interaction we have is arguably a form of improvisation. Many mundane non-social situations could also involve improvisation, such as choosing a seat on the train in the morning on our daily commute, or opening a beer bottle when there is no bottle opener handy. For situations like these, improvisation is largely voluntary. However, often we improvise involuntarily, because the necessity to do so has been thrust upon us due to the occurrence of some unforeseen circumstance: inventing a story to pacify a child who you thought was asleep but has caught you in the act of throwing away an old toy; devising a new meal for dinner after discovering the main ingredient for the dish you planned to make had gone bad; or more serious; providing an impromptu work presentation to your boss in a sudden, unscheduled meeting. These kinds of unplanned situations, particularly when they involve our career, can be stressful. It follows then that our ability to mitigate this stress, and successfully cope and thrive under such conditions, is greatly dependent upon our comfort and skill at improvisation.

By the same token, our willingness to voluntarily put ourselves in new or unpredictable situations could also be said to be contingent upon our willingness and ability to improvise. Moreover, new or unpredictable situations are usually richly rewarding experiences. Consider activities such as: attendance of social gatherings to connect and network with new people; travel to new countries to experience different cultures; communication in a foreign language. These activities are indispensable for professional development, and for broadening our understanding of the world. With respect to travel in particular, Mark Twain once wrote, “Travel is fatal to prejudice, bigotry, and narrow-mindedness, and many of our people need it sorely on these accounts. Broad, wholesome, charitable views of men and things cannot be

acquired by vegetating in one little corner of the earth all one's lifetime.” Metaphorically speaking, travel is the voluntary deviation from the ordinary and routine, to accept, engage, and learn from new experiences. It intrinsically involves circumstances that are novel and cannot be planned, and therefore requires us to improvise. Hence, we could argue that improvisational ability is a key with which to unlock the richness of life. Seen in this light, improvisation is thus an extremely important and useful skill to train and develop.

According to its very definition, improvisation could be deliberately trained through any activity simply by making it spontaneous. However, as with any skill, training improvisation requires time and repetition. To this end, not all activities have the same practicability. For instance, to improvise through travel we must have money and an abundance of spare time. To improvise through sports we must have physical ability and access to the facilities to engage in the sport. To improvise through cooking we must either be hungry or have people available to eat the food. For improvisational training to be the most practical and have the widest applicability, the activity used for improvisation training should ideally be implementable with minimal space and equipment, require minimal mental, physical or technical ability, and be intrinsically understandable to the learner. One activity that meets these criteria, that is universal to people of all cultures, and inherently expressed from a very early age, is music.

The inspiration for this thesis incidentally was born out of me teaching improvisation to others through music. One of my students in particular started out as someone who was petrified by performance anxiety, and could literally and figuratively only play the notes on the page. After regular musical improvisation training, he became braver and more outgoing socially, leading events in the community, and now continues to apply his improvisational skills on and off the stage. Thus the effect of musical improvisation training was not limited to his musical ability, but extended to his behavior and personality in everyday life. The

result suggested a fundamental change had occurred in the function of his brain. I was amazed. Surely I was not the only one who had noticed the power of musical improvisation. As it turns out, no, I was not.

I soon learned that musical improvisation training was already being used widely in clinical therapies targeting those with cognitive impairment. Therapies using musical improvisation training were even being touted as potentially excellent rehabilitative intervention following stroke because of the simultaneous involvement of auditory, motor, emotional, and social processing. I furthermore discovered that there were some fascinating links between musical improvisation ability and creative ability. Correspondingly, there was a small but growing field in neuroimaging interested in the brain activity underlying musical improvisation as a window into creative cognition. Nevertheless, neuroimaging studies conducted with the therapeutic use of musical improvisation in mind remain scant, meaning that their addition to the field is needed if the results of my student and those of therapy in general are to be better understood and supported.

Improvisation training has been of invaluable benefit to my life, and I firmly believe in its power to benefit others and society at large. My long term vision is to see musical improvisation training become more widely promoted as a therapeutic and educational intervention for people of all ages, cultures and abilities, based a strong foundation of neurophysiological evidence. This thesis represents my attempt to contribute not merely evidence, but a realistic and practical paradigm that will drive a new line of neurophysiological research towards this long-term end. Over the next chapter I will provide background details regarding various aspects of this paradigm, beginning first with sections dedicated to the neurophysiological measurement modality employed: magnetoencephalography (MEG).

2 Background

2.1 MEG Overview

Pioneered by Cohen (1968), MEG is a completely non-invasive method for recording the magnetic fields emitted due to neural signaling within the brain. MEG is also completely silent, and therefore ideal for music studies. Based on the magnetic fields recorded with MEG, the source of the brain activity can be estimated or localized. Thus MEG permits the examination not only of how brain activity modulates over time, but also of where in the brain this modulation occurs. This section will go on to provide a basic overview regarding the origins of MEG signals, common signal types measured, and the instrumentation used for measurement.

2.1.1 Origin of MEG signals

The origin of MEG signals begins with the transmission of signals through our brain cells via the propagation of tiny electric action potentials, a fantastic process made possible through the pumping of positively and negatively charged chemical ions (e.g. potassium, sodium, calcium, and chlorine) in and out of countless locations along the nerve cell. Although incomparable to the speed of charged electrons flowing through a copper wire, the ionic conduction of action potentials within a nerve cell is still quite fast (between 70–120 m/s in large diameter peripheral nerves; Principals of Neuroscience, 5th Ed., Table 22–1). As discovered by Hans Christian Ørsted, moving electrical charge, or current, is accompanied by a magnetic field that, as André-Marie Ampère later showed, propagates perpendicular and counterclockwise to it (i.e. the right hand rule). This is true whether the moving charge be in a copper wire or a neuron in our brain. The strength of this magnetic field is proportional to the electric current. In mammalian nerve cells, the strength or amplitude of action potentials varies with the nerve's location and function. Postsynaptic potentials (PSP) in pyramidal cells

are very weak, and tend to range around 5 mV, as measured directly with electric probes (Biedenbach & Stevens, 1966). However, it is pyramidal cell PSP conduction that is thought to be most responsible for the generation of magnetic fields that can be measured non-invasively outside the skull. To generate magnetic fields strong enough from PSP conduction such that they can be detected with present day MEG technology is thought to require the coordinated firing of tens of thousands of neurons (Murakami & Okada, 2006).

An additional caveat for non-invasive measurability of MEG signals is that they need to have originated in neurons where it is possible to form open magnetic fields (i.e. the electric potentials need to have a net flow in one particular direction lest the magnetic fields generated cancel themselves out). Thus, it is generally assumed that the neurons mainly contributing to the MEG signal are the pyramidal neurons of the cortex, which are neatly arranged in palisades with their apical dendrites aligned perpendicularly to the cortical surface. Moreover, because the coils used to detect the magnetic fields are typically oriented parallel to the scalp surface (to be discussed more in section 2.1.3), MEG signals need to originate from electric current moving tangentially to the surface of the scalp in order for the resulting magnetic field to radiate out of the skull and be “seen” by the magnetic sensor. Consequently, signals originating in the sulci (i.e. inside the folds or fissures of the cortex) are “seen” more strongly by MEG than those originating in the gyri (i.e. on the crowns or convex surfaces of the cortex). To illustrate this, Figure 1 shows a cross section of the cortex where a brain signal (i.e. electric current) is flowing through pyramidal neurons in the fissural cortex in the direction indicated. This coordinated conduction of electric potentials thus gives rise to a magnetic field that can be seen and measured outside the head with an MEG sensor.

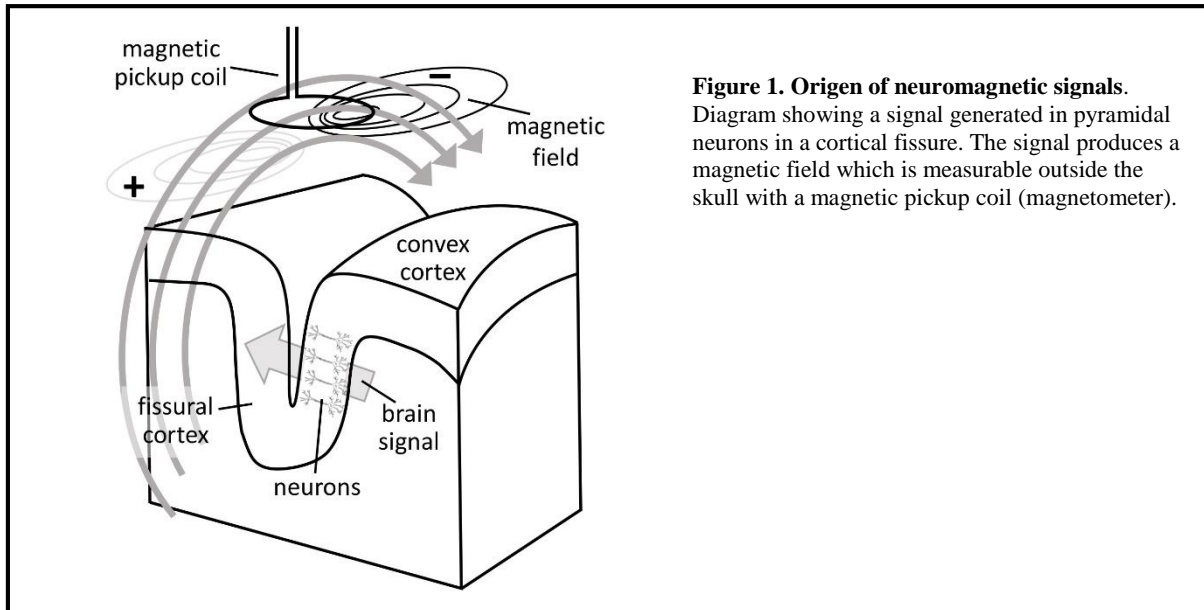


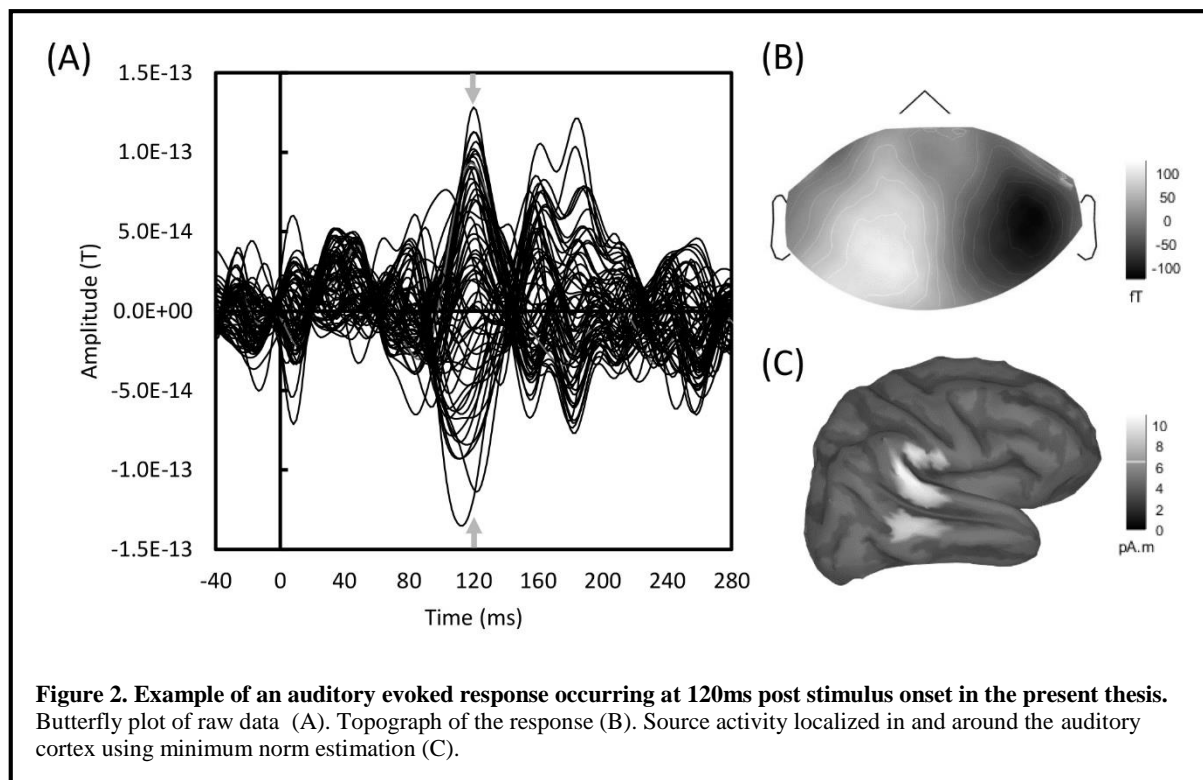
Figure 1. Origin of neuromagnetic signals. Diagram showing a signal generated in pyramidal neurons in a cortical fissure. The signal produces a magnetic field which is measurable outside the skull with a magnetic pickup coil (magnetometer).

2.1.2 MEG signal types

MEG signals are typically categorized into one of two types: evoked signals, and spontaneous oscillatory activity. Evoked signals are phase-locked responses to stimuli, and are generally only observed within a few hundred milliseconds of stimulus onset. The first MEG evoked signals were recorded in response to sensory stimulation by Brenner et al. in 1975. Since then, many studies have focused on evoked brain responses to numerous kinds of stimuli. For instance, Reite et al. (1994) reported on a typical evoked response to auditory stimuli that occurs approximately 100 ms after stimulus onset, called the M100 response. Figure 2 shows a typical M100 evoked response to auditory stimulation seen in study two of this thesis. Spontaneous oscillatory activity meanwhile is not phase-locked, but nevertheless does modulate in response to stimuli or event-related action, and can reveal how the brain changes in activation over a broad time course. The first report regarding spontaneous oscillatory activity was made by Berger in 1929 using electroencephalography (EEG). Often referred to as rhythms due their specificity to certain frequencies or frequency bands, spontaneous oscillations are generally categorized into the following types, in order from lowest to highest

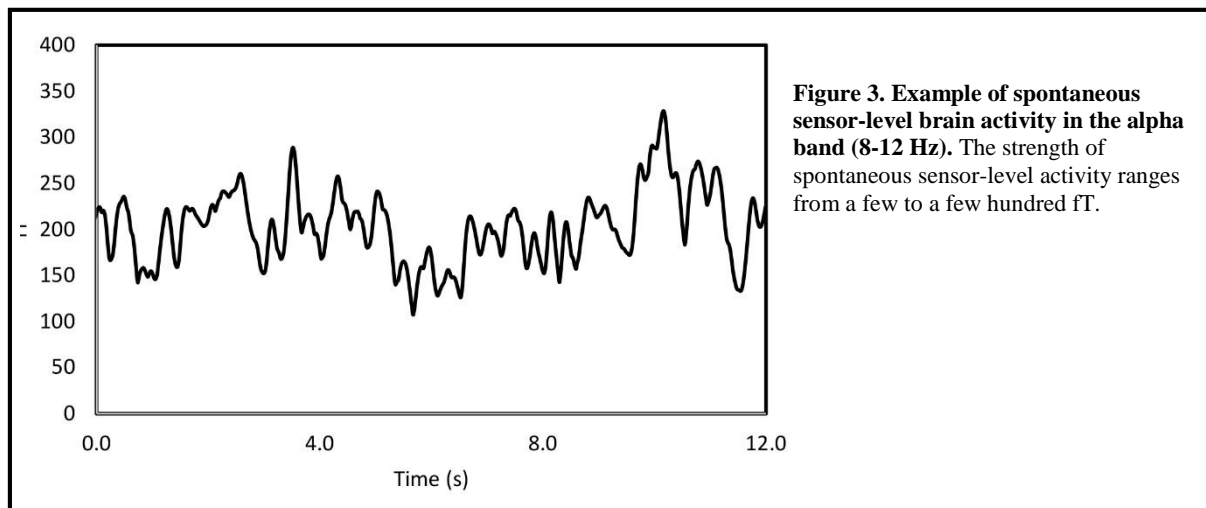
frequency: delta, theta, alpha, beta, gamma (Buzsáki, 2009). There are other types of oscillatory activity as well that refer to specific frequencies of activity originating from specific areas of the brain. For instance, tau rhythm refers to oscillations at 10 Hz generated in the auditory cortex (Lehtelä et al., 1997). Mu rhythm refers to oscillations between 8-13 Hz and 15-25 Hz generated in the sensorimotor cortex (Pineda, 2005). The general oscillatory types have also come to be associated with specific spatial and functional characteristics. For instance, alpha (8~13 Hz) modulation in parietal-occipital brain regions is reportedly associated with memory performance (Zanto et al., 2014), and attention (Forschack et al., 2017). Theta (4~8 Hz) modulation in temporal brain regions is reportedly important for decoding speech (Ghitza, 2012). Beta (15~30 Hz) modulation in frontal brain regions has been associated with inhibition processing (Swann et al., 2010).

This thesis will focus primarily on analyses of spontaneous oscillatory activity. Details regarding the frequency bands examined and the methods for extracting this data will be explained in later sections.



2.1.3 MEG instrumentation

Neuromagnetic signals are very weak. The neuromagnetic field strength produced by the simultaneous firing of 50,000 pyramidal neurons is thought to be only around 12 fT (Murakami and Okada, 2006). The sensor-level field strength of spontaneous brain activity detected in the studies involved in this thesis ranged from a few to a few 100 fT in strength (see Figure 3). For comparison, the Earth's magnetic field is about 50-90 microT, or about one million times stronger. In order to detect such weak magnetic fields from neuromagnetic signals, specialized sensors are needed. At present, the predominant sensor used in MEG is a superconducting quantum interference device, or SQUID.

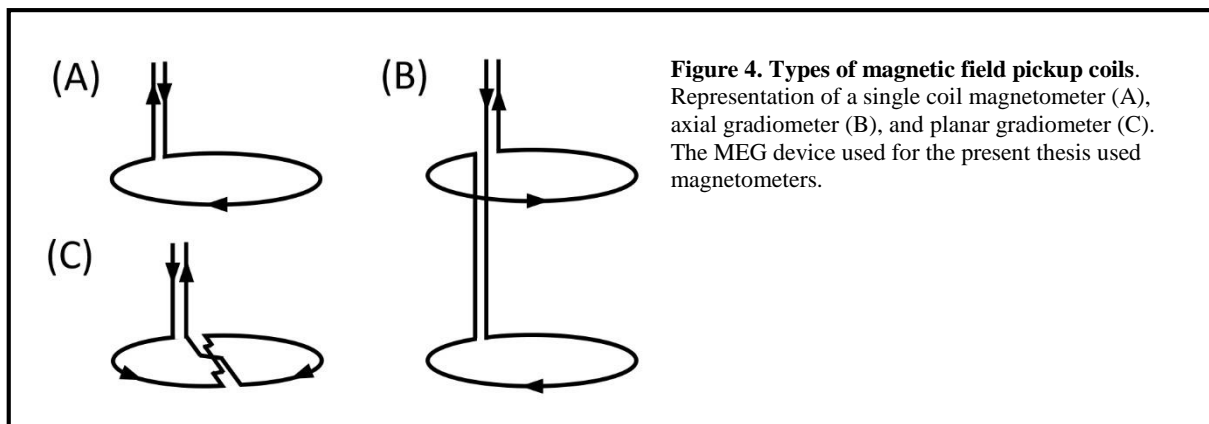


SQUIDs sense the magnetic field via pickup coils that are generally designed as one of three types: magnetometers, planar-gradiometers, or axial-gradiometers (See Figure 4).

Gradiometers are inherently insensitive to homogeneous magnetic fields (i.e. magnetic fields generated from distant sources), but have weak sensitivity to deep brain sources.

Magnetometers are capable of measuring brain signals from deeper sources than gradiometers, but are conversely sensitive to interference from homogeneous magnetic fields, and therefore require proper magnetic shielding for reliable measurements. Magnetometers and axial gradiometers have peak sensitivity to magnetic fields originating at the edge of the

detection coil, whereas planar-gradiometers have peak sensitivity to magnetic fields originating directly under the detection coil.



Modern MEG systems generally comprise an array of detection coils arranged such that magnetic fields can be recorded across the entire scalp surface. Furthermore, the detection coils are oriented parallel to the scalp surface such that they can be as close to the signal source as possible. The MEG system used for the present thesis comprises 76 SQUIDs connected to magnetometers, and covers approximately three quarters of the scalp surface.

As with any other MEG device employing SQUIDs, the SQUIDs are housed inside vacuum-insulated, helmet-shaped Dewar, into which liquid helium is filled to keep the SQUIDs at superconducting temperatures (a requirement for them to function). To minimize interference from external magnetic fields, the entire MEG measurement apparatus (i.e. the helmet/dewar containing the detection coils/SQUIDs) is usually housed within a magnetically shielded room. Shielded rooms are generally constructed of alternating layers of aluminum and mu-metal. The MEG measurement apparatus used for the present thesis is housed within a shielded room containing two shells: one of 1 mm thick aluminum, and another of 1 mm thick mu-metal. The total magnetic shielding provided by our shielded room is 40 dB.

In addition to the MEG measurement apparatus, our shielded room houses other items which are important for conducting MEG experiments. These items include: a chair, for the subject

to sit on, whose position can be adjusted for proper fit of the subject's head into the MEG helmet; a video camera and microphone to monitor the subject during recording; an electrostatic speaker to deliver auditory stimuli; a table which can be fixed upon the subject chair; and a response device (an electronic drum and keyboard were used in the present thesis). In principal, items housed within the shielded room are non-metallic, although non-magnetic metallic items may be present so long as their position is rigidly fixed, as was the case for experiments in the present thesis.

Other critical components of the MEG system are located outside the shielded room. For the present study, these components include: data converter/regulator, MEG data recorder, a computer for stimulus generation and delivery, a circuit board and computer for processing subject responses input via the response device, and a zero-latency audio mixer for processing stimuli and auditory feedback sound.

A general diagram showing set-up for the MEG system and related components used for experiments in the present thesis is shown in Figure 5.

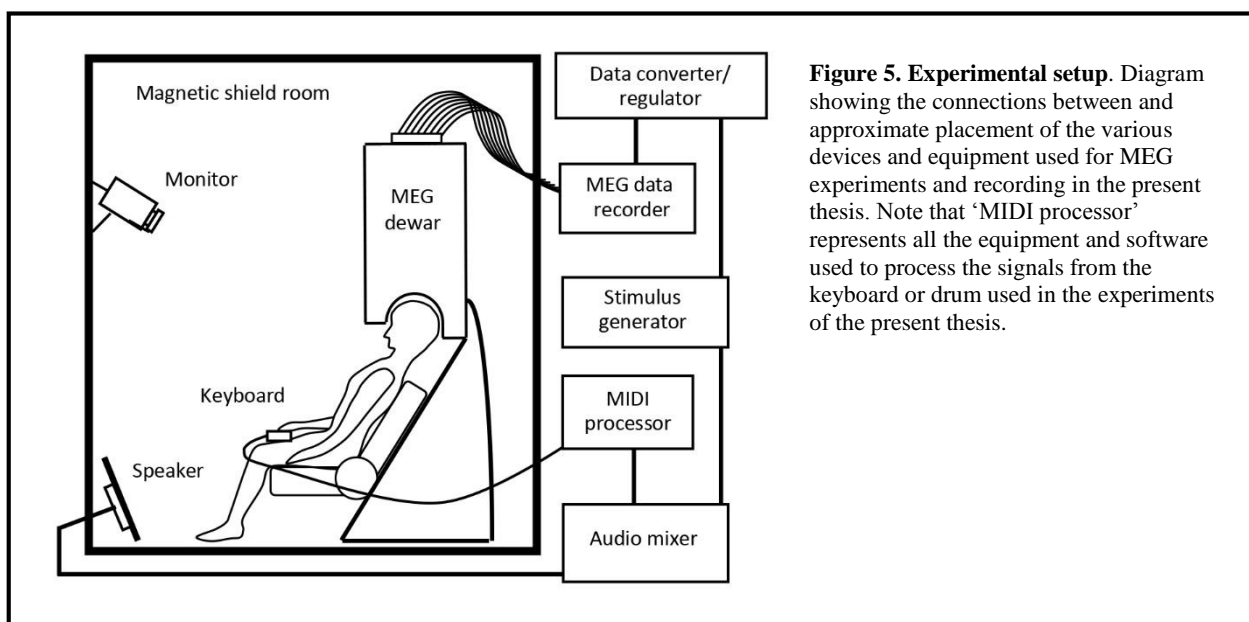


Figure 5. Experimental setup. Diagram showing the connections between and approximate placement of the various devices and equipment used for MEG experiments and recording in the present thesis. Note that 'MIDI processor' represents all the equipment and software used to process the signals from the keyboard or drum used in the experiments of the present thesis.

2.2 MEG Data Acquisition and Processing

The following sub-sections will describe the basic methods for MEG data acquisition and processing, as well specific aspects pertinent to this thesis.

2.2.1 Recording subject head shape and position

Prior to MEG recording, the subject's head shape is digitized and recorded, including the position of three landmark fiducials: the nasion, and the left and right preauricular points. Additionally, head position indicator (HPI) coils (three were used for experiments in the present thesis) are attached to the head, and their positions digitized. The HPI coils serve to help verify the position of the subject's head with respect to the MEG sensor array when positioned inside the MEG helmet. This is accomplished by pulsing a small amount of current through the HPI coils, which generates magnetic fields. As the position of the HPI coils relative to each other is known, along with the theoretical magnetic field strength produced by the current pulsed into them, their position can be accurately calculated. As for the fiducials and other digitized head points, they permit coregistration of the head position with structural anatomical data (T1 images) obtained via MRI.

2.2.2 MEG sampling and recording

The neuromagnetic signals strong enough to be measured by MEG are generally of low spectral energy (between 0.1-200 Hz). However, to prevent aliasing, sampling rates of at least twice the target analysis frequency must be used. For this thesis, MEG signals were online band-pass filtered from 0.6-200 Hz, and sampled at 600 Hz. Sampled MEG signals were then recorded on a computer hard drive with stimulus related events additionally recorded as trigger signals.

2.2.3 Cleaning the Data

Before a meaningful analysis of MEG signals can be conducted, the raw data must be cleaned of noise and other artifacts. For the analyses conducted in this thesis, the following steps were taken, the principals of which apply to any MEG data analysis.

First, the signals were filtered to a range more appropriate for the intended analyses via application of a band-pass filter from 1-40 Hz. Additionally, a comb filter was also applied at 50 Hz and related harmonic frequencies to remove line noise. Then, the recordings and power profiles from each sensor were scanned, and those which were overly noisy, poorly responding, or unresponsive (e.g. due to charge trapping) were excluded from further analysis. Next, the raw signals were scanned for physiological and environmental artifacts using what is known as an independent component analysis (ICA).

Simply put, ICA involves scanning the signals within a certain frequency band and dividing noise patterns into numerous individual or independent components. The topographies and wave forms of these components can then be visually inspected to confirm their relevance and contribution as noise artifacts (for a more detailed discussion on ICA and other artifact correction methods, please see Haumann et al., 2016). For this thesis, ICA was performed on raw signals from 1-30 Hz. The most common artifacts detected and removed by ICA were heartbeat and eye blinks.

2.2.4 Epoching and averaging

In general, even after cleaning and filtering MEG signals, a fair amount of noise will remain. This is because the magnetic fields produced by brain signals are so weak, and thus the signal to noise ratio (SNR) is very low. In order to improve the SNR, MEG experiments are designed with many stimulus-response events or epochs. During data processing, these

epochs are averaged together, effectively canceling out the noise, and leaving the stimulus-driven brain response. The number of epochs required for meaningful and appropriate analysis of MEG signals depends on factors such as the nature of the stimulus and the response to be measured, target analysis frequencies, etc. For this thesis, which analyzed spontaneous oscillatory activity, a minimum of 16 epochs per condition in each subject were sufficient for observation of significant differences between conditions and groups. However, the averaging of epochs did not occur until source activity was estimated and the spontaneous oscillatory source activity was extracted. Background for these aspects of MEG data analysis are provided in the next sub-sections.

2.2.5 Normalization to template brain anatomy

Before we can begin to estimate the origins of MEG signals, we must have a structural representation of brain upon which to model our estimations. This is where coregistration of fiducials and headpoints to MRI-based structural T1 imaging comes into play, as mentioned in the beginning of this chapter. For this thesis, in lieu of actual T1 images of each subject, which are time-consuming and costly to acquire, fiducials and headpoints were aligned and coregistered to a common template brain (ICBM152). The template anatomy was furthermore normalized to match the head shape of each subject in a process called, warping, resulting in a unique anatomical representation of the brain representative of each subject.

2.2.6 Source Estimation

One of the most meritorious aspects of MEG that sets it apart from other neurophysiological measurement methods is the ability to analyze spectral activity at the level where it originates spatially (i.e. at the source level). There are a number of methods in existence for estimating

the location of source activity, each with their own advantages and disadvantages. A detailed explanation of all of these methods is beyond the scope of this thesis. For those that are so inclined, an excellent primer on the subject is provided by Baillet, (Ch. 5 of MEG - an introduction to methods, 2010), or for further detail see Hämäläinen et al., (1993). Here, a basic explanation of the methods employed in the present thesis will be provided.

Estimating the spatial location of brain activity based on spectral information measured outside the head is mathematically very ill-posed. That is because for any given measurement of spectral activity, there are an infinite number of source activation patterns that could have produced it. Thus finding a unique solution for source activity based on MEG signals is impossible. However, we can reasonably and accurately estimate the source of MEG-based brain activity by making some key assumptions, and adding certain reasonable constraints to our calculations.

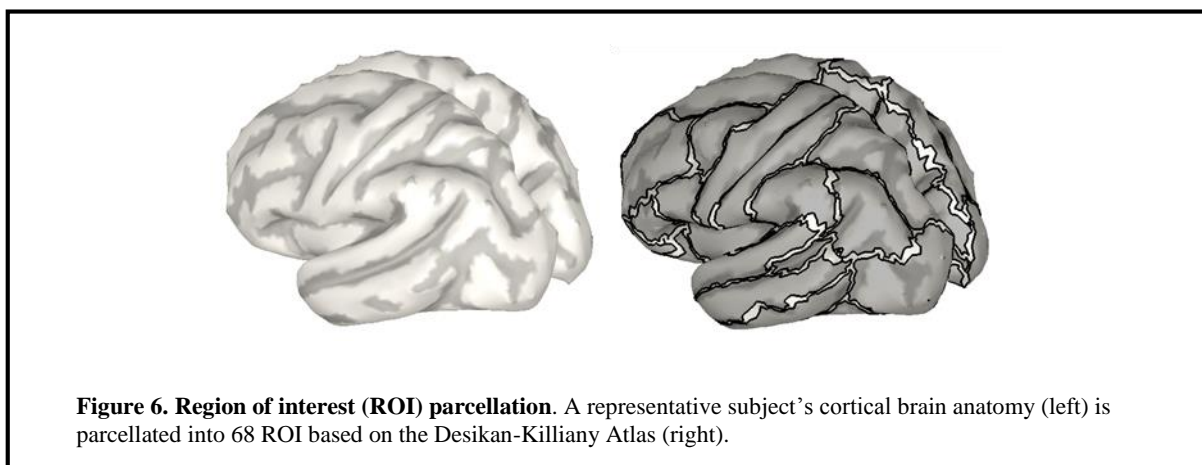
The first part of the estimation process begins by modeling how a neural activation at a given source location would look in our MEG recording. This is called the forward problem, and is where our assumptions and constraints begin. One of the most computationally friendly ways of solving the forward problem is to model the head as a sphere, and constrain the origins of neural activity to its surface, a reasonable approach as the main contributors to neuronal signaling are the pyramidal neurons in the cortex (see section 2.1.1). For this thesis, the forward problem was solved by using an overlapping spheres surface model. In this model, neural activity is fit to a spherical model of the head in correspondence with each MEG sensor (Huang et al., 1999). Thus, for a multi-sensor array, the head would be modeled as multiple overlapping spheres.

With this forward model complete, we can then move on to solve the inverse problem, that is estimate the origin of neural activity. The method used for this thesis was L-2 minimum norm

estimation (MNE). The L-2 MNE method is based on current source densities, three dimensional spatial vectors that indicate the direction and strength of current flow, and applies a constraint that favors solutions that have minimum energy (ref). Note that all MNE solutions in this thesis were constrained to the cortex surface in correspondence with the forward model used.

2.2.7 Region of interest parcellation

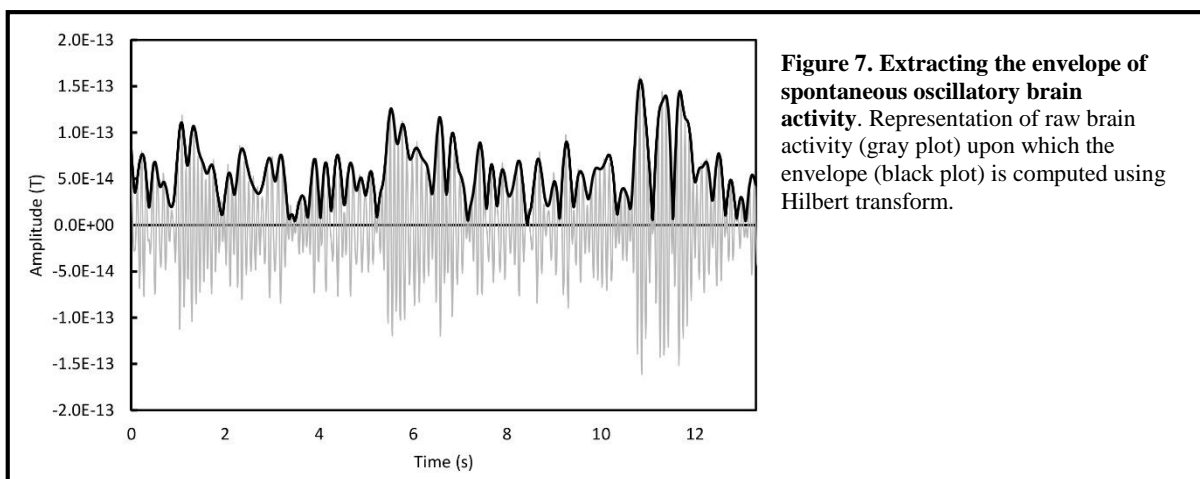
The results of the source estimation process permit investigation of brain activity across every point along the cortical surface. However, the purpose of this thesis was to explore brain activity more generally in discrete regions of the brain. To facilitate this kind of exploration of brain activity, the anatomical brain images of each subject were parcellated into regions of interest (ROI). The ROI used for this thesis corresponded to those in an established brain atlas called the Desikan-Killiany Atlas (Desikan et al., 2006). It comprises 68 ROI (34 bilateral homologues) based on the anatomical location of the gyri. A representation of the brain divided into these ROI can be seen in Figure 6.



2.2.8 Extracting spontaneous source oscillatory brain activity

This thesis focused on analyses of spontaneous oscillatory activity at the source level. To do this, source brain activity was first averaged across each ROI. This permitted decomposition and visualization of brain activity in specific frequency bands for each ROI, over each stimulus-response epoch. However, as mentioned earlier in section 2.2.4, in order to overcome the inherently low SNR of MEG signals, the brain activity must be averaged across a number of stimulus-response epochs. Furthermore, because spontaneous oscillatory activity is not phase-locked, additional processing is necessary prior to averaging, otherwise the spontaneous activity will be nullified (i.e. we will be left with mean phase-locked or evoked activity only). For this thesis, this additional processing step involved computing the Hilbert transform using the function included in the MATLAB Signal Processing Toolbox (MATLAB, MathWorks; see <http://www.mathworks.com/help/signal/ref/hilbert.html> for more details).

Simply put, the Hilbert transform extracts the envelope of activity in a given frequency band, as shown in Figure 7. This extracted envelope reveals how the spontaneous oscillatory activity modulates in amplitude over time. For this thesis, these envelopes were calculated for source-level brain activity in each ROI in targeted frequency bands for each stimulus-response epoch, and then averaged across epochs in each subject for each condition.



2.3 Improvisation in music

Music is composed of a number of elements such as pitch, tone, loudness, and rhythm, that can all conceivably be improvised. Musicians will generally make use of all these elements during their improvisation, simultaneously weaving them together into a distinct musical expression. However, the manner in which these elements are chosen, combined, and expressed generally varies in accordance with the type of improvisation a musician is performing.

Broadly speaking, musical improvisation can be divided into two types: idiomatic, and free (i.e. non-idiomatic). These can be further categorized into the subtypes: solo improvisation, and ensemble improvisation. Idiomatic solo improvisation would involve the musician playing alone within the confines of some stylistic or syntactic structure (e.g. a 12-bar blues in the key of A). Conversely, free solo improvisation would involve a single musician playing alone, unbound by a set metric, temporal, or even harmonic structure. The resulting music therefore does not adhere to any syntactic rules (Stenström, 2009: 318), and its characteristics are, "...established only by the sonic musical identity of the person or persons playing it." (Bailey, p.83. 1993). Idiomatic ensemble improvisation meanwhile would involve two or more musicians playing within the confines of some stylistic or syntactic structure, often with the improvisation being performed in turns. Lastly, free ensemble improvisation would involve two or more musicians playing non-idiomatically, with the music played by each musician strongly influencing that played by the other/s. As Fugate observed, "...each player can only impact the end result in direct relation to the percentage of the group which he/she constitutes." (1988: p46). However, precisely because of this influence or interdependence, free ensemble improvisation will often take on a syntactic structure. As Nachmanovitch relates, "There is no agree-on structure or measure, but once we have played for five seconds there is a structure, because we've started something." (1990: pp 94-95). This implies that the

very act of playing with others demands that the music take on some kind of structure by which the participants can interpret and communicate their musical expressions. In this light, ensemble improvisation appears very similar to language, and indeed has been referred to as synonymous with conversation (Monson, 1996). Ensemble improvisation can also permit deep psychological penetration into the emotions and thoughts of the participating players, or as Nachmanovitch puts it, “We open each other’s minds like an infinite series of Chinese boxes.” (1990: pp 94-95).

2.4 Psychological correlates of therapeutic and practical musical improvisation training

Ensemble musical improvisation’s two-fold quality of communication and psychological insight gives it therapeutic utility. Correspondingly, musical improvisation is frequently used in clinical therapies with patients who struggle with verbal, social, or emotional processing (Nordoff Robbins Research Department, 2012; Tomaino, 2013). Called improvisational (or active) music therapy, the improvisation permits the therapist and patient/s to communicate via their instruments using music instead of words in an ongoing musical conversation. In patients with depression, dementia, autism spectrum disorder, or other forms of cognitive dysfunction, improvisational music therapies have been reported to improve well-being, along with communication, sociability, and emotional and creative expression (Rylatt, 2012; Erkkilä, et al., 2011; Kim et al., 2008). Naturally, the focus of the patient’s music performance is therapeutic and is not concerned with musical quality. Indeed, the therapies are conducted in a way such that musical experience is unnecessary. To do this, the musical element that is improvised, and the instrument that the patient uses is simplified. Although the musical elements of pitch, tone, rhythm, and loudness are all conceivable options to focus

on, rhythm is arguably the most fundamental musical element, and hence it is used extensively in improvisational music therapy (Montello & Coons, 1998; Burns et al., 2001; Rickson & Watkins, 2003).

The benefits to social and creative expression garnered through musical improvisation may not be limited to therapy. Indeed, training ensemble musical improvisation has long been phenomenologically recognized to develop skills that are important for social communication such as adaptability, efficiency, fluency, flexibility, expressiveness, and creativity (Sparrow 1983). Regular practice or training of musical improvisation has also been tied to higher creative and communication ability as measured via tests of verbal divergent thinking. A study by Benedek et al. (2014a) found that compared to classical musicians and folk musicians, jazz musicians had significantly higher creativity scores, a result the authors attributed to the jazz musicians' more extensive improvisational training. Kleinmintz et al. (2014) similarly found that musicians trained in improvisation scored higher on creative fluency and originality compared with non-improvisational musicians and non-musicians. Even training the concept of improvisational communication using musical improvisation as a model has been shown by Haidet et al. (2017) in medical students to lead to high engagement in and creativity with verbal communication compared to students that did not undergo training.

This therapeutic and non-therapeutic evidence together regarding the effects of musical improvisation training demonstrates something very important. That is that verbal communication, which is itself a form of improvisation, can be improved by training improvisationally in a non-verbal medium – music. This implies that the cognition underlying improvisation involves common neurophysiological processes and substrates, and that the plastic improvements to them due to improvisation training are accessible regardless of the medium one is improvising in. Clarifying the neurophysiological processes and substrates

associated with improvisation would be of great clinical value for assessing the neurophysiological creative and social health of individuals, as well as monitoring the effects of improvisational therapy or training. Work towards this end is already underway in numerous fields using experiments employing musical improvisation tasks with improvisationally experienced musicians. These studies form an important backdrop for this thesis, and therefore are introduced along with some of their more pertinent results in the following section.

2.5 Neurophysiological processes and substrates associated with musical improvisation

At its essence, musical improvisation (and arguably language as well) could be said to involve processing related to auditory feedback and production, emotional interpretation, executive control, motor commands, somatosensory feedback, and memory, all of which must be simultaneously integrated and executed continuously in real-time. With such a complex array of processing occurring all at once, it might seem like an impossible task to isolate brain activity specific to musical improvisation. However, with appropriate experimental design, it can and has been done.

A number of neurophysiological studies regarding musical improvisation have been conducted via functional magnetic resonance imaging (fMRI) (Limb & Braun, 2008; Manzano & Ullén, 2012; Berkowitz & Ansari, 2008). Simply speaking, fMRI is a method for assessing changes in neurohemodynamics (i.e. cerebral blood flow). Increases and decreases in cerebral blood flow are thought to respectively reflect increases and decreases in brain activation. Particularly notable is a study by Donnay et al. (2014) which used a communicative style of improvisation akin to that employed in improvisational music

therapy, and observed activation of temporal brain areas associated with communication and sensorimotor integration. Donnay et al. (2014) also observed deactivation of frontal areas associated with executive processing. Similar frontal deactivation, albeit in a slightly different area, was also observed in jazz musicians during right-handed improvisational piano performance by Limb and Braun (2008). They proposed that this deactivation may be key to the spontaneity or disinhibition intrinsic to musical improvisation.

Electroencephalographic (EEG) studies, which measure the electrical potential of brain activity using electrodes placed on the scalp, have also made valuable contributions regarding brain activity during musical improvisation. Some of these studies have identified frequency bands and oscillatory characteristics of interest during musical improvisation. For example, Lopata et al. (2017) proposed increased oscillatory alpha power during musical improvisation compared to non-improvisational performance as a sign of increased spontaneous or bottom-up processing. Dikaya & Skirtach (2015) found higher levels of theta oscillatory coherence between left temporal-frontal electrodes, and higher beta spectral power over left frontal sensors during musical improvisation compared to other kinds of musical activity.

Meanwhile, Müller et al. (2013) found greater inter-brain synchronization of theta and delta oscillatory activity compared to higher frequency oscillatory activity during musical improvisation between two guitarists. Additionally, Adhikari et al. (2016) attributed decreased coherence with frontal oscillatory brain activity during musical improvisation compared to during performance of pre-learned music as important to the spontaneity of improvisation. Network-based analysis has also been used to identify potential regions of interest during musical improvisation. For instance, Wan et al. (2014) used causality analyses, and found that the frontal, parietal, and temporal regions were important for differentiating between brain activity during improvisational and non-improvisational music performance.

These neurophysiological studies shed light on the nature of brain hemodynamics and spontaneous oscillatory activity during improvisational cognition. However, how brain activity in different oscillatory frequency bands is modulated in different brain areas due to improvisational music cognition remains unclarified. To this end, studies employing magnetoencephalography (MEG), which permits spectral-spatial analyses of brain activity, would be well suited. Some MEG studies regarding music performance have been reported, such as one regarding mu rhythm suppression due to finger tapping on a drum (Caetano et al., 2007), and another regarding rhythmic brain activities related to singing (Gunji et al., 2007). However, at the time of this writing, the only report I have found regarding improvisational music performance in MEG is my own work (Boasen et al., 2018), which forms a significant portion of this thesis.

2.6 Neurophysiological correlates to creativity

Musical improvisation is a form of creative ideation. Moreover, as mentioned in section 2.4, musical improvisation experience and training has been correlated to higher scores on creativity tests, such as the Alternative Uses Task and the Torrance Test of Creative Thinking. These tests measure a sub-type of creativity called, divergent thinking ability, which is essentially the ability to come up with multiple ideas to a given problem. Moreover, the tests require subjects to come up with as many ideas as possible for each question within a brief set time limit, hence the fluency of creative ideation is an important index evaluated by these tests. Kleinmintz et al. (2014) proposed a model for creative ideation that involves a cycle of spontaneous or automatic associative processing for idea generation, and executive processing for the evaluation and refinement of these ideas for a given goal. They further suggest that improvisational training makes this cyclical process more efficient. While this

model seems very reasonable, it begs the question, is there any neurophysiological basis to support it. The answer, although still an active field of research, appears to be, yes.

With regard to spontaneous or automatic associative processing, a candidate network already exists called the default mode network (DMN). In a review on creative ideation literature, Jung et al. (2013) proposed that it is carried out on circuitry within the DMN. The DMN mainly comprises the medial prefrontal cortex, the posterior cingulate cortex (PCC), bilateral inferior parietal lobes, and temporal-parietal areas (Fox et al., 2005; Gusnard & Raichle, 2001). Individually, these areas are respectively thought to play roles in working memory, emotion and intrinsic control, sensorimotor integration, and auditory and temporal processing (Smith et al., 2018; Leech and Sharp, 2014; Behrmann et al., 2004; Bengtsson et al. 2007), functions which are arguably essential for musical improvisation. Perhaps unsurprising then is the finding by Bashwiler et al. (2016) that higher self-ratings of creativity in musicians correlated with greater surface area in DMN areas. Presumably, increased cortical surface area should correspond with increased processing speed or efficiency, and correspondingly increased creative output, though whether this is really the case with creative or improvisationally experienced musicians has yet to be directly investigated. However, Jung et al. (2013) make clear that their proposed involvement of the DMN in creative ideation is an approximation, and that more likely, various neural hubs (Sporns et al., 2007) throughout the brain are additionally involved and connected via circuitry within areas of the DMN. This is perhaps recognition of the fact that creative ideation involves more than just spontaneous processing. Indeed, returning to the model put forward by Kleinmuntz et al. (2014), spontaneous processing is only one of two essential aspects of creative ideation, the other being executive processing for evaluation of creative output.

Radel et al. (2015) astutely observed that the amount of executive processing required for effective creative ideation likely differs depending on the sub-type of creativity involved.

With respect to divergent thinking, the kind of creative ideation linked to musical improvisation experience, Radel et al. (2015) propose that there should be less constraint placed on automatic associative processing in order to maximize that quantity and variety of ideas, and therefore less executive processing is desirable. In line with this, they found that when cognitive resources for inhibition (a specific kind of executive function) were taxed, the fluency of ideas generated on a subsequent divergent thinking test was improved. In other words, a cognitive state involving decreased inhibition, or disinhibition, appears to enhance creative output.

It is perhaps not difficult to imagine how disinhibition would facilitate improvisational performance. For improvisational musicians, this notion it is taken as a matter of course. Indeed, in the report by Limb and Braun (2008) mentioned in Section 2.5, the concept of disinhibition during improvisation forms a central theme of their discussion as they seek to explain decreased activity in the right DLPFC. A review on inhibitory function by Aron et al. (2014) proposes that inhibition is implemented by the right inferior frontal cortex (rIFC), which in addition to the DLPFC, is given to comprise the pars triangularis (PTG), pars orbitalis (POB), and pars opercularis (POP). They further note beta band power increases in the rIFC prior to successful execution of inhibitory control, and go on to implicate the rDLPFC particularly in the regulation of the rules of inhibitory control. Incidentally, the DLPFC largely overlaps with the rostral middle frontal (RMF) region of the Desikan-Killany brain atlas used in this thesis. Meanwhile, the right precentral gyrus (PrCG) also appears to play a role in action inhibition (Spierer et al., 2013), with higher beta activity observed here prior to successful execution of inhibitory control.

Given the association of musical improvisation with divergent thinking-based creativity, and divergent thinking-based creativity with inhibition, the brain areas implicated in inhibitory function are of great interest to me and this thesis. The evidence in this section suggests that

creative musicians may have improved spontaneous processing ability. This may be due to their ability to limit inhibitory control, thereby entering a disinhibited cognitive state. Thus, I hypothesized that musicians with higher creative ability may also have augmented ability to control brain function associated with inhibition. In the latter part of this thesis, I attempt to investigate the validity of this hypothesis.

2.7 MEG experimental design considerations

Improvisational music performance inherently involves physical movement. However, it is known that physical movement affects MEG (and EEG) recording (Gross et al., 2013). To avoid this confound when the brain activity pertaining to physical action is desired, neurophysiological studies will often record brain activity during mental imagery of the physical action of interest. Although the degree to which brain activity during mental imagery corresponds with that during real action is an area of continuing research (Pearson et al. 2015), the existence of correspondence is undeniable. As far as mental imagery of music and actual listening are concerned, numerous overlapping areas of brain activation have been shown to be involved including: bilateral auditory antereolateral belt, Wernicke's area, and intraparietal sulcus; and left premotor cortex and supplementary motor area (Zhang et al., 2017). During physical music performance, mental imagery of the played audio and actual listening of the played audio has been shown to exhibit similarities with respect to modulation and cortical location of high frequency brain activity (Martin et al., 2017). Mental imagery of music performance has also been shown to reflect the structure of the imagined music by modulating in accordance with targeted beat and meter frequency (Okawa et al., 2017). Mental imagery of improvisational music performance was found to exhibit brain activity in the occipital lobe that correlated highly with that exhibited during passive listening

of the subject's own prior improvisational music performance (Sanyal et al., 2016). Additionally, brain activity during mental imagery of music performance and that during actual performance has been shown to share numerous causal network connections (Adhikari et al., 2016). Collectively, these findings indicate that brain activity during mental imagery of music perception and music performance (improvisational or otherwise) is relevant to and shares many commonalities with brain activity during actual perception and performance. Thus mental imagery is an insightful and useful design strategy for neurophysiological experimentation.

3 Goal of Thesis

The present thesis sought to demonstrate the feasibility of musical improvisation performance experimentation in MEG, and produce results that would not only have practical relevance, but also drive future studies regarding musical improvisation training/therapy and contribute neurophysiological evidence supportive of their wider implementation. To accomplish this, it was first necessary to develop an MEG-compatible music instrument that would permit engaging and realistic improvisational music performance without interfering with MEG recording. Then, it was necessary to establish an experimental design that minimized movement artifacts through the incorporation of mental imagery, and implement a conversational performance style resembling that used in therapies and actual musical improvisation performance. These goals were achieved over the course of two studies: Study 1, and Study 2. In Study 1, a prototype MEG-compatible instrument was constructed, and a pilot musical improvisation performance paradigm was tested on a subject population composed mainly of non-musicians. Study 2 was divided into two parts: A, and B. In Study 2A, the instrument was upgraded into a 5-key keyboard, and an improved musical improvisation performance paradigm which permitted more fluid and natural performance was tested on improvisationally experienced musicians. In Study 2B, which included subjects from Study 2A, in addition to the MEG experiment, improvisationally experienced musicians underwent assessments of creative (i.e. divergent thinking) ability and intelligence. Based on their resulting creativity scores, the musicians were split into either a high creativity or a low creativity group, and between-group comparisons were made regarding performance behavior and inhibition-related brain activity.

To ensure that the musical improvisation performance paradigms of both Study 1 and 2 would be therapeutically relevant and simple enough for non-musicians to do, focus was

placed on differences due to improvisation or non-improvisation of just the musical element of rhythm. Moreover, the metric structure of the performance paradigms was fixed (i.e. a set tempo was used). Consequently, rhythmic improvisation equated to the free execution of the number of notes in congruence with the metric structure, within a given time-frame (e.g. one measure). Correspondingly, performance behavioral differences between conditions and groups could be assessed by analyzing the number of notes performed. Meanwhile, data from the MEG recordings were used to explore and differentiate brain areas and spontaneous brain oscillatory modulation associated with mental imagery of improvisational music performance. In consideration of oscillatory frequencies shown by EEG studies to be relevant during improvisational cognition, analyses of brain activity focused on the theta (5-7 Hz), alpha (8-12 Hz), and beta (15-29 Hz) bands. Additionally, considering the hemispheric laterality of certain results from prior fMRI studies, analyses furthermore focused on the left and right hemispheres separately. Finally, considering Study 2B's focus on the neural correlates to creativity, and given the importance of brain areas associated with inhibition control in creative cognition, analyses of spontaneous brain activity for Study 2B focused specifically on the right POP, POB, PTG, RMF, and PCG, which are implicated in inhibition control.

4 Methods: Study 1

As mentioned in the introduction, Study 1 involved the development of a prototype MEG-compatible musical instrument, which was then tested on predominantly non-musicians in an MEG musical improvisation performance paradigm employing mental imagery.

4.1 Subjects

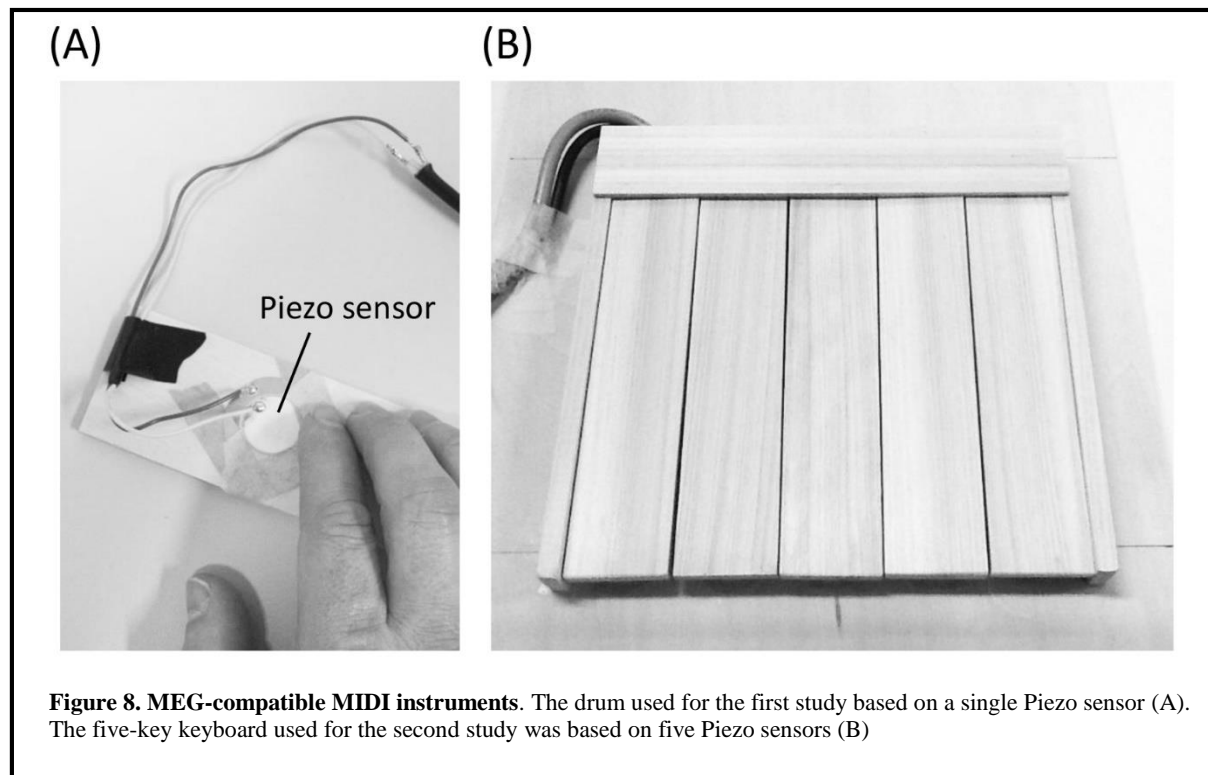
The pilot study targeted 13 right-handed students from the present institution (8 males and 5 females; mean \pm SD age, 21.8 ± 0.9). Two regularly practiced a musical instrument. None had any musical improvisation experience. Written informed consent was obtained from all subjects prior to participation in this study, which was approved by the Ethics Committee of the Faculty of Health Sciences and the Ethics Committee of the Graduate School of Medicine, Hokkaido University, and conformed to the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

4.2 MEG drum

For Study 1, an MEG-compatible musical instrument digital interface (MIDI) drum was constructed using a single, circular Piezo sensor. Anode and cathode wires were soldered onto the Piezo sensor, which was then simply fixed with cloth tape to a one centimeter thick piece of plywood. Serial signals from the Piezo sensor were fed outside the shielded room into an Arduino circuit board connected to a notebook PC. An open-source program was used to convert the Piezo sensor signals into MIDI. This program was purposely modified to eliminate velocity effects of Piezo sensor activation. In other words, regardless of the strength the Piezo sensor was activated, the loudness of the sound generated from its activation was

uniform. Free software was used to feed the MIDI signals into a virtual MIDI port (Hairless) that was then read by music production software (Ableton Live 8) and played through a MIDI drum plugin (Addictive Drums). Here, the serial to MIDI conversion program was further modified such that the MIDI signals produced the sound of a tom drum. Drum sound output was routed to an electrostatic speaker within the shielded room to provide subjects with auditory feedback of their performance. Of note, the Piezo sensor was left as is, without any covering to protect the sensor surface or soldered connections to the anode and cathode wires. This lack of protection resulted in accidental breakage of a few sensors. On one occasion, breakage occurred during an experimental recording, which had to then be rescheduled following replacement of the broken Piezo sensor with a new one. The fragility of this design was expressly addressed in the upgraded instrument design used for the main study.

The modified serial to MIDI program for the drum can be viewed in the appendix of this manuscript (Supplemental Information, I). A picture of the instrument can be viewed in Figure 8A.

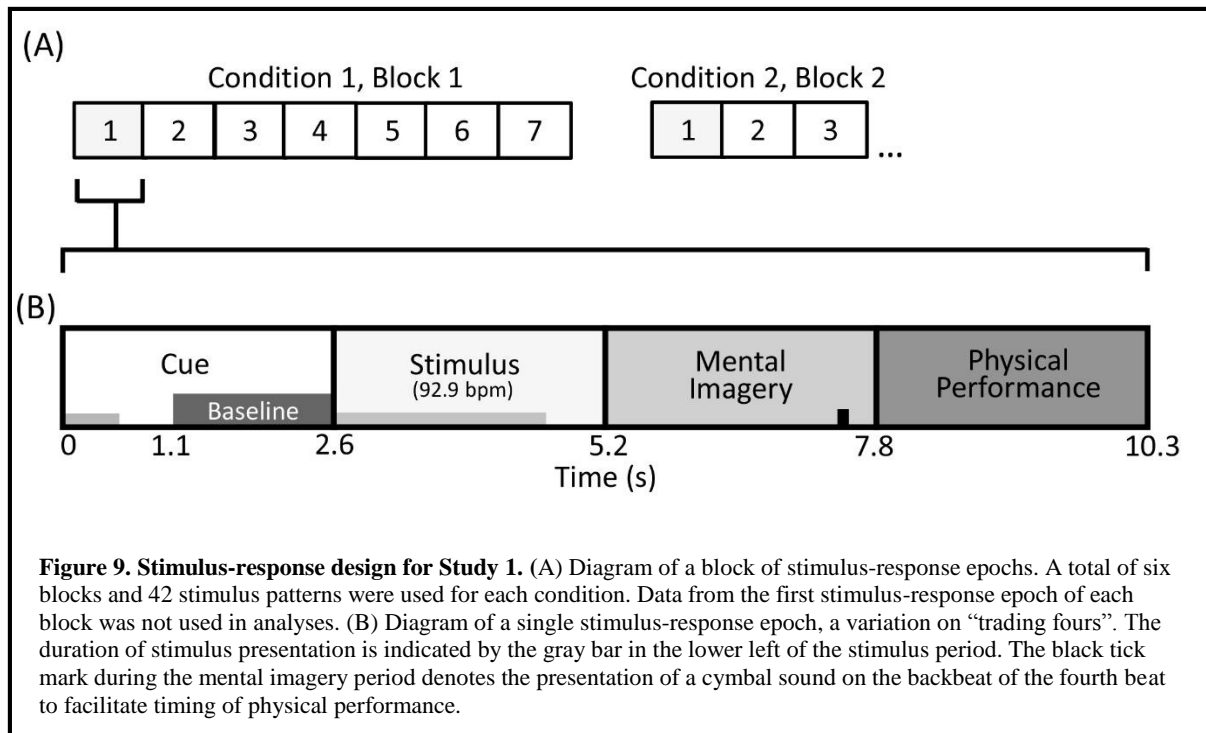


4.3 Experimental paradigm and procedure

Study 1 was designed with three conditions: Copy, Improvise, and Beat. In all three conditions, subjects use their index finger to respond to the stimulus by tapping on the drum. In Copy, the subjects copied the rhythm of the stimulus. In Improvise, subjects improvised a novel rhythm in response to the stimulus. In Beat, subjects responded with four quarter-note beats in time with the tempo, irrespective of the stimulus pattern presented. Thus, every Beat condition response was identical, permitting the Beat condition to serve as a kind of control condition.

The experiment was performed in two sessions. Each session consisted of three blocks of seven stimulus-response epochs for each task condition. Block order was randomized between subjects. No two blocks of the same condition were presented consecutively. The condition associated with any given block was distinguished by one of three specific auditory cues, which were also randomized between subjects. The auditory cues used were: a drop of water, gravel, and a bell. The sound duration for each auditory cue was time matched using audio software (Ableton Live8). The auditory cues were presented at the start of every stimulus-response epoch. Each stimulus-response epoch corresponded to a unique rhythm stimulus pattern composed of a tom drum sound with identical tonal properties as those produced by the MEG drum. There were thus a total of 42 stimulus patterns. The exact timing of the rhythmic notes and their number varied with each pattern. The same stimulus patterns were used for each condition, and presented in the same order for each block in each session. The stimulus-response epoch was designed to comprise four musical measures in 4/4 time at a tempo of 92.88 bpm with a total length of 10.3 s. In the first period (0-2.6 s, hereafter cue period), the auditory condition cue was presented during the first quarter-note beat. A two

second portion of the cue period (1.1-2.6 s) was used for calculating baseline activity. In the second measure (2.6-5.2 s, hereafter stimulus period), one of the rhythm patterns was presented via an electrostatic speaker in the shielded room. In the third measure (5.2-7.7 s, hereafter mental imagery period), subjects performed their response to the stimuli according to the given condition via mental imagery. In the fourth measure (7.7-10.3 s, hereafter physical performance period), the rhythm that was mentally imagined was recalled and physically performed on the MEG drum. To facilitate the timing of physical performance, a cymbal sound was presented on the backbeat of the fourth beat of the mental imagery period. Please see Figure 9 for further details.



This design permitted musical performance akin to a commonly used improvisational structure in jazz and blues called “trading fours,” in which two musicians take turns improvising and conversing to one another via their instruments. A similar design was used by Donnay et al. (2014). Conventionally, a “trading fours” structure would only comprise a stimulus period (i.e. a musical phrase played by another musician), and a physical

performance period (i.e. a musical phrase played by oneself in response to the musical phrase played by the other musician). The design used in the present study maintained the conversational structure of “trading fours,” albeit with modifications to facilitate MEG experimentation. Specifically, the mental imagery period permitted analysis of brain activity that was free from noise or confounds due to physical movement. The mental imagery period was also the only time where cognition related to improvisational performance was occurring. Thus, the present study focused exclusively on comparisons of brain activity between conditions during the mental imagery period. The physical performance period served merely to keep subjects enjoyably and musically engaged.

Prior to the experiment, subjects were given detailed instructions on how to perform the experimental conditions during a training session conducted outside the shielded room. With respect to Improvise responses, subjects were encouraged to play whatever they felt based on the preceding stimulus pattern, the only restriction being that the stimulus pattern should not be duplicated. During the training session, a series of continuous stimulus-response epochs were played over two external computer speakers while subjects sat upright in a chair. During the physical performance period of each stimulus-response epoch, subjects used their right index finger to tap a desk top. They were also specifically instructed to not move their heads, trunk, or other extremities, and to move their right index finger for performance during the physical performance period only. Once it was clear that subjects understood the instructions and could perform the experiment without difficulty, they were prepared for MEG recording.

4.4 MEG recording and processing

All MEG measurements were done within a magnetically shielded room using a 76 ch. custom-type helmet MEG system (Elekta-Neuromag). Head position indicators, fiducials, and

head points were digitized according to standard MEG operating procedure (Hansen et al., 2010). The subject was positioned in an upright position in the MEG measurement chair, onto which a table was attached. Upon the table, the drum was fixed with tape at a comfortable position for right-handed performance. The subject then placed their right hand in position on the drum. Throughout the experiment, the subject was visually and aurally monitored to ensure comfort and compliance with all experimental instructions and performance conditions.

MEG signals were band-pass filtered from 0.6 to 200 Hz and recorded at a 600 Hz sampling frequency. All MEG data processing was performed in Brainstorm (<http://neuroimage.usc.edu/brainstorm>). This processing began with removal of noisy or dead channels. Components of physiological artifacts and periodic noise were isolated and removed using independent component analysis. A comb filter was applied at 50 Hz and related harmonic frequencies to remove line noise. A band-pass filter was then applied from 1-40 Hz. Cleaned and filtered data was then epoched at -1 to 11.3 s relative to stimulus onset. Each epoch was visually scanned, and those with movement artifacts were removed. Subject head points and fiducials were normalized to a common template brain. An overlapping-sphere forward model was computed, and minimum-norm estimation was used to calculate cortical currents without dipole orientation constraints. The cortical surface was then parcellated into 68 areas (34 in each hemisphere) based on the Desikan-Kilany cortical surface atlas. The time-series of cortical currents in each brain area was decomposed into the theta (5-7 Hz), alpha (8-12 Hz) and beta (16-29 Hz) frequency bands, and their corresponding envelopes computed using Hilbert transform. Time-frequency envelopes in each frequency band in each brain area were averaged across epochs within subjects for each condition. The amplitude of the time-frequency envelopes was furthermore standardized in each subject as a

percent deviation from baseline using the following equation where x is the amplitude of the time-frequency envelope at each time point, and μ is the time-average over baseline.

$$X_{\text{std}} = \frac{x - \mu}{\mu} \times 100$$

Standardized time-frequency envelopes were averaged over the mental performance period in each brain area for each frequency band in each subject. Resulting values were used in statistical analyses.

4.5 Statistical analysis

Mean standardized brain activity over the mental imagery period in each hemisphere in each frequency band of interest was analyzed using two-way repeated measures analyses of variance (RM ANOVA) ((brain area: 34 areas per hemisphere) x (condition: Copy, Beat, Improvise)). Homogeneity of data from each hemisphere was assumed based on Levene's tests. All statistical tests were two-tailed and conducted using SPSS (IBM), with significance determined at $p \leq 0.05$.

5 Methods: Study 2

For Study 2, the MEG-compatible instrument was upgraded to a 5-key keyboard, and the performance paradigm was improved to permit more natural improvisational performance. The impetus for these changes was due to limited results produced by Study 1, which led to the hypothesis that the paradigm used in Study 1 may be too simple for generating robust differences in brain activity between conditions, particularly in musicians. Study 2 was furthermore divided into two parts: A and B. The aim of Study 2A was to spatial-spectrally explore and differentiate brain activity associated with improvisational music performance in improvisationally experienced musicians. Meanwhile, Study 2B sought to explore potential differences in musical improvisation-associated brain activity based on the creative ability of improvisationally experienced musicians. To do this, in addition to the MEG experiment used in Study 2A, Study 2B employed a psychological assessment of creative ability to divide the improvisationally experienced musicians into two groups of either high or low scorers (high creativity (HC) group, and low creativity (LC) group, respectively) in accordance with whether they scored higher or lower than the mean. Study 2B analyses then focused on between-group differences in performance behavior and brain activity in areas associated with inhibitory function. The intelligence of the subjects was additionally assessed to examine whether or not it was a confounding factor to creativity.

5.1 Subjects

Study 2 targeted musicians with improvisational experience in the Sapporo metropolitan area of Hokkaido prefecture, Japan. Subjects were recruited via flyer postings at our institution and via online social media. Subjects' playing frequency and frequency of improvisation were

assessed via a music experience questionnaire modeled after that used by Bashwiner et al. (2016). Study 2A targeted 13 right-handed musicians (10 males and 3 females; mean \pm SD age, 35.7 ± 8.6 years) with an improvisational playing frequency ranging from several days a week to several hours per day. Study 2B targeted 14 right-handed musicians, 13 of whom were from Study 2A, and an additional female subject with only marginal improvisation experience (10 males and 4 females; mean \pm SD age, 35.7 ± 8.9 years). As with Study 1, written informed consent was obtained from all subjects prior to participation in this study, which was approved by the Ethics Committee of the Faculty of Health Sciences and the Ethics Committee of the Graduate School of Medicine, Hokkaido University, and conformed to the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Further details regarding the subjects' characteristics and music experience can be seen in Supplemental Table 1.

5.2 MEG Keyboard

For Study 2, we constructed an MEG-compatible keyboard with five keys whose depression activated a corresponding circular Piezo sensor. The frame, keys, and hinges of the keys were built out of wood. The frame was glued onto a one centimeter thick plywood base. The hinges of the keys, 5 mm wooden dowels, were glued onto the ends of the keys made from 5 mm thick flat wooden dowels cut to dimensions of 16 cm x 3 cm. The ends of the keys where the hinges were attached were tapered by 1 cm² on each side to permit the keys to rotate freely about the wooden hinge holders. The Piezo sensors were fixed with wood glue on the plywood base, centered under their corresponding key. A rubber computer keyboard spring was glued to the bottom of each key to permit direct contact with the activating surface of the Piezo sensor and allow the key to naturally return to neutral position after being depressed.

The wires from the Piezo sensors were secured with tape flush to the plywood base such that contact was avoided during key depression. The wires were furthermore soldered to an open end of a 12 wire, insulated serial cable. The serial cable was fed out of one end of the keyboard frame and down to a serial pin connector that allowed quick and easy installation and de-installation of the keyboard in the shielded room. Hinge fitting and key spacing was stabilized using packing foam. Hinge connections and stabilizing foam were furthermore secured by a fascia board made from the same material as the keys across the top of the keyboard. Similar to the single Piezo sensor MIDI drum used in the pilot study, serial signals from the Piezo sensors in the keyboard were fed outside the shielded room to an Arduino circuit board which was connected to a notebook PC. The same open-source program was used to convert individual Piezo sensor signals into MIDI, and likewise modified to eliminate velocity effects of Piezo sensor activation. MIDI signals from each key were further programmed to play a major pentatonic scale beginning from the leftmost key with middle C (C3; 261.6 Hz). MIDI signals were read from the virtual MIDI port (Hairless) by music production software and played through a native MIDI piano instrument plugin (Ableton Live 8). Piano sound output was routed to the electrostatic speaker within the shield room for auditory feedback.

The modified serial to MIDI program for the keyboard can be viewed in the appendix of this manuscript (Supplemental Information, II). A picture of the completed instrument can be viewed in Figure 8B. The Piezo sensors were wired together as shown in Figure 10.

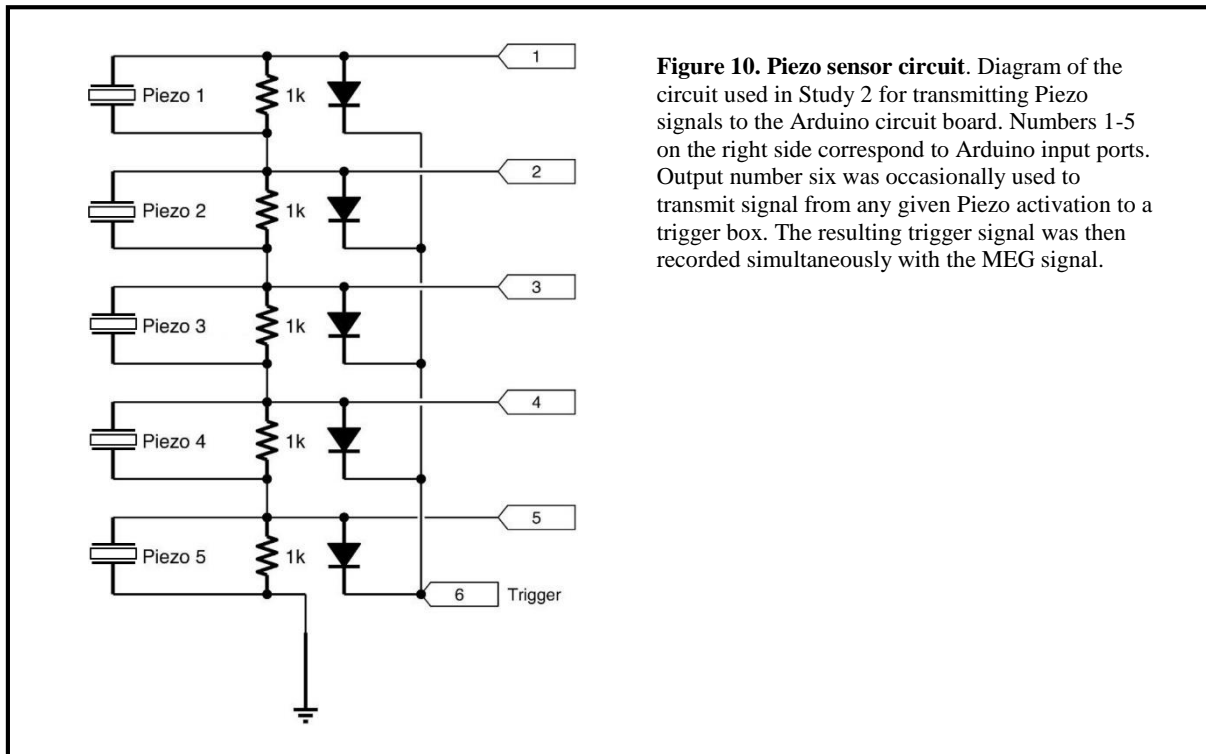


Figure 10. Piezo sensor circuit. Diagram of the circuit used in Study 2 for transmitting Piezo signals to the Arduino circuit board. Numbers 1-5 on the right side correspond to Arduino input ports. Output number six was occasionally used to transmit signal from any given Piezo activation to a trigger box. The resulting trigger signal was then recorded simultaneously with the MEG signal.

5.3 MEG experimental paradigm and procedure

The MEG experiment used for Study 2 was designed with two types of tasks, Single-finger and Multi-finger. Each task type comprised two response conditions, Copy and Improvise. In Single-finger Copy, the subject monotonically copied the rhythm of the stimulus using a single finger. In Single-finger Improvise, the subject monotonically improvised a novel rhythm in response to the stimulus using a single finger. In Multi-finger Copy, the subject polytonically copied the rhythm of the stimulus using any combination of fingers. In Multi-finger Improvise, the subject polytonically improvised the rhythm via any combination of fingers. The underlying difference between Copy and Improvise in each task was improvisation or non-improvisation of rhythm. The addition Multi-finger task (and correspondingly the keyboard) to the paradigm was based on the limited results from Study 1A, and the expectation that

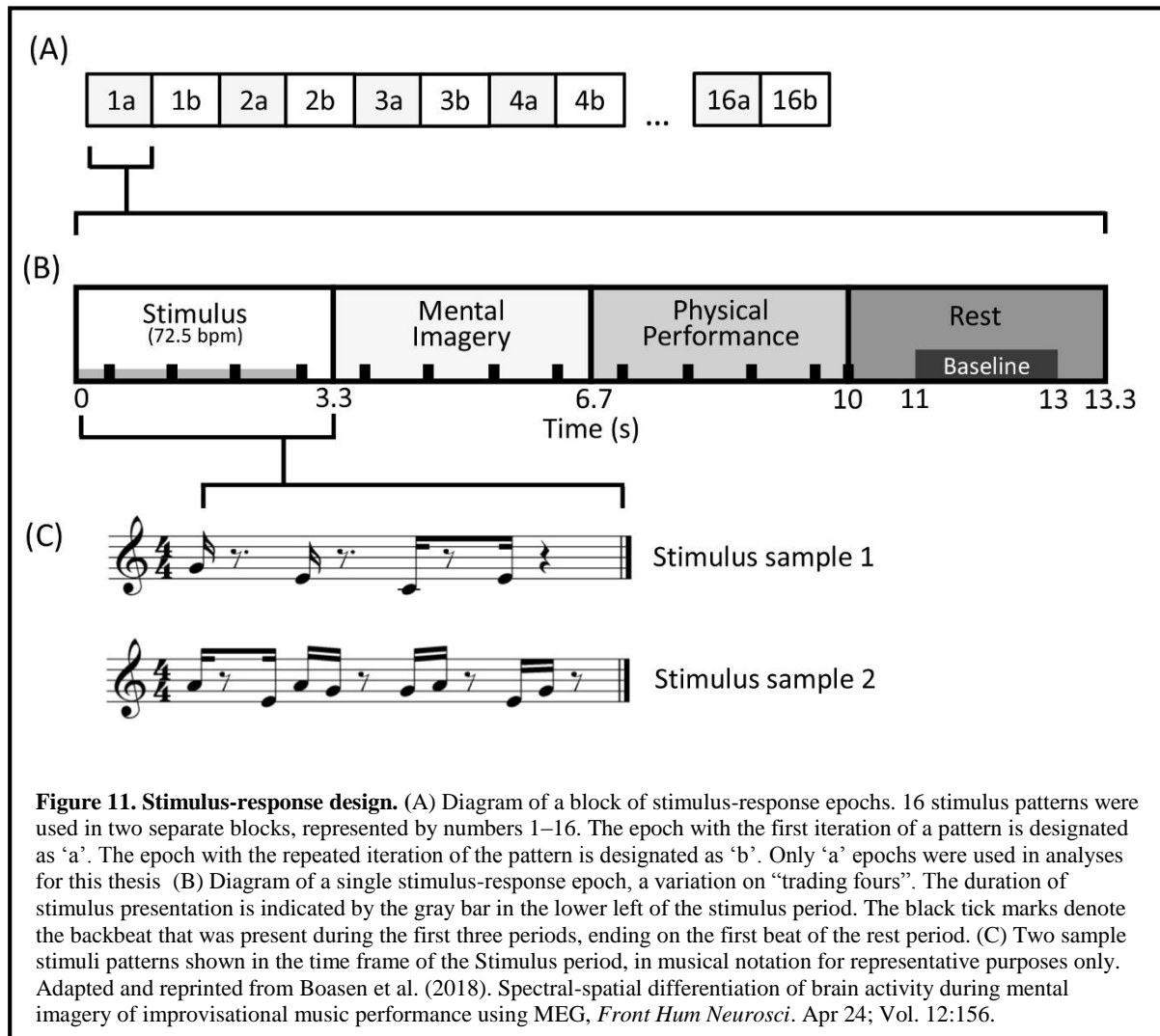
The experiment was performed in two sessions. Each session consisted of one block of 16 stimulus-response epochs for each task condition, with block order randomized between subjects. Within any given block, stimulus-response epochs were presented with no interruption to the musical continuum (i.e. they were presented continuously with no interval or jitter between epochs). Every two stimulus-response epochs within a given block corresponded to a unique polytonic keyboard stimulus pattern composed of the same five notes, with identical tonal properties, as those produced by the MEG keyboard. Thus, eight stimulus patterns were used in each block, with each presented twice in consecutive stimulus-response epochs. The exact notes used and their number varied with each pattern. The same stimulus patterns were used for each task/condition, and presented in the same order for each block in each session. Only stimulus-response epochs for the first iteration of any given stimulus pattern were used for analyses in this study.

The stimulus-response epoch was designed to comprise four musical measures in 4/4 time at a tempo of 72.5 bpm with a total length of 13.3 s. In the first measure (0-3.3 s; hereafter, stimulus period), one of the polytonic keyboard stimulus patterns was presented via an electrostatic speaker in the shielded room. In the second measure (3.3-6.7 s; hereafter, mental imagery period), subjects performed their response to the stimuli according to the given condition via mental imagery. In the third measure (6.7-10.0 s; hereafter, physical performance period), the notes that were mentally imagined were recalled and physically performed on the MEG keyboard. In the fourth measure (10-13.3 s; hereafter rest period), the subjects rested. A two second portion of the rest period (11-13 s) was used for calculating baseline activity. Meanwhile, a percussive quarter note backbeat played throughout the first three periods, ending on the first beat of the fourth period. The backbeat served to help subjects maintain the timing-accuracy of their responses (see Figure 11).

This design built upon the “trading fours” concept employed in Study 1. Here, the musicality of the design was improved by eliminating the condition cue, a redundant feature in a block design, and replacing it with a stimulus free rest period. Additionally, the stimulus period was moved to the first measure. This provided subjects with a clear foundation for determining musical tempo, which was markedly reduced compared to Study 1, and reinforced via the backbeat stimuli. As with Study 1, the mental imagery period of Study 2 was also the only time where cognition related to improvisational performance was occurring. Thus, the present study focused exclusively on comparisons of brain activity between conditions during the mental imagery period. The physical performance period served merely as a means for measuring behavior response (see section 2.5), and keeping the subjects enjoyably and musically engaged. The rest period meanwhile provided a reference frame to which the modulation of brain activity could be normalized (i.e. it permitted calculation of baseline activity levels).

Prior to the experiment, subjects were given detailed instructions on how to perform the experimental tasks and conditions during a training session conducted outside the shielded room. During the training session, a series of continuous stimulus-response epochs were played over two external computer speakers while subjects sat upright in a chair. During the physical performance period of each stimulus-response epoch, subjects used their right hands to tap an iPad running a digital keyboard application (Garage Band) which was programmed to a C3 major pentatonic scale (i.e. the iPad mimicked the MEG keyboard that subjects would use during the actual experiment inside the shielded room). Subjects were instructed to fix the performance of each finger to just one key on the scale (i.e. the thumb played C3, the index finger played D3, etc.). They were also specifically instructed to not move their heads, trunk, or other extremities, and to move their right hands for performance during the physical

performance period only. Once it was clear that subjects understood the instructions and could perform the experiment without difficulty, they were prepared for MEG recording.



5.4 MEG recording and processing

MEG recording and processing was performed identically to Study 1. The only difference was that the instrument in Study 2 was the five-key MIDI keyboard, instead of the single-Piezo MIDI drum.

5.5 Psychological assessments

For Study 2B, subjects were given two psychological assessments on a day separate to the MEG experiment. The first assessment evaluated their creative ability. The second assessment evaluated their intellectual ability, to ensure it was not a confounding factor to creativity. Both assessments were administered either at the present institution, at the subject's home, or at quiet public location. Every effort was made to make the test taking atmosphere cordial and relaxed. Details regarding each of these assessments, including their administrative and evaluative procedures are provided below.

5.5.1 Creativity

The creative ability of subjects was assessed first using the S-A creativity test (Society_For_Creative_Minds 1969), a timed, validated, Japanese language-based test which evaluates creative ability via divergent thinking. The test was originally designed in English by J.P. Guilford and developed under his guidance. The test was later standardized for Japanese speaking adults. The S-A creativity test is conceptually akin to the English language-based test of creative ability, the Torrance tests of creative thinking (TTCT; Torrance 1996).

The S-A creativity test comprises three tasks. In the first task, subjects must think of novel ways to use ordinary objects (e.g., 'What uses for a cup can you think of, other than to hold liquid? Write down as many answers as possible' A sample answer might be, 'to make cogs on a giant toy gear.') In the second task, subjects must think of imaginary and desirable functions for ordinary objects (e.g., 'What functions of a pen can you imagine that would be fun? Write down as many answers as possible' A sample answer might be, 'To draw magical portals to anywhere I want to go simply by making the outline of a door and writing the name

of the location inside.’) In the third task, subjects must think of consequences to fantastical hypothetical situations. (e.g., ‘How would the world be different if humans had no mouths? Write down as many answers as possible.’ A sample answer might be, ‘We would obtain energy and nutrients through our skin via photosynthesis and osmosis.’).

The S-A creativity test provides a total creativity score that is determined based on sub scores for the following dimensions: fluency, flexibility, originality, elaboration. Fluency reflects the ability to generate numerous alternative ideas and is measured based on the number of relevant responses provided. Flexibility reflects the ability to generate ideas that are categorically different and is measured based on the number or responses of different category types. Originality reflects the ability to generate ideas that are different from others and is measured based on the rarity of the response in comparison to an established database of responses. Elaboration reflects the ability to provide detail to an idea and is measured based on the level of detail of responses in comparison to that in an established database of responses. All scores are based on a ten-point scale.

The S-A creativity test has two versions, Version A and Version C. Both versions of the test are identical except that the questions are different, which allows them to be used in interventional studies to measure potential changes in creative ability due to the intervention. For this thesis, only Version A was used. Additionally, only the total creativity score was used in our analyses. Notably, S-A creativity scores have been significantly correlated to personality factors such as problem solving ability (Shimonaka & Nakazato, 2007).

Completed tests were submitted to and scored by the Tokyo Shinri Corporation. Subjects in Study 2B who scored above the mean were placed in the HC group, and those who scored below the mean were placed in the LC group.

5.5.2 Intelligence

After a five minute break following the completion of the S-A creativity test, subjects' intelligence was assessed using the Raven's Standard Progressive Matrices (SPM) Plus test, an untimed, non-verbal test of observational skills and thinking ability. The test is a psychometric measure of intelligence that is highly correlated with general intelligence (Raven et al., 1998). We chose to use the SPM Plus test due to the possibility that intelligence may correlate with creative ability, something that has been shown among subjects of low to average intelligence (Barron & Harrington, 1981). However, considering that all the subjects participating in this thesis were college educated, it is unlikely that intelligence will be a significant confounding factor to creative ability. Another reason for choosing the SPM Plus test is its non-verbal nature, which allows it to be used irrespective of language and cultural background, and thus permits the adaptation of the experimental paradigm used in this thesis to non-Japanese subject populations, an important future goal of this work.

The SPM Plus test is organized into five sets of 12 problems. Each problem consists of a matrix of patterns with one pattern missing. Subjects must choose from a list of patterns which one is most appropriate based on the matrix. The matrices are designed to progressively increase in complexity, while incorporating aspects of previous solutions. Thus, the test also gauges one's ability to learn and apply new knowledge towards solving novel problems. The SPM Plus test produces a raw total score, which can also be converted to a percentile rank. For this thesis, only raw total scores were used. Scoring for the SPM Plus test is done in house, and is automatic when using Easy Score Answer Sheets, as was done for this thesis.

5.6 Behavioral analysis

Although the present study expressly focused on brain activity during the mental imagery period, a time when there was no behavioral response, the experiment was designed such that the notes imagined during the mental imagery period are recalled and physically played during the physical performance period. Thus, we assumed that the notes played during the physical performance period were a reasonable representation of the behavioral response during the mental imagery period. As the number of notes imagined and correspondingly physically played (hereafter, note count) in each epoch was not controlled in this study, it is conceivable that note count may have affected brain activity during the mental imagery period. To assess this, concurrent with MEG recording, keyboard responses during the physical performance period were recorded for each subject in the form of MIDI data. From this MIDI data, mean note counts in each task and condition for each subject were calculated for use in statistical analyses.

5.7 Statistical analysis

5.7.1 Study 2A

Mean note counts for Copy and Improvise were contrasted with the mean stimulus note count across all 16 stimulus patterns (7.06 notes) via one-sample t tests to assess behavioral adherence to the task conditions. Additionally, differences in mean note count between Copy and Improvise were analyzed using paired t tests. Mean standardized brain activity over the mental imagery period in each hemisphere in each frequency band of interest was analyzed using two-way repeated measures analyses of variance (RM ANOVA) ((brain area: 34 areas per hemisphere) x (condition: Copy, Improvise)). Homogeneity of data from each hemisphere was assumed based on Levene's tests. In cases where RM ANOVA revealed brain areas with

significant differences between conditions, the relationship of performance note count to the level of frequency-specific brain activity in that corresponding area was analyzed using Pearson's correlation analyses (within and across conditions) and multiple regression analyses (with note count and condition as regressors).

All statistical tests for Study 2A were two-tailed and conducted using SPSS (IBM), with significance determined at $p \leq 0.05$.

5.7.2 Study 2B

For the second series of analyses, Pearson's correlation analysis was performed to assess the correlation between creative ability and intelligence. Mean note counts for Copy and Improvise in HC and LC groups separately were contrasted with the mean stimulus note count across all 16 stimulus patterns via one-sample t tests to assess behavioral adherence to the task conditions. Additionally, differences in mean note count between creativity groups and conditions were analyzed using mixed ANOVA (creativity: HC, LC) x (condition: Copy, Improvise).

As for brain activity, Study 2B focused only on the following right hemispheric areas associated with inhibitory function: rostral middle frontal, pars opercularis, pars orbitalis, pars triangularis, and precentral gyrus. Mean standardized brain activity over the mental imagery period in each area in each frequency band of interest during Copy was subtracted from that during Improvise in each subject (hereafter, I-C value). I-C values were thus positive or negative depending on whether Improvise values were greater or less than Copy values, respectively. The I-C values at the five inhibition brain areas were analyzed using mixed ANOVA ((brain area: 5) x (creativity group: high, low)). In cases where the mixed ANOVA revealed brain areas with significant differences between groups, the relationship of

performance note count during *Improvise* to the level of frequency-specific I-C brain activity in that corresponding area was analyzed using multiple regression analyses (with note count and creativity group as regressors).

All statistical tests for Study 2B were two-tailed and conducted using SPSS (IBM), with significance determined at $p \leq 0.10$ for interactions, and at $p \leq 0.05$ for all other measures.

The choice of a higher interaction threshold was due to the lower statistical power of Study 2B.

6 Results: Study 1

RM ANOVA of theta band activity during mental performance in the left hemisphere revealed no significant main effect of area or condition, nor interaction between area and condition ($F_{(33, 396)} = 1.086, p = 0.345$; $F_{(2, 24)} = 0.426, p = 0.658$; $F_{(66, 792)} = 0.336, p = 0.623$; respectively). Subsequent simple main effects tests were not performed. In the right hemisphere, there was no significant main effect of area or condition ($F_{(33, 396)} = 0.036, p = 0.964$; $F_{(2, 24)} = 1.084, p = 0.348$). There was also no interaction between area and condition ($F_{(66, 792)} = 0.93, p = 0.59$), and therefore subsequent simple effects tests were not performed. Thus, RM ANOVA revealed no brain areas with significantly different levels of theta activity between conditions during the mental performance period. This lack of difference between conditions during the mental performance period can be discerned in Figure 12 (top panel), which shows the mean theta activity envelope for each condition in the left middle temporal gyrus (MTG). Theta activity for all conditions appears to synchronize strongly at the performance period cue and then remain elevated throughout the physical performance period.

In the alpha band, results in the left hemisphere revealed significant main effects of area and condition ($F_{(33, 396)} = 2.556, p < 0.001$; $F_{(2, 24)} = 4.616, p = 0.020$), but no significant interaction between area and condition ($F_{(66, 792)} = 0.868, p = 0.762$). Subsequent simple main effects tests were therefore not performed. However, pairwise comparisons between conditions indicated that left-hemispheric alpha levels were significantly lower for *Improvise* than both *Copy* and *Beat* ($p = 0.047$ and $p = 0.014$, respectively). In the right hemisphere, although results revealed no main effects of area or condition ($F_{(33, 396)} = 0.703, p = 0.891$; $F_{(2, 24)} = 2.901, p = 0.074$), there was a significant interaction between area and condition ; $F_{(66, 792)} = 1.459, p = 0.012$; respectively). Subsequent simple main effects tests revealed that

right-hemispheric alpha levels were significantly lower for Improve than Beat in the superior temporal sulcus (STS) ($p = 0.029$), cuneus (CUN) ($p = 0.008$), isthmus cingulate cortex (ICC) ($p = 0.018$), pericalcarine cortex (PEC) ($p = 0.034$), precuneus cortex (PCu) ($p = 0.014$). Additionally, alpha levels were significantly lower for Improve than Copy and Beat in the right superior parietal cortex (SPC) ($p = 0.034$ and 0.030 , respectively). A representative plot of the mean alpha activity envelope in the right SPC (Figure 12, second panel from top) reveals that alpha activity for Improve remains roughly around baseline levels during the stimulus period, undergoes gradual desynchronization throughout the mental imagery period, and then exhibits a sharp drop that coincides with the start of the physical performance period. Conversely, alpha activity for Copy and Beat remains above baseline levels for the greater part of the mental performance period before similarly dropping sharply in correspondence with the start of the physical performance period. Interestingly, alpha activity desynchronization for Improve in the left hemisphere overall (Figure 12, third from top) begins from the start of the stimulus period and continues through the mental imagery period until the physical performance period. In contrast, although Copy and Beat show brief alpha desynchronization during the stimulus period, levels return to baseline until the latter half of the mental imagery period. The desynchronization dynamics exhibited by all three conditions have parallels that which many studies have observed during idea generation and periods of planning prior to physical movement (Schwab et al., 2014; Fumuro, et al., 2015; Deiber, et al., 2012; Caetano et al., 2007). A visual summary of the brain areas where simple main effects revealed significantly different alpha activity between Improve and the other conditions is provided in Figure 13 (left).

In the beta band, results in the left hemisphere revealed a significant main effect for area ($F_{(33, 396)} = 5.514$, $p < 0.001$), but no main effect of condition ($F_{(2, 24)} = 2.236$, $p = 0.129$). However, there was a significant interaction between area and condition ($F_{(66, 792)} = 1.365$, $p = 0.033$).

Subsequent simple main effects tests were performed which revealed significantly lower beta levels for *Improvise* than *Beat* in the left hemisphere in the cuneus ($p = 0.038$), fusiform gyrus (FFG) ($p = 0.045$), inferior temporal gyrus (ITG) ($p = 0.037$), isthmus cingulate cortex (ICC) ($p = 0.030$), lateral occipital cortex (LOC) ($p = 0.020$), lingual gyrus (LNG) (0.013), paracentral lobule (PCL) ($p = 0.046$), pericalcarine cortex (PEC) ($p = 0.022$), postcentral gyrus (PoCG) ($p = 0.043$), precentral gyrus (PrCG) ($p = 0.020$), superior parietal cortex (SPC) ($p = 0.020$), and the superior temporal gyrus (STG) ($p = 0.049$). Beta levels for *Improvise* were also significantly lower than *Copy* in the caudal anterior cingulate (CAC) ($p = 0.029$), and lower than *Copy* and *Beat* in the PCu ($p = 0.032$, and 0.006 , respectively). A representative plot of the mean beta activity envelope in the left PCu (Figure 12, bottom) reveals that beta activity for all conditions drops below baseline during the stimulus period, and then continues a gradual decline throughout the mental imagery period before dropping sharply in preparation for physical performance.

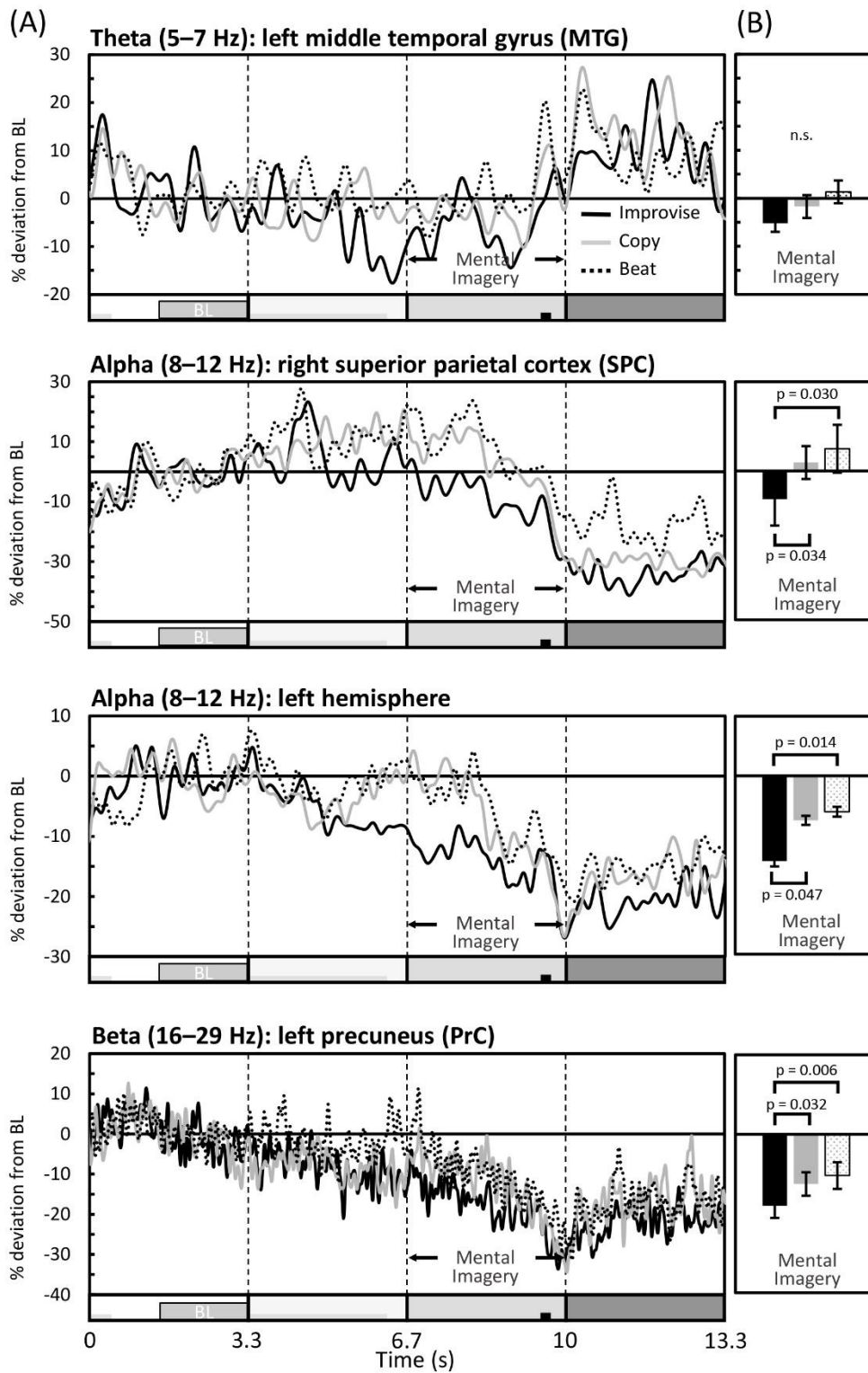


Figure 12. Differential modulation of spectral activity during Study 1. (A) Mean brain activity across the entire stimulus-response epoch in representative brain areas (N = 13). The X axis is represented by a minimized version of the stimulus-response epoch diagram which is detailed in Figure 9. BL denotes the baseline period. (B) Respective mean activity over the mental imagery period. Error bars are standard error

For beta results in the right hemisphere, there was a significant main effect of area ($F_{(33, 396)} = 3.871, p < 0.001$), but no main effect of condition ($F_{(2, 24)} = 0.960, p = 0.397$). However, there was a significant interaction between area and condition ($F_{(66, 792)} = 1.835, p < 0.001$).

Subsequent simple main effects tests revealed significantly lower levels of beta activity for Improvise than Beat in the right: ICC ($p = 0.049$), and PCu ($p = 0.007$). It is worth noting that both of these are situated in the interhemispheric fissure, and that their left-hemispheric homologues also exhibited similar differences in beta activity between Improvise and Beat.

Figure 13 (right) visually summarizes brain areas with significantly different beta activity between Improvise and the other conditions.

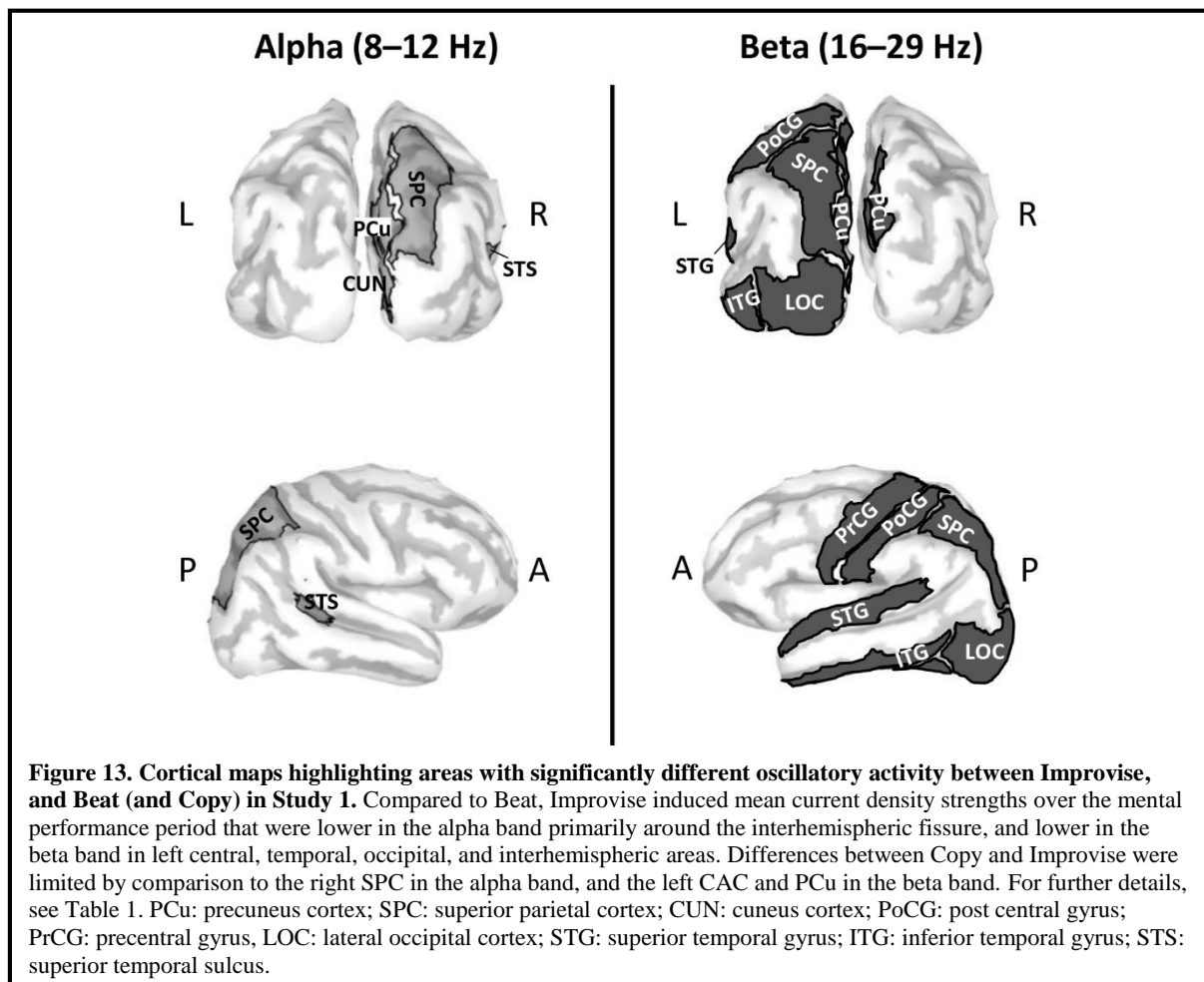


Table 1, summarizes the results from significant interactions and simple main effects as per the RM ANOVAs for the Multi-finger task in Study 1.

Table 1. Piezo drum, RM ANOVA results summary

Frequency	L/R	Interaction p value	Difference I vs. C, B	Brain areas	Simple main effect p value
<i>Alpha</i> 8–12 Hz	R	0.012	I < B	Superior temporal sulcus (STS)	0.029
			I < B	Cuneus cortex (CUN)	0.008
			I < B	Isthmus cingulate cortex (ICC)	0.018
			I < B	Pericalcarine cortex (PEC)	0.034
			I < B	Precuneus cortex (PCu)	0.014
			I < C,B	Superior parietal cortex (SPC)	0.034, 0.030
<i>Beta</i> 16–29 Hz	L	0.033	I < C	Caudal anterior cingulate (CAC)	0.029
			I < B	Cuneus (CUN)	0.038
			I < B	Fusiform gyrus (FFG)	0.045
			I < B	Inferior temporal gyrus (ITG)	0.037
			I < B	Isthmus cingulate cortex (ICC)	0.03
			I < B	Lateral occipital cortex (LOC)	0.02
			I < B	Lingual gyrus (LNG)	0.013
			I < B	Paracentral lobule (PCL)	0.046
			I < B	Pericalcarine cortex (PEC)	0.022
			I < B	Postcentral gyrus (PoCG)	0.043
			I < B	Precentral gyrus (PrCG)	0.02
I < C, B	Precuneus cortex (PCu)	0.032, 0.006			
<i>Beta</i> 16–29 Hz	R	< 0.001	I < B	Superior parietal cortex (SPC)	0.02
			I < B	Superior temporal gyrus (STG)	0.049
<i>Beta</i> 16–29 Hz	R	< 0.001	I < B	Isthmus cingulate cortex (ICC)	0.049
			I < B	Precuneus cortex (PCu)	0.007

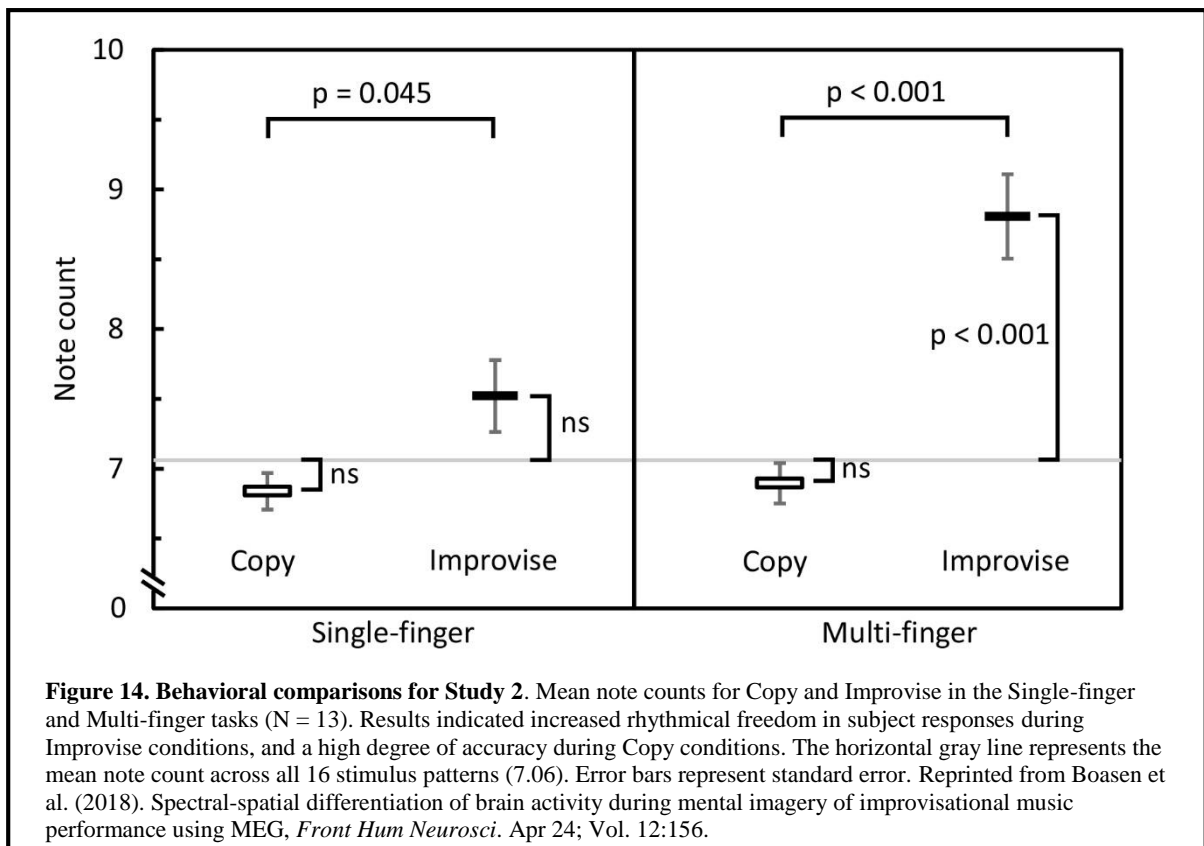
L, R, I, B and C refers to left, right, Improvise, Beat and Copy, respectively.

7 Results: Study 2

7.1 Study 2A

In the Single-finger task, one-sample t tests revealed that note counts for Improvise (mean \pm SE, 7.587 ± 0.257) and Copy (mean \pm SE, 6.803 ± 0.130) were not significantly different from the mean note count for all 16 stimulus patterns (7.06 notes) ($p = 0.072$ and $p = 0.063$, respectively), indicating that responses in neither condition deviated significantly from the level of rhythmic complexity in the stimulus patterns. This result also implied a high degree of accuracy for Copy responses. Meanwhile, the fact that mean note count and standard error were larger for Improvise indicated a tendency towards expression of increased rhythmic freedom, a notion that was corroborated by the paired t test which revealed that note counts for Improvise were significantly greater compared to Copy ($p = 0.045$) (see Figure 14 left panel).

As for brain activity in the Single-finger task, RM ANOVA revealed no significant effects of condition nor interactions between brain area and condition in any frequency. As such, my report will hereafter focus on results from the Multi-finger task.



RM ANOVA of theta band activity during mental imagery in the left hemisphere revealed no significant main effect of area or condition ($F_{(33, 12)} = 1.280, p = 0.143$; $F_{(1, 12)} = 2.103, p = 0.173$; respectively). However, there was a significant interaction between area and condition ($F_{(33, 396)} = 1.763, p = 0.007$). Simple main effects tests revealed greater levels of activity for Improve than Copy in the left: fusiform gyrus (FFG) ($p = 0.047$), inferior temporal gyrus (ITG) ($p = 0.023$), middle temporal gyrus (MTG) ($p = 0.009$), superior temporal gyrus (STG) ($p = 0.030$), and parahippocampal gyrus (PHG) ($p = 0.049$). In the right hemisphere, there was a significant main effect of area ($F_{(33, 12)} = 1.725, p = 0.009$), but no main effect of condition nor interaction between area and condition ($F_{(1, 12)} = 0.581, p = 0.461$; $F_{(33, 396)} = 0.93, p = 0.59$; respectively). Thus, areas having significantly different theta activity were concentrated in the left temporal cortex (see Figure 15 left). A plot of representative mean theta activity across subjects in the left MTG reveals that theta band activity for Improve was strongly modulated in correspondence with the stimulus and physical performance

periods, and that it remained higher compared to Copy throughout the mental imagery period (Figure 16 top panel).

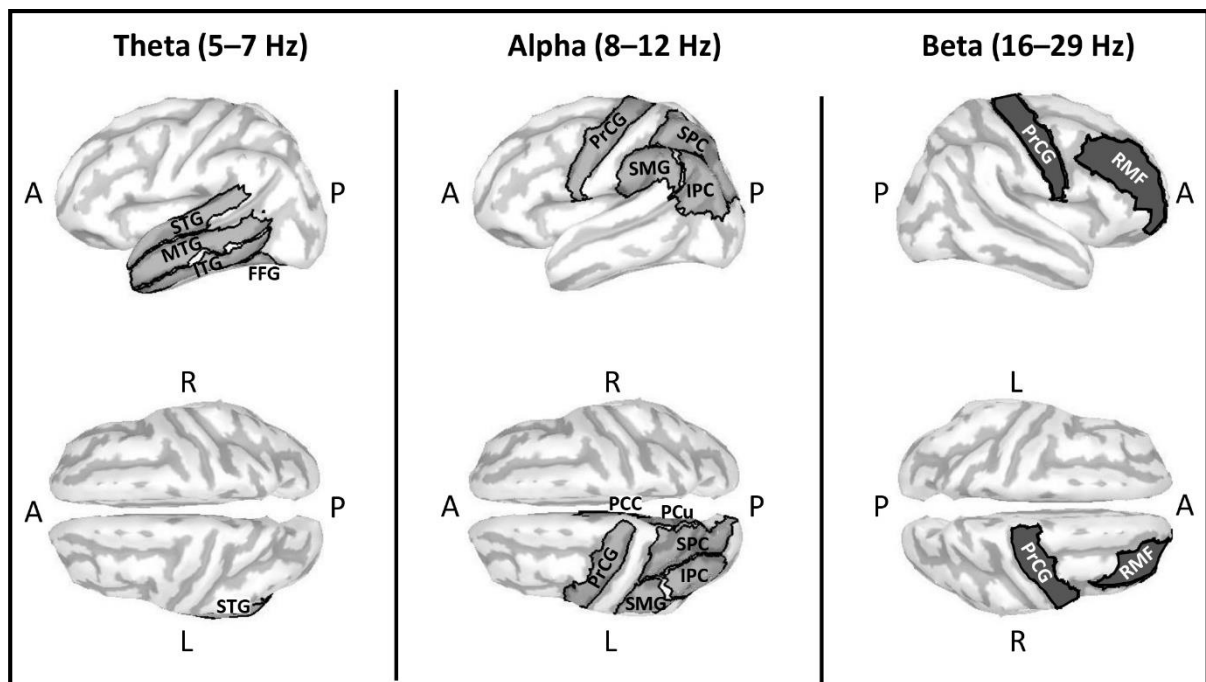


Figure 15. Cortical maps highlighting areas with significantly different oscillatory activity between conditions for the Multi-finger task in Study 2. Compared to Copy, Improvise induced mean current density strengths over the mental performance period that were higher in the theta band in the left temporal cortex, higher in the alpha band primarily in the left posterior parietal cortex, and lower in the beta band in right prefrontal areas. Improvisational cognition was thus differentiated according to the frequency of oscillatory activity in non-overlapping brain regions. A, P, L, and R, respectively denote anterior, posterior, left, and right. For further details, see Table 1. STG: superior temporal gyrus; MTG: middle temporal gyrus; ITG: inferior temporal gyrus; FFG: fusiform gyrus; PrCG: precentral gyrus; SMG: supramarginal gyrus; IPC: inferior parietal cortex; SPC: superior parietal cortex; PCC: posterior cingulate cortex; PCu: precuneus cortex; RMF: rostral middle frontal cortex. Adapted from Boasen et al. (2018). Spectral-spatial differentiation of brain activity during mental imagery of improvisational music performance using MEG, *Front Hum Neurosci.* Apr 24; Vol. 12:156.

In the alpha band, results in the left hemisphere revealed a significant main effect of area ($F_{(33, 12)} = 3.653, p < 0.001$), a marginal main effect of condition ($F_{(1, 12)} = 4.553, p = 0.054$), and a significant interaction between area and condition ($F_{(33, 396)} = 2.080, p = 0.001$). Simple main effects tests revealed significantly greater levels of activity for Improvise than Copy in the left: precentral gyrus (PrCG) ($p = 0.019$), superior parietal cortex (SPC) ($p = 0.017$), inferior parietal cortex (IPC) ($p = 0.017$), supramarginal gyrus (SMG) ($p = 0.045$), precuneus (PCu) ($p = 0.021$), and posterior cingulate cortex (PCC) ($p = 0.040$). In the right hemisphere, results revealed no main effects of area or condition, nor interaction between area and

condition ($F_{(33, 12)} = 1.297$, $p = 0.131$; $F(1, 12) = 0.508$, $p = 0.49$; $F_{(33, 396)} = 0.698$, $p = 0.90$; respectively). Thus, areas having significant different alpha band activity did not overlap with those relevant to the theta band, were also left hemispheric, and were predominantly concentrated in the posterior parietal cortex, which comprises the SPC, IPC, SMG, and PCu (see Figure 15 middle). A plot of representative average alpha activity in the left IPL (Figure 16 middle panel) reveals that activity for both condition exhibited desynchronization dynamics during the mental imagery period similar to that which many studies have observed during idea generation and periods of planning prior to physical movement (Schwab et al., 2014; Fumuro, et al., 2015; Deiber, et al., 2012; Caetano et al., 2007). Activity for Improve was higher however throughout the stimulus period and well into the mental imagery period, where it remained at or above baseline levels until dropping in preparation for physical performance.

In the beta band, results in the left hemisphere revealed a significant main effect for area ($F_{(33, 12)} = 3.886$, $p < 0.001$), but the main effect of condition and interaction between area and condition were not significant ($F_{(1, 12)} = 0.227$, $p = 0.64$; $F_{(33, 396)} = 1.284$, $p = 0.140$; respectively). In the right hemisphere, there was a significant main effect of area ($F_{(33, 12)} = 3.886$, $p < 0.001$), but no main effect of condition ($F_{(1, 12)} = 0.812$, $p = 0.39$). However, there was a weakly significant interaction between area and condition ($F_{(33, 396)} = 1.473$, $p = 0.048$). Simple main effects tests revealed significantly lower levels of activity for Improve than Copy in the right: rostral middle frontal cortex (RMF) ($p = 0.040$), and the PrCG ($p = 0.045$) (see Figure 15 right). A plot of representative average beta activity in the right RMF reveals that activity steadily decreased for both conditions from the stimulus through the performance

periods. However, lower activity for *Improvise* is apparent, particularly during early mental imagery (Figure 16 bottom panel).

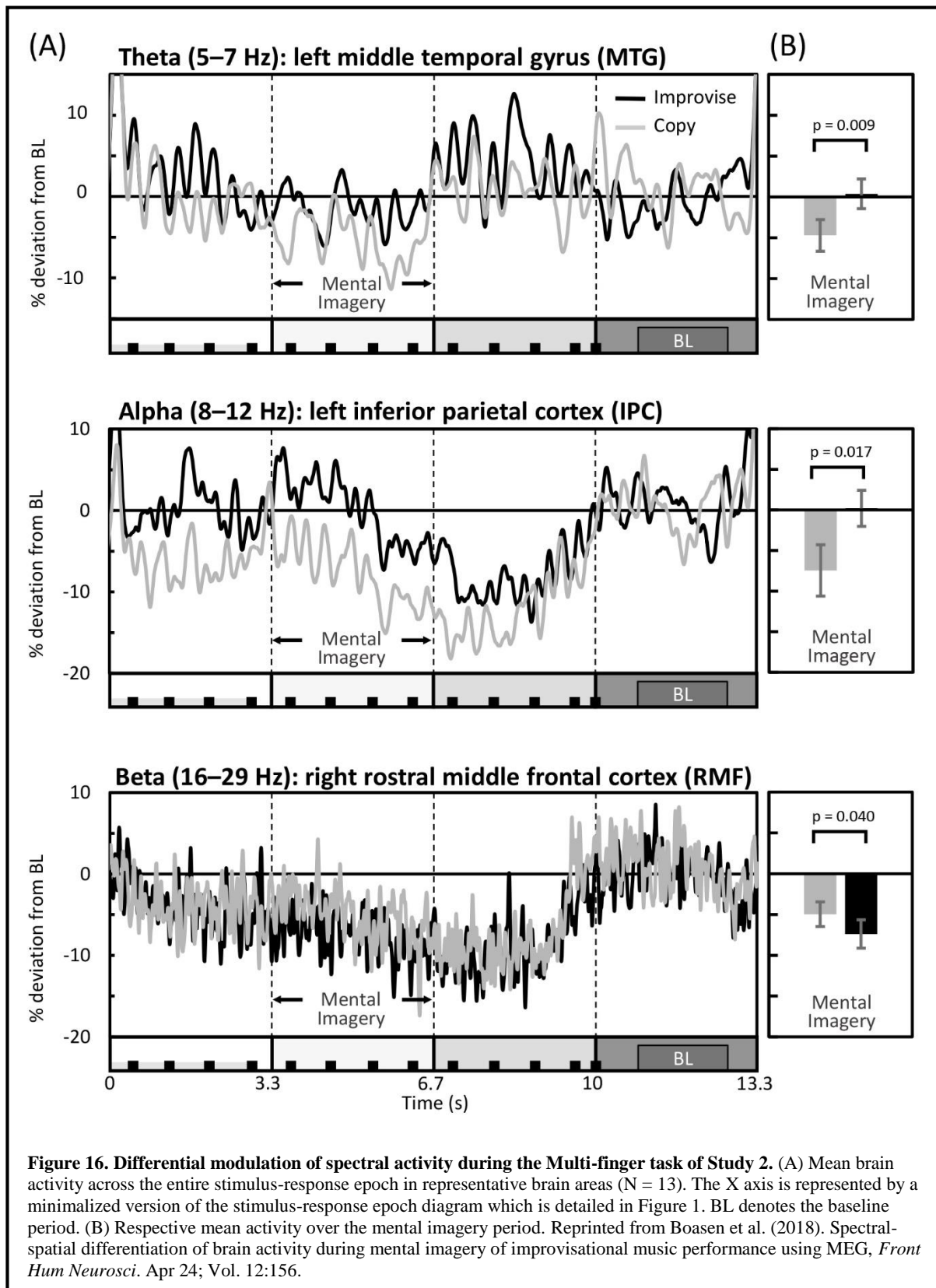


Table 2, summarizes the results from significant interactions and simple main effects as per the RM ANOVAs for the Multi-finger task in Study 2A.

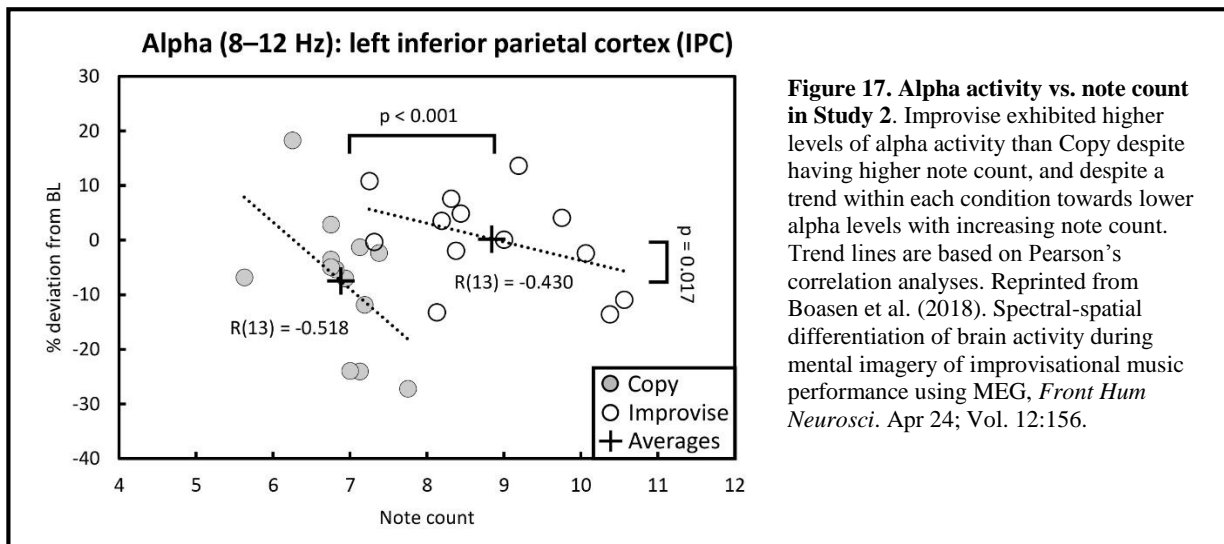
Table 2. Multi-finger task RM ANOVA results summary

Frequency	L/R	Interaction p value	Difference I vs. C	Brain areas	Simple main effect p value
<i>Theta</i> 5–7 Hz	L	0.007	I > C	Fusiform gyrus (FFG)	0.047
				Inferior temporal gyrus (ITG)	0.023
				Middle temporal gyrus (MTG)	0.009
				Superior temporal gyrus (STG)	0.030
				Parahippocampal gyrus (PHG)	0.049
<i>Alpha</i> 8–12 Hz	L	0.001	I > C	Precentral gyrus (PrCG)	0.019
				Superior parietal cortex (SPC)	0.017
				Inferior parietal cortex (IPC)	0.017
				Supramarginal gyrus (SMG)	0.045
				Precuneus (PCu)	0.021
<i>Beta</i> 15–29 Hz	R	0.048	C > I	Posterior cingulate cortex (PCC)	0.040
				Rostral Middle Frontal Cortex (RMF)	0.040
				Precentral gyrus (PrCG)	0.045

L, R, I and C refers to left, right, Improve, and Copy, respectively. Adapted from Boasen et al. (2018). Spectral-spatial differentiation of brain activity during mental imagery of improvisational music performance using MEG, *Front Hum Neurosci.* Apr 24; Vol. 12:156.

Behaviorally in the Multi-finger task, note counts for Improve (mean ± SE, 8.841 ± 0.302) were significantly higher than Copy (mean ± SE, 6.880 ± 0.145) ($p < 0.001$), and significantly greater than the mean note count for all 16 stimulus patterns ($p < 0.001$), again reflecting expression of increased rhythmical freedom during Improve. Meanwhile for Copy, standard error was less than that for Improve, and note count was not significantly different from the mean note count for all 16 stimulus patterns, implying a high degree of accuracy during Copy responses (see Figure 14 right panel). Pearson’s correlation analyses revealed no significant relationship between note count and brain activity in any frequency band, in any area, within or across conditions. Nevertheless, multiple regression analyses revealed that note count was predictive of brain activity in the alpha frequency band in the left IPC ($F_{(2, 23)} = 4.207$, $p = 0.028$, $R^2 = 0.268$) and the left PCC ($F_{(2, 23)} = 3.439$, $p = 0.049$, $R^2 = 0.230$). Standardized beta coefficients for the contribution of note count in these two areas were respectively $\beta = -0.593$ ($p = 0.044$) and $\beta = -0.663$ ($p = 0.029$), indicating a trend towards decreased alpha band brain activity with higher note count. However, the

standardized beta coefficients for the contribution of condition in these two areas were respectively $\beta = 0.806$ ($p = 0.008$) and $\beta = 0.730$ ($p = 0.017$), indicating the greater importance of condition over note count at predicting alpha activity, and corroborating the RM ANOVA finding that alpha activity levels are higher for Improvise than for Copy. Figure 17 helps illustrate these multiple regression findings, using Pearson's correlation results for alpha band activity vs. note count within conditions at the left IPC. The figure indicates that alpha activity levels are higher for Improvise than Copy despite trends towards lower alpha activity with higher note count within each condition.



7.2 Study 2B

The subjects targeted in Study 2B demonstrated a fairly wide range of creative ability with a mean total S-A Creativity score of 6.88 points out of 10 points possible, and a standard deviation of 1.87 points. Meanwhile, the intelligence of this particular subject population was quite homogeneous, with a mean SPM Plus test score of 49 points out of 60 points possible, and a standard deviation of 4.5 points. For a summary of the assessment scores please see Table 3. It is worth noting that, although the SPM Plus test has not been validated for age-

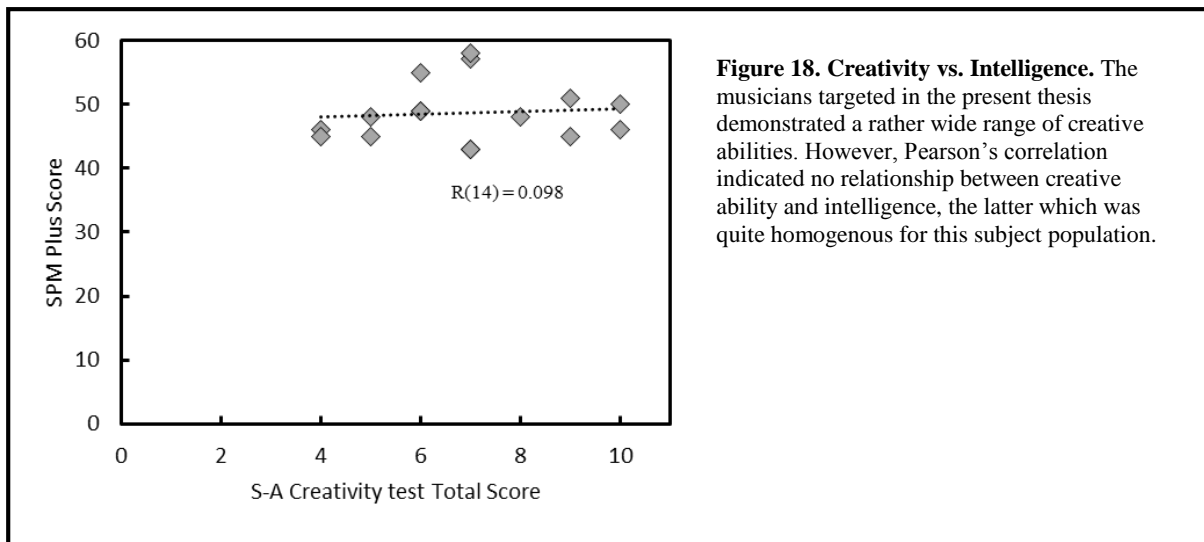
corrected, percentile conversion of scores for Japanese populations, when converted to age corrected percentiles based on validated data from German populations, the scores of the subjects in the present study averaged in the 80th to 90th percentile. This is unsurprising when considering that all of the subjects had at least two to four years of post-secondary education.

Table 3. Study 2B assessment results

Subjects	Creativity group	SPM Plus	S-A creativity test scores							Total
			Ta	Tb	Tc	F	X	O	E	
1	HC	46	9	8	9	8	8	7	10	10
2	HC	58	8	6	5	5	6	8	6	7
3	HC	50	10	7	9	9	10	10	10	10
4	HC	57	7	6	6	6	5	8	6	7
5	HC	51	9	8	7	8	8	10	9	9
6	HC	57	8	8	7	8	7	6	9	8
7	HC	43	6	6	8	6	7	6	7	7
8	HC	45	10	5	9	10	7	7	10	9
9	LC	49	6	6	4	5	5	5	6	6
10	LC	49	8	6	4	6	7	7	5	6
11	LC	45	3	4	6	4	4	4	4	4
12	LC	46	6	3	5	4	4	7	3	4
13	LC	45	6	4	5	5	5	5	5	5
14	LC	48	5	5	5	5	5	6	5	5

Ta, Tb, Tc: total score on sections a, b, and c, respectively. F, X, O, E: fluency, flexibility, originality, and elaboration, respectively

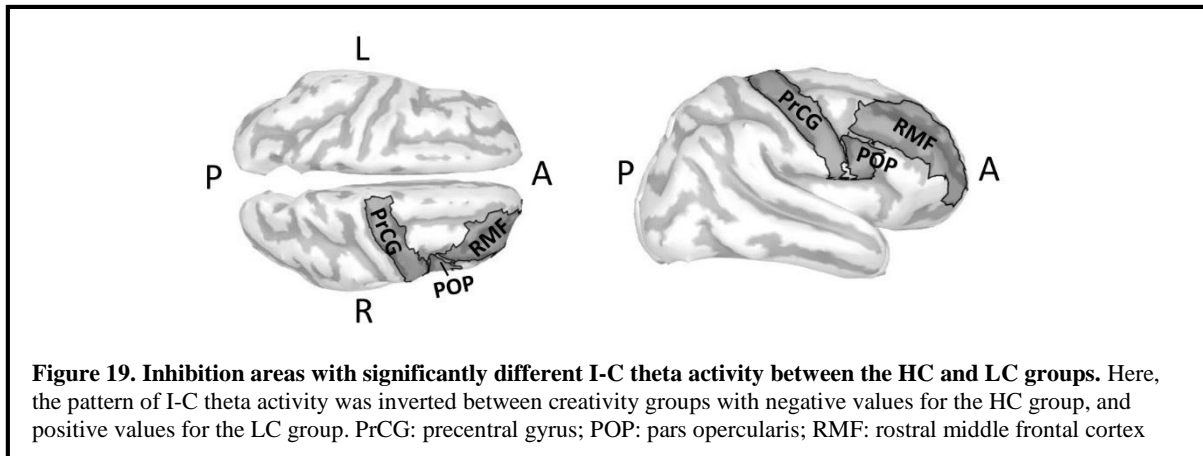
Pearson’s correlation test did not reveal a significant relationship between creative ability and intelligence ($p = 0.716$, $R = 0.099$) (see Figure 18), indicating that intelligence was not a confounding factor for creativity. Thus, the subjects were split into groups based on their creativity scores as per the methodology of this study. Consequently, those with scores of 7 points or higher were placed in the HC group ($N = 8$, 6 males and 2 females, average age \pm SD: 35.3 ± 9.3 years), and those with scores of 6 points or lower were placed in the LC group ($N = 6$, 4 males and 2 females, average age \pm SD: 36.3 ± 7.5). The average total creativity scores of the HC and LC groups were (average \pm SD) 8.4 ± 1.2 points and 5.0 ± 0.8 points respectively. The results presented hereafter will be based on the division of subjects into these two creativity groups.



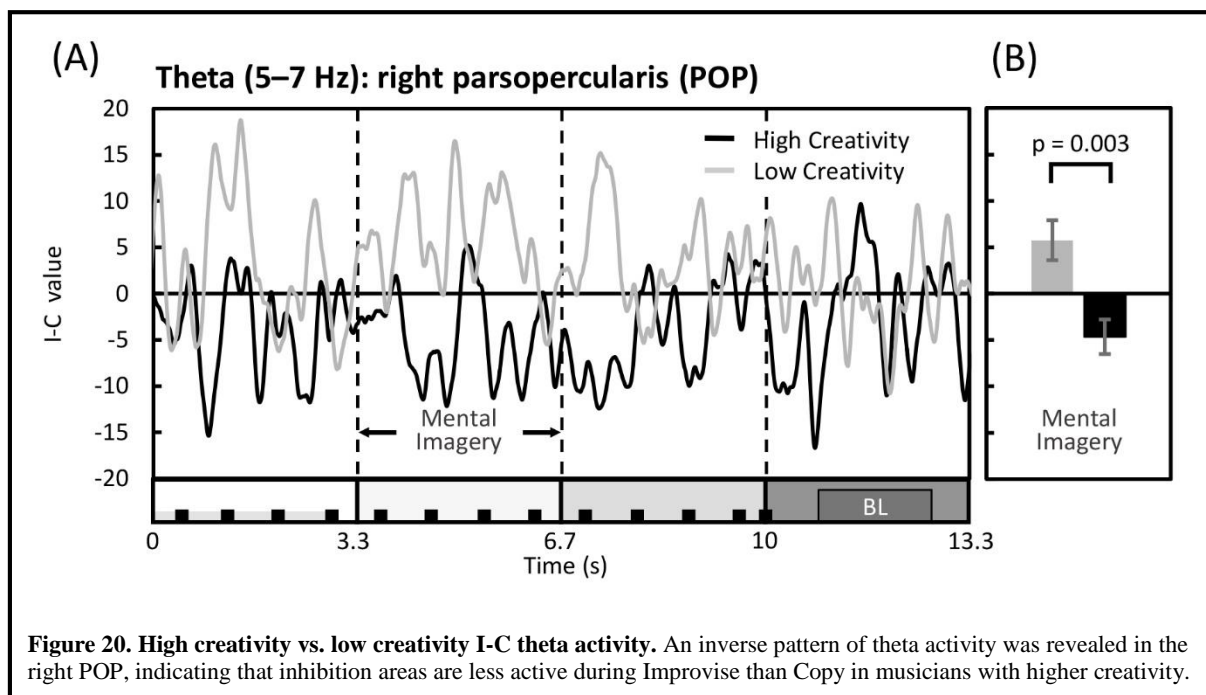
As for brain activity in the Single-finger task, mixed ANOVA revealed no significant effects of condition nor interactions between brain area and condition in any frequency. As such, my report on brain activity will hereafter focus on results from the Multi-finger task.

Mixed ANOVA of theta band I-C brain activity during mental imagery revealed a significant between subjects effect of creativity group ($F_{(1, 12)} = 5.249$, $p = 0.041$), with I-C values in the HC group negative, and those in the LC group positive (mean \pm SE; 4.357 ± 2.018 ; -1.760 ± 1.748). There was also a significant interaction between creativity group and brain area ($F_{(33, 396)} = 5.255$, $p = 0.001$). Simple main effects revealed that I-C values were significantly lower for the HC group compared to the LC group in the pars opercularis (POP) (mean \pm SE; -4.640 ± 1.873 vs. 5.760 ± 2.163 ; $p = 0.003$), RMF (mean \pm SE; -5.227 ± 1.521 vs. 1.554 ± 1.757 ; $p = 0.013$), and PrCG (mean \pm SE; -1.008 ± 1.993 vs. 7.777 ± 2.301 ; $p = 0.014$) (see Figure 19 for a cortical map of these areas). Intriguingly, the pattern of I-C theta activity in each of these three brain areas was opposite between groups, with negative mean values for the HC group, and positive mean values for the LC group. This means that theta activity for Improve was lower than Copy in the HC group, and higher than Copy in the LC group. A plot of representative mean normalized I-C theta activity for both groups in the right POP reveals that I-C theta band values for the HC group were negative from the time of stimulus

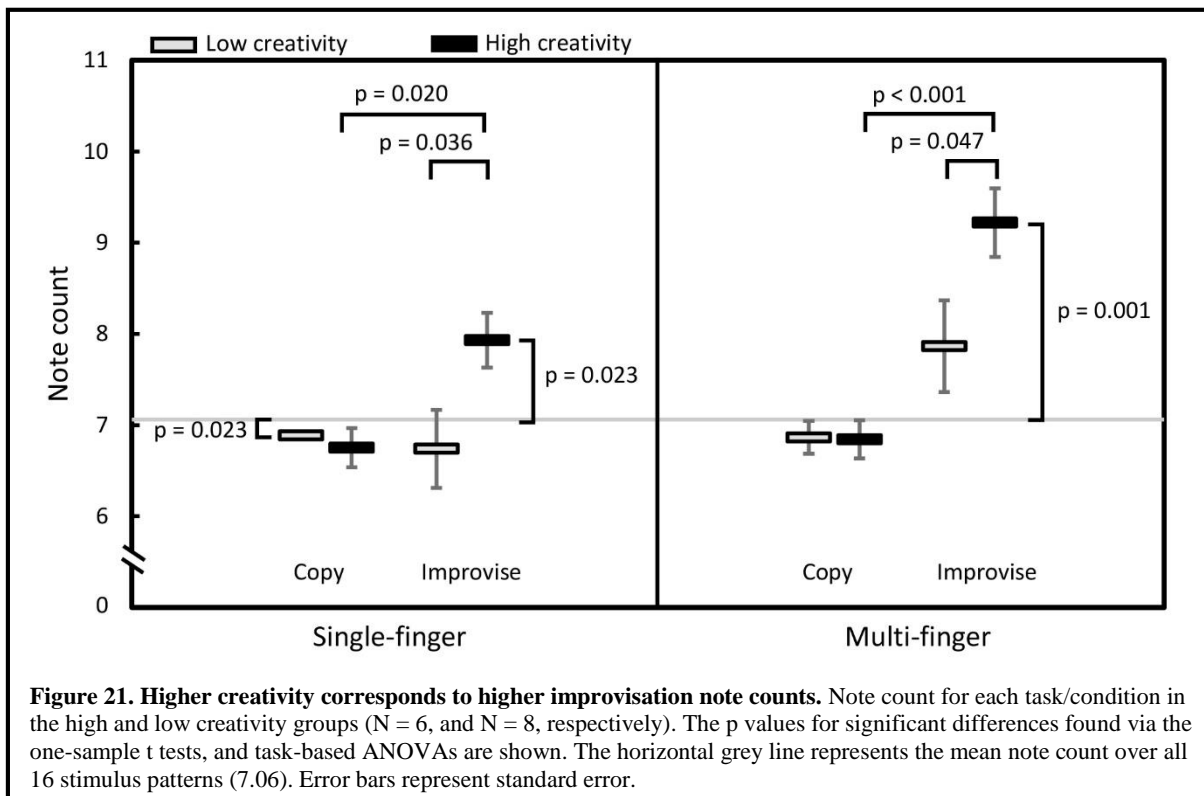
presentation through the end of performance, whereas the inverse was the case for the LC group (see Figure 20).



In the alpha band, results revealed no between-subjects effect of creativity group ($F_{(1, 12)} = 0.563$, $p = 0.468$), nor interaction between creativity group and brain area ($F_{(33, 396)} = 0.461$, $p = 0.764$). Similarly in the beta band, results revealed no between-subjects effect of creativity group ($F_{(1, 12)} = 0.187$, $p = 0.297$), nor interaction between creativity group and brain area ($F_{(33, 396)} = 0.409$, $p = 0.801$). However, mean beta activity in the RMF and PrCG did reveal a tendency towards the same inverse pattern between the HC and LC groups seen in the theta band: -1.418 ± 4.50 vs. 0.690 ± 3.525 , and -1.267 ± 3.421 vs. 0.550 ± 3.567 , respectively.



Behaviorally for the Single-finger task, mixed ANOVA comparing note count between conditions and between groups revealed that there was no significant main effect of condition ($F_{(1, 12)} = 2.384$, $p = 0.149$). However, there was a significant interaction between condition and creativity group in the ($F_{(1, 12)} = 3.919$, $p = 0.071$). There was also a significant between-subjects effect of creativity ($F_{(1, 12)} = 5.873$, $p = 0.032$), with higher note counts for those in the HC group (mean \pm SE, 7.340 ± 0.142) than the LC group (mean \pm SE, 6.813 ± 0.164). Simple main effects revealed that the between-subjects effect of creativity was limited to Improvise, where note counts for the HC group (mean \pm SE, 7.930 ± 0.331) were significantly higher than the LC group (mean \pm SE, 6.740 ± 0.382) ($p = 0.036$). Looking at groups separately, there was no significant difference in note count between Improvise (mean \pm SE, 6.740 ± 0.382) and Copy (mean \pm SE, 6.885 ± 0.190) in the LC group, whereas note count was significantly higher for Improvise (mean \pm SE, 7.930 ± 0.331) than Copy (mean \pm SE, 6.750 ± 0.164) in the HC group ($p = 0.020$). It is worth noting here that standard error was roughly double for Improvise compared to Copy in both groups, reflecting increased rhythmical freedom during Improvise regardless of creativity. One sample t test results for the Single-finger task revealed that compared to the mean note count for all 16 stimulus patterns, note counts for Improvise in the HC group (mean \pm SE, 7.930 ± 0.301) were significantly higher. Surprisingly, note counts for Copy in the LC group (mean \pm SE, 6.885 ± 0.034) were significantly lower than the mean note count for all 16 stimulus patterns. With a standard error of only 0.034, it appears that LC subjects were not only conservative, but extremely consistent in their Single-finger Copy responses. Subjects in the HC group were also conservative for Copy, but had higher standard error (mean \pm SE, 6.750 ± 0.214) (see Figure 21, left side).



Behaviorally for the Multi-finger task, mixed ANOVA comparing note count between conditions and between groups revealed a significant main effect of condition ($F_{(1, 12)} = 21.159, p = 0.001$). There was also a significant interaction between condition and creativity group ($F_{(1, 12)} = 3.512, p = 0.085$), as well as a marginally significant between-subjects effect of creativity ($F_{(1, 12)} = 4.703, p = 0.051$), with higher note counts for those in the HC group (mean \pm SE, 8.031 ± 0.201) than the LC group (mean \pm SE, 7.365 ± 0.232). Simple main effects revealed that the between-subjects effect of creativity was limited to Improve, where note counts for the HC group (mean \pm SE, 9.219 ± 0.401) were significantly higher than the LC group (mean \pm SE, 7.865 ± 0.463) ($p = 0.047$). Looking at groups separately, there was no significant difference in note count between Improve (mean \pm SE, 7.865 ± 0.463) and Copy (mean \pm SE, 6.865 ± 0.217) in the LC group, whereas note count was significantly higher for Improve (mean \pm SE, 9.219 ± 0.401) than Copy (mean \pm SE, 6.844 ± 0.188) in the HC group ($p < 0.001$). It is worth noting here that, akin to the Single-finger task, standard error was roughly double for Improve compared to Copy in both groups in the Multi-finger

task, reflecting increased rhythmical freedom during *Improvise* regardless of creativity. One sample t test results for the Single-finger task revealed that compared to the mean note count for all 16 stimulus patterns, note counts for *Improvise* in the HC group (mean \pm SE, 7.930 ± 0.301) were significantly higher. The lack of significant differences for *Copy* conditions in both groups, and their low standard error, implies there was a high degree of accuracy during *Copy* responses regardless of creativity (see Figure 21, right side).

Multiple regression analyses revealed that note count during *Improvise*, and creativity group, together were significantly predictive of I-C brain activity in the theta frequency band in the right POP ($F_{(2, 11)} = 6.079$, $p = 0.017$, $R^2 = 0.525$), the right RMF ($F_{(2, 11)} = 4.004$, $p = 0.049$, $R^2 = 0.421$), and the right PrCG ($F_{(2, 11)} = 4.799$, $p = 0.032$, $R^2 = 0.466$). However, standardized beta coefficients for the contribution of note count during *Improvise* were not significant in any of these areas at $\beta = 0.036$ ($p = 0.886$), $\beta = -0.094$ ($p = 0.737$), and -0.281 ($p = 0.305$). Instead, the contribution towards I-C theta activity appeared to be based on creativity group, whose beta coefficients for POP, RMF, and PrCG were respectively, $\beta = -0.743$ ($p = 0.012$), $\beta = -0.594$ ($p = 0.052$), and $\beta = -0.489$ ($p = 0.088$). Figure 22 helps illustrate these multiple regression findings, using regression lines for I-C theta band activity vs. *Improvise* note count in each group at the right POP. The figure indicates that theta activity levels are lower for the HC group compared to the LC group regardless of *Improvise* note count.

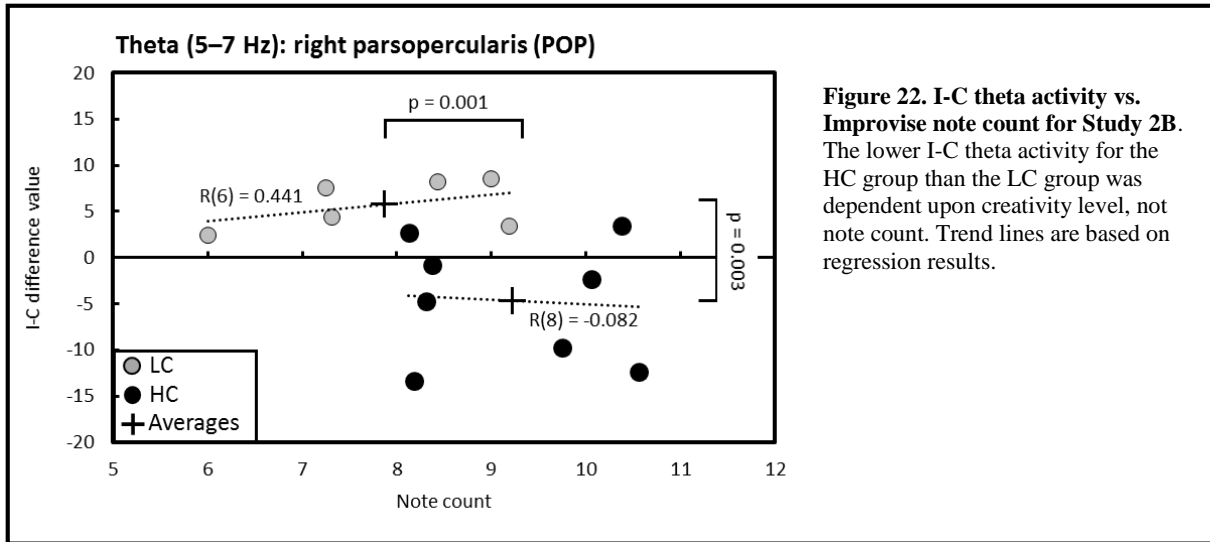


Figure 22. I-C theta activity vs. Improvise note count for Study 2B. The lower I-C theta activity for the HC group than the LC group was dependent upon creativity level, not note count. Trend lines are based on regression results.

8 Discussion

The present thesis sought to differentiate brain areas and oscillatory frequency bands relevant to improvisational cognition by comparing brain activity during mental imagery of music performance in conditions where rhythm was either improvised, copied. The thesis also sought to investigate the relationship between creative ability and inhibition-associated brain activity in improvisationally experienced musicians. The following discussion will address the results of each of the studies in turn, beginning with Study 1 which targeted predominantly non-musicians, then Study 2A which targeted improvisationally experienced musicians, and finally Study 2B regarding creativity and inhibition.

8.1 Study 1

The majority of significant differences in brain activity between conditions found in Study 1 were between Beat and Improve. To explain this, it is important to recall that Beat was originally conceived as a kind of control condition for Study 1. During Beat, subjects merely playback a quarter note, metronomic response. The response is the same every time, regardless of the stimulus pattern that was presented. It was precisely because the response was independent of the stimulus that led to the usefulness of the Beat condition to be called into question. Indeed, for Beat, there was no need to pay close attention to the stimuli aside from ascertaining tempo. In contrast, for both Copy and Improve, subjects had to pay close attention to the stimuli not only to ascertain tempo, but also to remember them, either duplicating them in their response for Copy, or playing something novel in response for Improve. Moreover, the novel response production of Improve arguably adds an additional level of cognitive engagement that further separates Improve from Beat. Considering this, the differences in brain activity between Beat and Improve is

unsurprising, and arguably more difficult to explain. It was for this reason that the Beat condition was eliminated from further iterations of the paradigm in Study 2. Consequently, to make this discussion on Study 1 more pertinent to other implementations of the paradigm, I will hereafter focus only on differences in brain activity between *Improvise* and *Copy*.

Alpha band brain activity in the right hemisphere was significantly lower for *Improvise* than *Copy* in the SPC. However, pairwise comparisons revealed alpha band activity for *Improvise* was also significantly lower than *Copy* in the left hemisphere. Furthermore, the lack of a significant interaction between condition and brain area in the left hemisphere indicates that lower alpha activity there for *Improvise* was widespread. Alpha activity is strongly associated with motor-related processing, and is known to desynchronize prior to movement or during movement planning (Caetano et al., 2007; Fumuro et al., 2015; Schalles & Pineda, 2015). Moreover, motor processing is known to occur contralateral to the body part that is moved (Yousry et al., 1997). In line with this, Study 1 involved right-handed performance, and left hemispheric alpha desynchronization was observed for *Improvise* leading up to physical performance. However, physical performance is also relevant to *Copy*, and indeed alpha desynchronization was also apparent for *Copy* prior to physical performance. Nevertheless, alpha desynchronization for *Improvise* appears to begin much earlier than for *Copy*, from the start of the mental imagery period or earlier. This suggests that the greater alpha desynchronization for *Improvise* was not due to the level of motor planning involved, but rather to the cognitive characteristics associated with musical improvisation imagery.

In the context of ideation, an intrinsic part of the mental imagery period in all studies of this thesis, numerous EEG studies have reported greater alpha levels when the ideation involved is divergent compared to convergent (Jaušovec, 1997; Mölle et al., 1999; Fink & Benedek, 2014). In other words, alpha levels tend to be higher when the cognition involves more spontaneous associative processing, as would be the case during *Improvise*, compared to

goal-directed processing such as that involved in the stimulus imitation of Copy. Specifically with respect to improvisation, greater alpha activity is thought indicative that the cognition involved is internally-directed, and is a phenomenon seen not only in musicians, but also in dancers (Lopata et al. 2017; Fink et al., 2009). Incidentally, results from Study 2A corroborated this, revealing comparatively higher alpha levels for Improvise than Copy. However, alpha levels were conversely lower for Improvise than Copy in Study 1. This paradoxically suggests that the brain activity for subjects in Study 1 was more goal-directed for Improvise, and more internally-directed for Copy. However, this logic is irreconcilable with the nature of improvisation, which should intrinsically involve more creative and internally-directed processing than stimulus mimicry. Clearly, the notion that internally-directed processing is reflected by greater alpha activity is an oversimplification. To explain it better, let us first consider that to say that spontaneous brain activity is less or greater is to respectively say that it is comparatively desynchronized or synchronized.

Simply put, desynchronized brain activity is the result of asynchronous neural signaling, which would produce deconstructive electromagnetic wave forms that would in turn be seen as activity with lower amplitude. Conversely, synchronized brain activity is the result of synchronous or coordinated neural signaling, which would produce constructive electromagnetic wave forms that would in turn be seen as activity with higher amplitude. Synchronous alpha activity in particular has been inversely associated with decreased blood metabolism (Laufs et al., 2003). Decreased blood metabolism, although sometimes considered a sign of deactivation, has alternatively been proposed to be a sign of more efficient neural processing (Haier et al., 1988). Neural processing efficiency meanwhile is thought to be enhanced by expertise and experience (Grabner et al., 2006; Strait et al., 2009). By this logic, one would expect the neural processing efficiency associated with expertise for a given experimental task to be reflected by comparatively more synchronous or higher alpha

activity. In support of this, two recent studies by Fink et al. (2018) and Camarda et al. (2018) demonstrate that those with expertise at creative ideation (an intrinsic aspect of musical improvisation) exhibit comparatively higher alpha levels during creative tasks. The subjects in Study 1 were predominantly non-musicians, and crucially, none had experience with musical improvisation. In light of the preceding evidence, the comparatively greater and widespread desynchronization exhibited by the non-musicians of Study 1 during *Improvise* compared to *Copy* arguably reflects their lack of familiarity with musical improvisation, and thus their lack of coordination and efficiency with the underlying spontaneous associative processing involved.

As for beta band activity in Study 1, levels for *Improvise* were significantly lower than *Copy* in the left CAC and PCu. Beta band activity is strongly associated with motor-related processing, with desynchronization typically exhibited prior to and during physical or imagined movement (Engel & Fries, 2010; Caetano et al., 2007; de Lange et al., 2008). Meanwhile, the CAC is functionally linked to decision making and high-level action planning processing (see review by Lavin et al., 2013), while the PCu is thought to play a central role in integrative processing including sensorimotor and mental imagery strategies (Cavanna & Trimble, 2006; Borsook et al., 2014). In line with the argument in the preceding paragraph, for non-musicians in particular who have not developed efficient automated motor processing for musical improvisation, *Improvise* may place a larger burden on decision making and sensorimotor integration than *Copy*. Thus, that the CAC and PCu would demonstrate differential activity in improvisationally inexperienced non-musicians is not surprising. That the differential activity in these areas was in the beta band would furthermore seem to cement the role of sensorimotor processing. However, other evidence and characteristics of beta activity suggest a potentially more complex story. For instance, Huebl et al. (2016) have shown that beta activity in the CAC desynchronizes in accordance with emotion and arousal,

suggesting that the greater desynchronization of beta activity for *Improvise* in Study 1 was due to it involving more emotional processing than *Copy*. Moreover, motor-related decreases in beta activity are regularly accompanied by increases in faster gamma-band activity (de Lange et al., 2008; Donner et al., 2009), indicating an increase in higher-order processing. It is reasonable to suppose that musical improvisation would demand more higher-order processing than stimulus mimicry. Therefore, although gamma activity was not verified in this thesis, the beta results could comprehensively be indicative of increased emotional processing, as well as increased higher-order processing for planning/decision making and sensorimotor integration in *Improvise* compared to *Copy*.

8.2 Study 2A

Study 2A involved two tasks, a *Single-finger* task and a *Multi-finger* task. In the *Single-finger* task, although behaviorally, the musicians played significantly more notes during *Improvise* than *Copy*, and demonstrated a marked increase in note count variance for *Improvise*, the mean note counts for *Improvise* were not significantly different from the mean note count of all stimuli. In other words, although behavioral differences between conditions were apparent, they were not robust. This lack of a strong behavioral difference between *Single-finger* conditions likely underscores why significant differences in brain activity between conditions were not seen. Granted this does not mean that differences in brain activity between *Improvise* and *Copy* did not exist. Rather, it suggests that the differences were too subtle to be discerned with the study design that was used. Recall that the potential for this result was predicted at the time of designing Study 2, which is precisely why the *Multi-finger* task was added to the paradigm. This design change proved fortuitous, as the differences between *Improvise* and *Copy* for the *Multi-finger* task in Study 2A were striking.

Behaviorally, the musicians clearly played more notes, and more varied patterns of notes for *Improvise* than *Copy*. Correspondingly, analyses of brain activity revealed significant interactions between condition and brain area, with significant differences in brain activity found between conditions for all three frequency bands of interest. Moreover, the brain areas where significant differences in brain activity were found differed depending on the oscillatory frequency band. Consequently, the results from the Multi-finger task of Study 2A served to support the publication of a major portion of this thesis (Boasen et al., 2018).

Considering first the results of theta band activity for the Multi-finger task of Study 2A, theta levels were significantly greater for *Improvise* compared to *Copy* comprehensively throughout the left temporal cortex in the STG, MTG, ITG, FFG, and PHG. Numerous studies have shown that event-related increases in theta activity localized within the temporal cortex including within the STG are important for auditory rhythm processing (Ghitza, 2012; Hyafil et al., 2015; Ahissar, et al., 2001; Luo & Poeppel, 2012). The left STG in particular has been implicated as important for the production of syllables and discrete rhythm elements of speech (i.e. sublexical speech) (Hickok & Poeppel, 2004), implying a functional role in rhythm-based auditory production. Additionally, activation of temporal areas, including the STG, was observed by Doney et al. (2014) during a similar style of musical improvisation, and has consistently been demonstrated during mental imagery of music (Zvyagintsev, et al., 2013; Halpern & Zatorre, 1999; Kraemer et al., 2005; Groussard, et al., 2010). During the *Improvise* condition of the present study, the need to improvise novel rhythm patterns likely placed more demand on rhythmic production processing, and may thus explain the greater theta activity found for *Improvise* at the STG.

Areas other than the STG where theta activity was significantly higher for *Improvise* may be functionally important to the improvisational nature of the rhythm production. For example, the ITG and MTG in the left hemisphere specifically, and the FFG, are all reportedly

important for linguistic semantic processing (Balsamo et al, 2006; Chee et al., 1999; Hickok & Poeppel, 2000). Left anterior temporal areas, including the left MTG, have also been linked to musical semantic processing (Platel et al., 2003). Theta power increases over left temporal areas are associated with increased demand on linguistic semantic processing (Bastiaansen et al., 2005), and may likewise occur with increased demand on musical semantic processing. Meanwhile, the PHG has been implicated in emotional processing, including that related to music (Koelsch, 2005; Aminoff et al., 2013). Processing the semantic and emotional context of sounds is arguably an intrinsic part of auditory communication, and likely more important for *Improvise* than *Copy* due to the conversational style of improvisation used. Thus, the higher theta activity found for *Improvise* may comprehensively reflect an increased demand on rhythmic communication processing.

As for differences in alpha band activity, here it seems important to recognize that memory processing is also essential for both *Improvise* and *Copy* during the mental imagery period of the present thesis. This is because mentally imagined musical information must be memorized for playback during the physical performance period. Note count could be considered an index of memory load during the mental imagery period. Increasing memory load reportedly results in lower alpha activity (Stipacek et al., 2003). In agreement with this, the contribution of note count found via multiple regression analyses indicated decreased alpha band activity with greater note count at the left IPC and PCC, areas known to be functionally important in memory tasks (Koenigs et al., 2009; Maddock et al., 2001). Based on the above, the fact that note count was significantly greater for *Improvise* than *Copy* suggests that memory load was higher for *Improvise*, and thus favors it having lower alpha band activity. Nevertheless, alpha band activity was significantly greater for *Improvise* than *Copy*. Moreover, contribution of condition via multiple regression analyses indicated the greater importance of condition over note count. This suggests that the difference in alpha

activity between conditions was being influenced apart from memory by another more important aspect of cognition.

I proposed this other aspect of cognition to be its directionality (i.e. internal vs. external) with respect to the imagined music performance in each condition. This notion is first of all supported by the fact that the left SMG, IPC, SPC, PCu, and PrCG, areas where significant differences in alpha activity were found, are all contralateral to the hand used in imagined music performance. Additionally, these areas have reported links to auditory-related sensorimotor integration (Knight et al., 1989; Bangert, et al., 2006; Rushworth et al., 2001; Koenigs et al., 2009; Wolpert et al., 1998), and mental imagination of motor activity (Caminiti et al., 1998; Kawashima et al., 1994; Simon, et al., 2002; Porro, et al., 1996; Lotze & Halsband, 2006; Sacco, et al., 2006). Secondly, during tasks employing mental imagination, divergent thinking, and analytical problem solving, alpha power is higher when cognition is internally-directed compared to when it is externally-directed (Cooper et al., 2003; Kounios, et al., 2008; Kounios & Beeman, 2014; Benedek et al., 2014b). As argued in the discussion regarding Study 1, particularly in subjects with expertise at creative tasks, alpha levels are higher during such tasks compared to those with less expertise and compared to alpha levels during non-creative tasks (Fink et al., 2018; Carmarda et al., 2018). This phenomenon is moreover attributed to the cognition involved being more bottom-up or internally-directed (Lopata et al., 2017; Fink et al., 2018). Indeed, internally-directed cognition is thought to be an intrinsic aspect of tasks such as musical improvisation which require generation of novel content (Beaty, 2015). In line this, I argue that cognition is directed more internally during the mental imagery period of the *Improvise* condition to produce novel rhythm responses, rather than externally to ensure accurate duplication of rhythm patterns as in the *Copy* condition. Furthermore, reiterating my argument in the discussion on Study 1, higher alpha levels could be a sign of increased processing efficiency.

Thus I propose that the higher alpha activity for *Improvise* is a sign that the cognitive processing underlying the imagined right-handed rhythmic improvisation is not only more internally-directed, but also more efficient in improvisationally experienced musicians.

Additionally, the inverse relationship of left hemispheric alpha levels between *Improvise* and *Copy* in improvisationally experienced subjects in Study 2A and the non-musicians in Study 1, suggests that left hemispheric alpha activity will be an important target for future studies using this paradigm to investigate changes in brain activity due to musical improvisation training.

With respect to the beta band, there was higher activity in the right RMF and PrCG for *Copy* compared to *Improvise* (see Figure 3). Higher beta power in the right dorsal lateral prefrontal cortex (which shares anatomy with the RMF) during response preparation to an anti-saccade task has also been implicated as a sign of inhibitory control (Hwang et al., 2014). In a review of functional evidence on inhibition control, As mentioned in the introduction to this thesis, Aron et al. (2014) argue that brain areas critical to inhibition are right-lateralized, and furthermore propose that the dorsal lateral prefrontal cortex is involved in regulating the rules of inhibition control. Meanwhile, the right primary motor cortex, which is within the PrCG, is also recognized as playing a role in action inhibition (Spierer et al., 2013), and a recent electrocortical study has found higher beta oscillatory power here prior to a successful stop during a no-go task (Fonken, et al., 2016), thus implicating higher beta oscillatory power in this brain area as a sign of inhibition.

Inhibition can be considered a form of conscious self-monitoring. Such processing is necessary for the *Copy* condition of the present study as subjects must ensure their imagined rhythmic pattern accurately matches that of the presented stimulus. Conversely less self-monitoring, or disinhibition, is arguably key to the spontaneous free flowing of ideas intrinsic to improvisational cognition. Neurological evidence that improvisation involves a

disinhibited cognitive state has previously been reported by Limb and Braun (2008), who similarly observed deactivation in the right DLPFC during free right-handed improvisation by professional jazz players. In the present study, both Multi-finger Improvise and Multi-finger Copy involve a degree of improvisational cognition pertaining to melody, as the subject is free to use any combination of notes to perform the task. However, it is only Improvise in which subjects are completely free to improvise their responses. Thus, cognition during Improvise should be more disinhibited, and may therefore explain why beta activity for Improvise was lower in frontal areas associated with inhibition control.

8.3 Study 2B

The importance of disinhibition not only to improvisation, but also to creative ideation was central to Study 2B, where I hypothesized that musicians with higher creativity may also have augmented ability to control brain function associated with inhibition. To investigate this, I separated subjects in the HC or LC groups according to whether they had higher or lower creativity. I then analyzed their performance behavior via note counts, and compared their differential I-C inhibition-associated brain activity in the theta, alpha, and beta frequency bands for both tasks.

Behaviorally, although the LC group demonstrated greater variability in note counts for Improvise compared to Copy in both the Single-finger and Multi-finger tasks, they did not play significantly more notes for Improvise than Copy in either task. In fact, the mean note count for Improvise was actually less than that for Copy for the LC group in the Single-finger task. In contrast, the HC group not only played significantly more notes for Improvise than they did for Copy in both tasks, they also played significantly more notes than the LC group did for Improvise in both tasks. More notes played could be a sign of greater performance

fluency, suggesting that among these improvisationally experienced musicians, those with higher creativity performed with greater fluency during improvisation than those with lower creativity. Ideational fluency is incidentally a sub-index on the S-A Creativity test, and is known to correlate strongly with its total creativity score that was used to categorize subjects into the HC and LC groups (Society_For_Creative_Minds, 1969). These behavioral results thus appear to indicate that creative ideational fluency and musical improvisation performance fluency are related. However, the question remains whether these behavioral differences between groups can be explained by differences in disinhibition.

For the Single-finger task, despite significant differences in behavior between the HC and LC groups, analyses of brain activity did not reveal any differences. Like Study 2A, this could simply have been due to the behavioral differences not being robust enough to discern differences in brain activity with this small sample size. Moreover, in the Single-finger task, all subjects must constrain their *Improvise* responses down to a single melodic dimension. This constraint likely required a certain level of inhibitory control. Accordingly, my hypothesis might predict musicians with higher creativity to exhibit greater inhibitory activity than musicians with lower creativity. However, it may also simply be that disinhibition is not a relevant differentiating cognitive factor for the Single-finger task in this paradigm.

As for the Multi-finger task, which did not involve melodic constraints on *Improvise* responses, differences in inhibition-associated brain activity were observed between the LC and HC groups in the theta band at the right POP, RMF, and PrCG. For all three areas, the pattern of I-C theta activity was inverted between groups, with negative I-C values for the HC group, and positive I-C values for the LC group. This means that subjects with higher creativity exhibited lower theta activity for *Improvise* than *Copy*, and vice versa for subjects with lower creativity. Theta band activity is often observed to be coupled with faster oscillatory activity (Schack et al., 2002; Sarnthein et al., 2003), and is believed to play a

fundamental role in regulating higher-order processing across distant cortical regions (Mölle & Born, 2010, Pascual-Marqui et al., 2017). In corroboration with this, although not significant, the mean beta band levels recorded during *Improvise* for the HC group in these areas followed a similar trend of reduced activity compared to the LC group. Thus, the pattern of lower theta could be interpreted as a sign that the right POP, RMF, and PrCG were more fundamentally disengaged during *Improvise* compared to *Copy* in the HC group, and furthermore implies a decrease in higher-order processing in these inhibition control areas. In short, musicians with higher creativity exhibited brain activity during *Improvise* that was indicative of increased disinhibition.

Interestingly, musicians with lower creativity conversely appeared to not employ a disinhibitory cognitive strategy during improvisation, as inhibition-associated theta activity was higher for *Improvise* than *Copy*. This implies that disinhibition is not a given for musicians during musical improvisation, even for those who have improvisational experience. Rather, disinhibition during improvisation appeared to depend upon creative ability. Multiple regression results corroborate this (see Figure 21), revealing that disinhibitory theta band activity (i.e. negative I-C theta activity) is only predicted by creativity group and not by *Improvise* note count. This finding could furthermore indicate that the beta band results in Study 2A were biased by the larger number of musicians with high creativity scores. Overall, the results of Study 2B favor my hypothesis regarding creative ability and control of inhibitory function, and highlight the importance of assessing inhibition-associated brain activity and creative ability in future studies examining the effects of musical improvisation training.

8.4 Limitations

The studies in this thesis were limited in that the time-frequency analyses used were based on average activity within relatively broad, pre-determined areas, which intrinsically lowered the spatial precision of spectral activity. However, I feel the method was justifiable and informative for this first-time, exploratory inquiry of improvisational music performance-related cognition in MEG. Meanwhile, the lack of significant results for the Single-finger task in improvisationally experienced musicians may indicate that, in subjects with musical expertise, the cognitive burden for both Single-finger conditions was insufficient to generate observable interactions between brain activity and brain area. This was not be the case with non-musicians however, and thus further experiments using the present paradigm should perhaps maintain the Single-finger task, particularly when targeting non-musician populations. Regarding Study 2B in particular, sample size was somewhat small. Although support for my hypothesis was gained, further large-scale studies are needed to clarify the beta-band activity results from Study 2A in the context of creativity. Finally, the tasks in the present study were not “yorked” (Engel & Keller, 2011). In other words, subjects did not respond to stimuli produced by another subject, as was the case in the improvisational music performance study by Donnay et al. (2014). By using a “yorked” performance design, the deviation in rhythmic complexity (i.e. note count) between Improvise and Copy could have been lessened, and may have resulted in more robust differences in brain activity between the conditions.

9 Conclusions

The studies comprised in this thesis are the first to successfully demonstrate the feasibility of musical improvisation experimentation in MEG. Comprehensively, the work herein resulted in the construction of two unique, MEG-compatible musical instruments, and establishment of a musical improvisation paradigm that incorporated mental imagery and mimicked conversational forms of improvisation used in real live performance or therapy. Using these instruments and paradigm, I was able to differentiate spectral-spatial brain activity associated with improvisational cognition in improvisationally inexperienced non-musicians, improvisationally experienced musicians, and in improvisationally experienced musicians with high creative ability. The inexperience of the non-musicians was reflected by greater alpha band and beta band desynchronization during mental imagery of musical improvisation performance compared to copied performance in parietal brain areas, a sign of inefficient integrative processing during creative ideation. Improvisationally experienced musicians meanwhile demonstrated greater theta activity in left temporal rhythm production and communication areas, greater alpha activity in left sensorimotor and premotor areas, and less beta-activity in areas associated with inhibition control. These findings highlighted the communicative nature of the improvisational style used, and support the notion that production of novel auditory content may be facilitated by more efficient integrative processing, and a disinhibited cognitive state. Finally, improvisationally experienced musicians with higher creative ability exhibited a pattern of theta activity in inhibition-associated brain areas indicative of a higher level of disinhibition during improvisation that corresponded with higher improvisational performance output. These results highlight the importance of disinhibition as a cognitive strategy during improvisation for those with higher creative ability. Overall, far more than merely demonstrating the feasibility of musical improvisation performance experimentation in MEG, the present thesis has produced results

that corroborate findings from other modalities, and deepen the knowledge in this field. Most importantly, the establishment of its practical paradigm provides a solid foundation for further direct neuromagnetic investigation into the effects of improvisational music training and therapy that will hopefully support its wider implementation.

10 References

- Adhikari, B. M., Norgaard, M., Quinn, K. M., Ampudia, J., Squirek, J., & Dhamala, M. (2016). The Brain Network Underpinning Novel Melody Creation. *Brain Connectivity*, 6(10), 772–785. <https://doi.org/10.1089/brain.2016.0453>
- Ahissar, E., Nagarajan, S., Ahissar, M., Protopapas, A., Mahncke, H., & Merzenich, M. M. (2001). Speech comprehension is correlated with temporal response patterns recorded from auditory cortex. *Proceedings of the National Academy of Sciences*, 98(23), 13367–13372. <https://doi.org/10.1073/pnas.201400998>
- Aminoff, E. M., Kveraga, K., & Bar, M. (2013). The role of the parahippocampal cortex in cognition. *Trends in Cognitive Sciences*. <https://doi.org/10.1016/j.tics.2013.06.009>
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2014). Inhibition and the right inferior frontal cortex: One decade on. *Trends in Cognitive Sciences*, 18(4), 177–185. <https://doi.org/10.1016/j.tics.2013.12.003>
- Bailey, D. (1993). *Improvisation: Its nature and practice in music*. Da Capo Press. ISBN-13: 978-0306805288
- Balsamo, L. M., Xu, B., & Gaillard, W. D. (2006). Language lateralization and the role of the fusiform gyrus in semantic processing in young children. *NeuroImage*, 31(3), 1306–1314. <https://doi.org/10.1016/j.neuroimage.2006.01.027>
- Bangert, M., Peschel, T., Schlaug, G., Rotte, M., Drescher, D., Hinrichs, H., ... Altenmüller, E. (2006). Shared networks for auditory and motor processing in professional pianists: Evidence from fMRI conjunction. *NeuroImage*, 30(3), 917–926. <https://doi.org/10.1016/j.neuroimage.2005.10.044>
- Barron, F., & Harrington, D. M. (1981). Creativity, Intelligence, and Personality. *Annual Review of Psychology*, 32(1), 439–476. <https://doi.org/10.1146/annurev.ps.32.020181.002255>
- Bashwiner, D. M., Wertz, C. J., Flores, R. A., & Jung, R. E. (2016). Musical Creativity “Revealed” in Brain Structure: Interplay between Motor, Default Mode, and Limbic Networks. *Scientific Reports*, 6(1), 20482. <https://doi.org/10.1038/srep20482>
- Bastiaansen, M. C. M., Van Der Linden, M., Ter Keurs, M., Dijkstra, T., & Hagoort, P. (2005). Theta responses are involved in lexical-semantic retrieval during language processing. *Journal of Cognitive Neuroscience*, 17(3), 530–541. <https://doi.org/10.1162/0898929053279469>
- Beaty, R. E. (2015). The neuroscience of musical improvisation. *Neuroscience and Biobehavioral Reviews*, 51, 108–117. <https://doi.org/10.1016/j.neubiorev.2015.01.004>
- Behrmann, M., Geng, J. J., & Shomstein, S. (2004). Parietal cortex and attention. *Current Opinion in Neurobiology*, 14(2), 212–217. <https://doi.org/10.1016/j.conb.2004.03.012>

- Benedek, M., Borovnjak, B., Neubauer, A. C., & Kruse-Weber, S. (2014a). Creativity and personality in classical, jazz and folk musicians. *Personality and Individual Differences*, 63, 117–121. <https://doi.org/10.1016/j.paid.2014.01.064>
- Benedek, M., Schickel, R. J., Jauk, E., Fink, A., & Neubauer, A. C. (2014b). Alpha power increases in right parietal cortex reflects focused internal attention. *Neuropsychologia*, 56(1), 393–400. <https://doi.org/10.1016/j.neuropsychologia.2014.02.010>
- Bengtsson, S. L., Csikszentmihályi, M., & Ullén, F. (2007). Cortical regions involved in the generation of musical structures during improvisation in pianists. *Journal of Cognitive Neuroscience*, 19(5), 830–842. <https://doi.org/10.1162/jocn.2007.19.5.830>
- Berger, H. (1929). Ueber das Elektroenkephalogramm des Menschen. *Archiv für Psychiatrie und Nervenkrankheiten*, 87(1), 527–570. <https://doi.org/10.1007/BF01797193>.
- Berkowitz, A. L., & Ansari, D. (2008). Generation of novel motor sequences: The neural correlates of musical improvisation. *NeuroImage*, 41(2), 535–543. <https://doi.org/10.1016/j.neuroimage.2008.02.028>
- Biedenbach, M. A., & Stevens, C. F. (1966). Intracellular postsynaptic potentials and location of synapses in pyramidal cells of the cat olfactory cortex. *Nature*, 212(5060), 361–362. <https://doi.org/10.1038/212361a0>
- Boasen, J., Takeshita, Y., Kuriki, S., & Yokosawa, K. (2018). Spectral-spatial differentiation of brain activity during mental imagery of improvisational music performance using MEG. *Frontiers in Human Neuroscience*, 12. <https://doi.org/10.3389/fnhum.2018.00156>
- Borsook, D., Maleki, N., & Burstein, R. (2014). *Migraine. Neurobiology of Brain Disorders: Biological Basis of Neurological and Psychiatric Disorders*. <https://doi.org/10.1016/B978-0-12-398270-4.00042-2>
- Brenner, D., Williamson, S. J., & Kaufman, L. (1975). Visually evoked magnetic fields of the human brain. *Science*, 190(4213), 480–2.
- Burns, S. J., Harbuz, M. S., Hucklebridge, F., & Bunt, L. (2001). A pilot study into the therapeutic effects of music therapy at a cancer help center. *Alternative Therapies in Health & Medicine*, 7(1), 48–56.
- Buzsáki, G. (2009). *Rhythms of the Brain. Rhythms of the Brain*. Oxford University Press. ISBN: 9780199828234 <https://doi.org/10.1093/acprof:oso/9780195301069.001.0001>
- Caetano, G., Jousmäki, V., & Hari, R. (2007). Actor's and observer's primary motor cortices stabilize similarly after seen or heard motor actions. *Proceedings of the National Academy of Sciences*, 104(21), 9058–62. <https://doi.org/10.1073/pnas.0702453104>
- Camarda, A., Salvia, É., Vidal, J., Weil, B., Poirel, N., Houdé, O., ... Cassotti, M. (2018). Neural basis of functional fixedness during creative idea generation: an EEG study. *Neuropsychologia*. <https://doi.org/10.1016/j.neuropsychologia.2018.03.009>

- Caminiti, R., Ferraina, S., & Mayer, A. B. (1998). Visuomotor transformations: Early cortical mechanisms of reaching. *Current Opinion in Neurobiology*, 8(6), 753–761. [https://doi.org/10.1016/S0959-4388\(98\)80118-9](https://doi.org/10.1016/S0959-4388(98)80118-9)
- Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, 129(3), 564–583. <https://doi.org/10.1093/brain/awl004>
- Chee, M. W., O’Craven, K. M., Bergida, R., Rosen, B. R., & Savoy, R. L. (1999). Auditory and visual word processing studied with fMRI. *Human Brain Mapping*. [https://doi.org/10.1002/\(SICI\)1097-0193\(1999\)7:1<15::AID-HBM2>3.3.CO;2-Y](https://doi.org/10.1002/(SICI)1097-0193(1999)7:1<15::AID-HBM2>3.3.CO;2-Y)
- Cohen, D. (1968). Magnetoencephalography: Evidence of Magnetic Fields Produced by Alpha-Rhythm Currents. *Science*, 161(3843), 784 LP-786. Retrieved from <http://science.sciencemag.org/content/161/3843/784>.
- Cooper, N. R., Croft, R. J., Dominey, S. J. J., Burgess, A. P., & Gruzelier, J. H. (2003). Paradox lost? Exploring the role of alpha oscillations during externally vs. internally directed attention and the implications for idling and inhibition hypotheses. *International Journal of Psychophysiology*, 47(1), 65–74. [https://doi.org/10.1016/S0167-8760\(02\)00107-1](https://doi.org/10.1016/S0167-8760(02)00107-1)
- de Lange, F. P., Jensen, O., Bauer, M., & Toni, I. (2008). Interactions Between Posterior Gamma and Frontal Alpha/Beta Oscillations During Imagined Actions. *Frontiers in Human Neuroscience*, 2, 7. <https://doi.org/10.3389/neuro.09.007.2008>
- de Manzano, Ö., & Ullén, F. (2012). Activation and connectivity patterns of the presupplementary and dorsal premotor areas during free improvisation of melodies and rhythms. *NeuroImage*, 63(1), 272–280. <https://doi.org/10.1016/j.neuroimage.2012.06.024>
- Deiber, M.-P., Sallard, E., Ludwig, C., Ghezzi, C., Barral, J., & Ibañez, V. (2012). EEG alpha activity reflects motor preparation rather than the mode of action selection. *Frontiers in Integrative Neuroscience*, 6(August), 1–11. <https://doi.org/10.3389/fnint.2012.00059>
- Desikan, R. S., Ségonne, F., Fischl, B., Quinn, B. T., Dickerson, B. C., Blacker, D., ... Killiany, R. J. (2006). An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. *NeuroImage*, 31(3), 968–980. <https://doi.org/10.1016/j.neuroimage.2006.01.021>
- Dikaya, L. A., & Skirtach, I. A. (2015). Neurophysiological correlates of musical creativity: The example of improvisation. *Psychology in Russia: State of the Art*, 8(3), 84–97. <https://doi.org/10.11621/pir.2015.0307>
- Donnay, G. F., Rankin, S. K., Lopez-Gonzalez, M., Jiradejvong, P., & Limb, C. J. (2014). Neural substrates of interactive musical improvisation: An fMRI study of “trading fours” in jazz. *PLoS ONE*, 9(2). <https://doi.org/10.1371/journal.pone.0088665>

- Donner, T. H., Siegel, M., Fries, P., & Engel, A. K. (2009). Buildup of Choice-Predictive Activity in Human Motor Cortex during Perceptual Decision Making. *Current Biology*, *19*(18), 1581–1585. <https://doi.org/10.1016/j.cub.2009.07.066>
- Engel, A. K., & Fries, P. (2010). Beta-band oscillations-signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156–165. <https://doi.org/10.1016/j.conb.2010.02.015>
- Engel, A., & Keller, P. E. (2011). The perception of musical spontaneity in improvised and imitated jazz performances. *Frontiers in Psychology*, *2*(MAY). <https://doi.org/10.3389/fpsyg.2011.00083>
- Erkkilä, J., Punkanen, M., Fachner, J., Ala-Ruona, E., Pöntiö, I., Tervaniemi, M., ... Gold, C. (2011). Individual music therapy for depression: Randomised controlled trial. *British Journal of Psychiatry*, *199*(2), 132–139. <https://doi.org/10.1192/bjp.bp.110.085431>
- Fink, A., & Benedek, M. (2014). EEG alpha power and creative ideation. *Neuroscience and Biobehavioral Reviews*, *44*, 111–123. <https://doi.org/10.1016/j.neubiorev.2012.12.002>
- Fink, A., Graif, B., & Neubauer, A. C. (2009). Brain correlates underlying creative thinking: EEG alpha activity in professional vs. novice dancers. *NeuroImage*, *46*(3), 854–862. <https://doi.org/10.1016/j.neuroimage.2009.02.036>
- Fink, A., Rominger, C., Benedek, M., Perchtold, C. M., Papousek, I., Weiss, E. M., ... Memmert, D. (2018). EEG alpha activity during imagining creative moves in soccer decision-making situations. *Neuropsychologia*, *114*(January), 118–124. <https://doi.org/10.1016/j.neuropsychologia.2018.04.025>
- Fonken, Y. M., Rieger, J. W., Tzvi, E., Crone, N. E., Chang, E., Parvizi, J., ... Krämer, U. M. (2016). Frontal and motor cortex contributions to response inhibition: evidence from electrocorticography. *Journal of Neurophysiology*. <https://doi.org/10.1152/jn.00708.2015>
- Forschack, X. N., Nierhaus, X. T., & Mu, M. M. (2017). Alpha-Band Brain Oscillations Shape the Processing of Perceptible as well as Imperceptible Somatosensory Stimuli during Selective Attention, *37*(29), 6983–6994. <https://doi.org/10.1523/JNEUROSCI.2582-16.2017>
- Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). From The Cover: The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences*, *102*(27), 9673–9678. <https://doi.org/10.1073/pnas.0504136102>
- Fugate, T. (1988). Notes toward an ontology of solo improvising. In *The Improvisor, Volume VIII*. Winter 1988–1999. 1705 12th Street, South Birmingham, Alabama.
- Fumuro, T., Matsushashi, M., Miyazaki, T., Inouchi, M., Hitomi, T., Matsumoto, R., ... Ikeda, A. (2015). Alpha-band desynchronization in human parietal area during reach planning. *Clinical Neurophysiology*, *126*(4), 756–762. <https://doi.org/10.1016/j.clinph.2014.07.026>

- Ghitza, O. (2012). On the role of theta-driven syllabic parsing in decoding speech: Intelligibility of speech with a manipulated modulation spectrum. *Frontiers in Psychology*, 3(JUL), 1–12. <https://doi.org/10.3389/fpsyg.2012.00238>
- Grabner, R. H., Neubauer, A. C., & Stern, E. (2006). Superior performance and neural efficiency: The impact of intelligence and expertise. *Brain Research Bulletin*, 69(4), 422–439. <https://doi.org/10.1016/j.brainresbull.2006.02.009>
- Gross, J., Baillet, S., Barnes, G. R., Henson, R. N., Hillebrand, A., Jensen, O., ... Schoffelen, J. M. (2013). Good practice for conducting and reporting MEG research. *NeuroImage*, 65, 349–363. <https://doi.org/10.1016/j.neuroimage.2012.10.001>
- Groussard, M., Rauchs, G., Landeau, B., Viader, F., Desgranges, B., Eustache, F., & Platel, H. (2010). The neural substrates of musical memory revealed by fMRI and two semantic tasks. *NeuroImage*, 53(4), 1301–1309. <https://doi.org/10.1016/j.neuroimage.2010.07.013>
- Gunji, A., Ishii, R., Chau, W., Kakigi, R., & Pantev, C. (2007). Rhythmic brain activities related to singing in humans. *NeuroImage*, 34(1), 426–434. <https://doi.org/10.1016/j.neuroimage.2006.07.018>
- Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: functional imaging and the resting human brain. *Nature Reviews Neuroscience*, 2(10), 685–694. <https://doi.org/http://dx.doi.org/10.1038/nrn1001-685a>
- Haidet, P., Jarecke, J., Yang, C., Teal, C., Street, R., & Stuckey, H. (2017). Using Jazz as a Metaphor to Teach Improvisational Communication Skills. *Healthcare*, 5(3), 41. <https://doi.org/10.3390/healthcare5030041>
- Haier, R. J., Siegel, B. V., Nuechterlein, K. H., Hazlett, E., Wu, J. C., Paek, J., ... Buchsbaum, M. S. (1988). Cortical glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography. *Intelligence*, 12(2), 199–217. [https://doi.org/10.1016/0160-2896\(88\)90016-5](https://doi.org/10.1016/0160-2896(88)90016-5)
- Halpern, A. R., & Zatorre, R. J. (1999). When that tune runs through your head: A PET investigation of auditory imagery for familiar melodies. *Cerebral Cortex*, 9(7), 697–704. <https://doi.org/10.1093/cercor/9.7.697>
- Hämäläinen, M., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics*, 65(2), 413–497. <https://doi.org/10.1103/RevModPhys.65.413>
- Hansen, P., Kringelbach, M., & Salmelin, R. (2010). *MEG: An introduction to methods. MEG: An Introduction to Methods*. <https://doi.org/10.1093/acprof:oso/9780195307238.001.0001>
- Haumann, N. T., Parkkonen, L., Kliuchko, M., Vuust, P., & Brattico, E. (2016). Comparing the Performance of Popular MEG/EEG Artifact Correction Methods in an Evoked-Response Study. *Computational Intelligence and Neuroscience*, 2016, 1–10. <https://doi.org/10.1155/2016/7489108>

- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, 92(1–2), 67–99. <https://doi.org/10.1016/j.cognition.2003.10.011>
- Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences*. [https://doi.org/10.1016/S1364-6613\(00\)01463-7](https://doi.org/10.1016/S1364-6613(00)01463-7)
- Huang, M. X., Mosher, J. C., & Leahy, R. M. (1999). A sensor-weighted overlapping-sphere head model and exhaustive head model comparison for MEG. *Physics in Medicine and Biology*, 44(2), 423–440. <https://doi.org/10.1088/0031-9155/44/2/010>
- Huebl, J., Brietzke, C., Merkl, A., Bajbouj, M., Schneider, G. H., & Kienhn, A. A. (2016). Processing of emotional stimuli is reflected by modulations of beta band activity in the subgenual anterior cingulate cortex in patients with treatment resistant depression. *Social Cognitive and Affective Neuroscience*, 11(8), 1290–1298. <https://doi.org/10.1093/scan/nsw038>
- Hwang, K., Ghuman, A. S., Manoach, D. S., Jones, S. R., & Luna, B. (2014). Cortical Neurodynamics of Inhibitory Control. *Journal of Neuroscience*, 34(29), 9551–9561. <https://doi.org/10.1523/JNEUROSCI.4889-13.2014>
- Hyafil, A., Fontolan, L., Kabdebon, C., Gutkin, B., & Giraud, A. L. (2015). Speech encoding by coupled cortical theta and gamma oscillations. *eLife*, 4(MAY), 1–45. <https://doi.org/10.7554/eLife.06213>
- Jaušovec, N. (1997). Differences in EEG Alpha Activity Between Gifted and Non-Identified Individuals: Insights into Problem Solving. *Gifted Child Quarterly*, 41(1), 26–32. <https://doi.org/10.1177/001698629704100104>
- Jung, R. E. (2013). The structure of creative cognition in the human brain. *Frontiers in Human Neuroscience*, 7(July), 1–13. <https://doi.org/10.3389/fnhum.2013.00330>
- Kandel, E. R., Schwartz, J. H., Jessell, T. M., Siegelbaum, S. A., & Hudspeth, A. J. (2014). *Principles of Neural Science, Fifth Edition*. Neurology (Vol. 3). <https://doi.org/10.1036/0838577016>
- Kawashima, R., Roland, P. E., & O'Sullivan, B. T. (1994). Fields in human motor areas involved in preparation for reaching, actual reaching, and visuomotor learning: a positron emission tomography study. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 14(6), 3462–3474. <https://doi.org/10.1523/JNEUROSCI.14-06-03462.1994>
- Kim, J., Wigram, T., & Gold, C. (2008). The effects of improvisational music therapy on joint attention behaviors in autistic children: a randomized controlled study. *J Autism Dev Disord*, 38(9), 1758–1766. <https://doi.org/10.1007/s10803-008-0566-6>
- Kleinmintz, O. M., Goldstein, P., Maysless, N., Abecasis, D., & Shamay-Tsoory, S. G. (2014). Expertise in musical improvisation and creativity: The mediation of idea evaluation. *PLoS ONE*, 9(7), 1–8. <https://doi.org/10.1371/journal.pone.0101568>

- Koelsch, S. (2005). Investigating Emotion with Music. *Annals of the New York Academy of Sciences*, 1060(1), 412–418. <https://doi.org/10.1196/annals.1360.034>
- Koenigs, M., Barbey, A. K., Postle, B. R., & Grafman, J. (2009). Superior Parietal Cortex Is Critical for the Manipulation of Information in Working Memory. *Journal of Neuroscience*, 29(47), 14980–14986. <https://doi.org/10.1523/JNEUROSCI.3706-09.2009>
- Kounios, J., & Beeman, M. (2014). The Cognitive Neuroscience of Insight. *Annual Review of Psychology*, 65(1), 71–93. <https://doi.org/10.1146/annurev-psych-010213-115154>
- Kounios, J., Fleck, J. I., Green, D. L., Payne, L., Stevenson, J. L., Bowden, E. M., & Jung-Beeman, M. (2008). The origins of insight in resting-state brain activity. *Neuropsychologia*, 46(1), 281–291. <https://doi.org/10.1016/j.neuropsychologia.2007.07.013>
- Kraemer, D. J. M., Macrae, C. N., Green, A. E., & Kelley, W. M. (2005). Musical imagery: Sound of silence activates auditory cortex. *Nature*, 434(7030), 158–158. <https://doi.org/10.1038/434158a>
- Laufs, H., Kleinschmidt, A., Beyerle, A., Eger, E., Salek-Haddadi, A., Preibisch, C., & Krakow, K. (2003). EEG-correlated fMRI of human alpha activity. *NeuroImage*, 19(4), 1463–1476. [https://doi.org/10.1016/S1053-8119\(03\)00286-6](https://doi.org/10.1016/S1053-8119(03)00286-6)
- Lavin, C., Melis, C., Mikulan, E., Gelormini, C., Huepe, D., & Ibañez, A. (2013). The anterior cingulate cortex: an integrative hub for human socially-driven interactions. *Frontiers in Neuroscience*, 7(May), 1–4. <https://doi.org/10.3389/fnins.2013.00064>
- Leech, R., & Sharp, D. J. (2014). The role of the posterior cingulate cortex in cognition and disease. *Brain*, 137(1), 12–32. <https://doi.org/10.1093/brain/awt162>
- Lehtelä, L., Salmelin, R., & Hari, R. (1997). Evidence for reactive magnetic 10-Hz rhythm in the human auditory cortex. *Neuroscience Letters*, 222(2), 111–114. [https://doi.org/10.1016/S0304-3940\(97\)13361-4](https://doi.org/10.1016/S0304-3940(97)13361-4)
- Limb, C. J., & Braun, A. R. (2008). Neural substrates of spontaneous musical performance: An fMRI study of jazz improvisation. *PLoS ONE*, 3(2). <https://doi.org/10.1371/journal.pone.0001679>
- Lopata, J. A., Nowicki, E. A., & Joannisse, M. F. (2017). Creativity as a distinct trainable mental state: An EEG study of musical improvisation. *Neuropsychologia*, 99(March), 246–258. <https://doi.org/10.1016/j.neuropsychologia.2017.03.020>
- Lotze, M., & Halsband, U. (2006). Motor imagery. *Journal of Physiology Paris*, 99(4–6), 386–395. <https://doi.org/10.1016/j.jphysparis.2006.03.012>
- Luo, H., & Poeppel, D. (2012). Cortical oscillations in auditory perception and speech: evidence for two temporal windows in human auditory cortex. *Front Psychol*, 3, 170. <https://doi.org/10.3389/fpsyg.2012.00170>

- Maddock, R. J., Garrett, A. S., & Buonocore, M. H. (2001). Remembering familiar people: The posterior cingulate cortex and autobiographical memory retrieval. *Neuroscience*, *104*(3), 667–676. [https://doi.org/10.1016/S0306-4522\(01\)00108-7](https://doi.org/10.1016/S0306-4522(01)00108-7)
- Martin, S., Mikutta, C., Leonard, M. K., Hungate, D., Koelsch, S., Shamma, S., ... Pasley, B. N. (2017). Neural Encoding of Auditory Features during Music Perception and Imagery. *Cerebral Cortex*, (January 2018), 1–12. <https://doi.org/10.1093/cercor/bhx277>
- Möller, M., & Born, J. (2011). Slow oscillations orchestrating fast oscillations and memory consolidation. *Progress in Brain Research*, *193*, 93–110. <https://doi.org/10.1016/B978-0-444-53839-0.00007-7>
- Möller, M., Marshall, L., Wolf, B., Fehm, H. L., & Born, J. (1999). EEG complexity and performance measures of creative thinking. *Psychophysiology*, *36*(1), 95–104. <https://doi.org/10.1017/S0048577299961619>
- Monson, I. (1996). *Saying Something: Jazz Improvisation and Interaction*. Chicago, IL: University of Chicago Press. (P.73). ISBN: 9780226534787
- Montello, L., & Coons, E. E. (1999). Effects of Active Versus Passive Group Music Therapy on Preadolescents with Emotional, Learning, and Behavioral Disorders. *J Music Ther*, *35*, 49–67. <https://doi.org/10.1093/jmt/35.1.49>
- Müller, V., Sängler, J., & Lindenberger, U. (2013). Intra- and Inter-Brain Synchronization during Musical Improvisation on the Guitar. *PLoS ONE*, *8*(9). <https://doi.org/10.1371/journal.pone.0073852>
- Murakami, S., & Okada, Y. (2006). Contributions of principal neocortical neurons to magnetoencephalography and electroencephalography signals, *3*, 925–936. <https://doi.org/10.1113/jphysiol.2006.105379>
- Nachmanovitch, Stephen (1990). *Free play: Improvisation in life and art*. Los Angeles: Jeremy P. Tarcher, Inc. ISBN 0-87477-578-7.
- Nordoff Robbins Research Department. (2012). *The Nordoff Robbins Evidence Bank 2012 - 2nd Edition*.
- Okawa, H., Suefusa, K., & Tanaka, T. (2017). Neural Entrainment to Auditory Imagery of Rhythms. *Frontiers in Human Neuroscience*, *11*(October), 1–11. <https://doi.org/10.3389/fnhum.2017.00493>
- Pascual-Marqui, R. D., Faber, P., Milz, P., Kochi, K., Kinoshita, T., Nishida, K., ... Ishii, R. (2017). The Cross-Frequency Mediation Mechanism Of Intracortical Information Transactions. *bioRxiv*. 119362. (preprint). <https://doi.org/10.1101/119362>
- Pearson, J., Naselaris, T., Holmes, E. A., & Kosslyn, S. M. (2015). Mental Imagery: Functional Mechanisms and Clinical Applications. *Trends in Cognitive Sciences*, *19*(10), 590–602. <https://doi.org/10.1016/j.tics.2015.08.003>

- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing.” *Brain Research Reviews*, *50*(1), 57–68.
<https://doi.org/10.1016/j.brainresrev.2005.04.005>
- Platel, H., Baron, J. C., Desgranges, B., Bernard, F., & Eustache, F. (2003). Semantic and episodic memory of music are subserved by distinct neural networks. *NeuroImage*, *20*(1), 244–256. [https://doi.org/10.1016/S1053-8119\(03\)00287-8](https://doi.org/10.1016/S1053-8119(03)00287-8)
- Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zuiani, C., ... di Prampero, P. E. (1996). Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *16*(23), 7688–7698. <https://doi.org/8922425>
- Radel, R., Davranche, K., Fournier, M., & Dietrich, A. (2015). The role of (dis)inhibition in creativity: Decreased inhibition improves idea generation. *Cognition*, *134*, 110–120.
<https://doi.org/10.1016/j.cognition.2014.09.001>
- Raven, J., Raven, J. C., & Court, J. (1998). *Manual for Raven’s progressive matrices and vocabulary scales*. Raven manual. <https://doi.org/10.1006/cogp.1999.0735>
- Reite, M., Adams, M., Simon, J., Teale, P., Sheeder, J., Richardson, D., & Grabbe, R. (1994). Auditory M100 component 1: relationship to Heschl’s gyri. *Cognitive Brain Research*, *2*(1), 13–20. [https://doi.org/10.1016/0926-6410\(94\)90016-7](https://doi.org/10.1016/0926-6410(94)90016-7)
- Rickson, D. J., & Watkins, W. G. (2003). Music Therapy to Promote Prosocial Behaviors in Aggressive Adolescent Boys--A Pilot Study. *Journal of Music Therapy*, *40*(4), 283–301.
<https://doi.org/10.1093/jmt/40.4.283>
- Rushworth, M. F., Ellison, A., & Walsh, V. (2001). Complementary localization and lateralization of orienting and motor attention. *Nature Neuroscience*, *4*(6), 656–661.
<https://doi.org/10.1038/88492>
- Sanyal, S., Banerjee, A., Mukherjee, S., Guhathakurata, T., & Dipak Ghosh, R. S. (2016). Musical Improvisation and Brain Correlates: An EEG Based Neurocognitive Study Using Hindustani Music. *Journal of Biomusical Engineering*, *4*(2).
<https://doi.org/10.4172/2090-2719.1000119>
- Sarnthein, J., Morel, A., von Stein, A., & Jeanmonod, D. (2003). Thalamic theta field potentials and EEG: High thalamocortical coherence in patients with neurogenic pain, epilepsy and movement disorders. *Thalamus and Related Systems*, *2*(3), 231–238.
[https://doi.org/10.1016/S1472-9288\(03\)00021-9](https://doi.org/10.1016/S1472-9288(03)00021-9)
- Schack, B., Vath, N., Petsche, H., Geissler, H. G., & Möller, E. (2002). Phase-coupling of theta-gamma EEG rhythms during short-term memory processing. *International Journal of Psychophysiology*, *44*(2), 143–163. [https://doi.org/10.1016/S0167-8760\(01\)00199-4](https://doi.org/10.1016/S0167-8760(01)00199-4)
- Schalles, M. D., & Pineda, J. A. (2015). Musical Sequence Learning and EEG Correlates of Audiomotor Processing. *Behavioural Neurology*, *2015*.
<https://doi.org/10.1155/2015/638202>

- Schwab, D., Benedek, M., Papousek, I., Weiss, E. M., & Fink, A. (2014). The time-course of EEG alpha power changes in creative ideation. *Frontiers in Human Neuroscience*, 8(May), 1–8. <https://doi.org/10.3389/fnhum.2014.00310>
- Shimonaka, Y., & Nakazato, K. (2007). Creativity and factors affecting creative ability in adulthood and old age. *JAPANESE JOURNAL OF EDUCATIONAL PSYCHOLOGY*, 55(2), 231–243. https://doi.org/10.5926/jjep1953.55.2_231
- Simon, S. R. S., Meunier, M., Pieltre, L., Berardi, A. M., Segebarth, C. M., & Boussaoud, D. (2002). Spatial attention and memory versus motor preparation: premotor cortex involvement as revealed by fMRI. *Journal of Neurophysiology*, 88(4), 2047–2057. [https://doi.org/Doi 10.1152/Jn.00965.2001](https://doi.org/Doi%2010.1152/Jn.00965.2001)
- Smith, R., Lane, R. D., Alkozei, A., Bao, J., Smith, C., Sanova, A., ... Killgore, W. D. S. (2018). The role of medial prefrontal cortex in the working memory maintenance of one's own emotional responses. *Scientific Reports*, 8(1), 1–15. <https://doi.org/10.1038/s41598-018-21896-8>
- Society_For_Creative_Minds. (1969). Manual of S-A Creativity Test. *Tokyo: Tokyo Shinri Corporation.*
- Sparrow, W. A. (1983). The efficiency of skilled performance. *Journal of Motor Behavior*, 15(3), 237–261. <https://doi.org/10.1080/00222895.1983.10735299>
- Spierer, L., Chavan, C. F., & Manuel, A. L. (2013). Training-induced behavioral and brain plasticity in inhibitory control. *Frontiers in Human Neuroscience*, 7(August), 1–9. <https://doi.org/10.3389/fnhum.2013.00427>
- Sporns, O., Honey, C. J., & Kötter, R. (2007). Identification and classification of hubs in brain networks. *PLoS ONE*, 2(10). <https://doi.org/10.1371/journal.pone.0001049>
- Stipacek, A., Grabner, R. H., Neuper, C., Fink, A., & Neubauer, A. C. (2003). Sensitivity of human EEG alpha band desynchronization to different working memory components and increasing levels of memory load. *Neuroscience Letters*, 353(3), 193–196. <https://doi.org/10.1016/j.neulet.2003.09.044>
- Stenström, H., & Högskolan för scen och musik vid Göteborgs universitet. (2009). *Free ensemble improvisation.*
- Swann, N., Tandon, N., Canolty, R., Ellmore, T. M., Mcevoy, L. K., Dreyer, S., ... Aron, A. R. (2010). Stopping Initiated Responses, 29(40), 12675–12685. <https://doi.org/10.1523/JNEUROSCI.3359-09.2009>.Intracranial
- Tomaino, C. M. (2013). Creativity and improvisation as therapeutic tools within music therapy. *Annals of the New York Academy of Sciences*, 1303(1), 84–86. <https://doi.org/10.1111/nyas.12224>
- Torrance, E. P. (1966). Torrance Tests of Creative Thinking. *Bensenville, IL: Scholastic Testing Service.*

- Wan, X., Crüts, B., & Jensen, H. J. (2014). The causal inference of cortical neural networks during music improvisations. *PLoS ONE*, *9*(12), 1–25. <https://doi.org/10.1371/journal.pone.0112776>
- Wolpert, D. M., Goodbody, S. J., & Husain, M. (1998). Maintaining internal representations the role of the human superior parietal lobe. *Nature Neuroscience*, *1*(6), 529–533. <https://doi.org/10.1038/2245>
- Yousry, T. A., Schmid, U. D., Alkadhi, H., Schmidt, D., Peraud, A., Buettner, A., & Winkler, P. (1997). Localization of the motor hand area to a knob on the precentral gyrus. A new landmark. *Brain*, *120*(1), 141–157. <https://doi.org/10.1093/brain/120.1.141>
- Zanto, T. P., Chadick, J. Z., & Gazzaley, A. (2014). Anticipatory alpha phase influences visual working memory performance. *NeuroImage*, *85*, 794–802. <https://doi.org/10.1016/j.neuroimage.2013.07.048>
- Zhang, Y., Chen, G., Wen, H., Lu, K.-H., & Liu, Z. (2017). Musical Imagery Involves the Wernicke’s Area in Bilateral and Anti-Correlated Network Interactions in Musicians. *bioRxiv*, (November), 1–13. <https://doi.org/10.1038/s41598-017-17178-4>
- Zvyagintsev, M., Clemens, B., Chechko, N., Mathiak, K. A., Sack, A. T., & Mathiak, K. (2013). Brain networks underlying mental imagery of auditory and visual information. *Eur J Neurosci*, *37*(9), 1421–1434. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=23383863

11 Supplemental Information

Supplemental Table 1. Study 2A and 2B subject characteristics and music experience

Subject #	Sex	Age	Study	Instrument	Years played	Education style				Song memorization method				Genre listened
						Formal	Informal	Written	Ear	Both	Practice freq.	Freq. of improv	Music listening freq.	
1	F	39	2A/2B	Voice	22	x	x			x	6	3	6	Rock, popular, Jazz
2	M	26	2A/2B	Guitar	13		x		x		6	5	5	Other
3	M	21	2A/2B	Drums	7	x				x	6	5	6	Jazz
4	M	44	2A/2B	Guitar	30	x				x	5	5	5	Jazz
5	M	31	2A/2B	Cello	13	x				x	5	5	6	Rock, popular
6	M	36	2A/2B	Guitar	20	x				x	6	6	6	Jazz
7	M	42	2A/2B	Guitar	25		x			x	5	5	6	Rock, popular
8	M	51	2A/2B	Guitar	38		x		x		6	3	6	Rock, popular
9	M	38	2A/2B	Drums	32	x				x	6	5	6	Jazz
10	M	34	2A/2B	Guitar	20	x	x			x	5	4	6	Rock, popular
11	M	24	2A/2B	Saxophone	12	x				x	6	6	6	Jazz
12	F	31	2A/2B	Percussion	6	x			x		5	4	6	Rock, popular
13	F	49	2A/2B	Piano	20		x			x	6	6	6	Everything
14	F	34	2B	Voice	nd	x			x		5	2	5	Rock, popular

nd: no data

MEG drum Arduino code

```
//Xylophone
//Adapted for an ArduinoMega
//from Jenna deBoisblanc and Spiekenzie Labs initial code
//*****
//*****

// User settable variables
//*****
//*****

int pinRead;
char pinAssignments[16]={'A2'};
byte PadNote[16] = {38}; // MIDI notes from 0 to 127 (Mid C = 60)
int PadCutOff[16] =
{500}; // Minimum Analog value to cause a drum hit
int MaxPlayTime[16] = {20}; // Cycles before a 2nd hit is allowed
#define midichannel 1; // MIDI channel from 0 to 15 (+1 in "real world")
boolean VelocityFlag = true; // Velocity ON (true) or OFF (false)
//*****
//*****

// Internal Use Variables
//*****
//*****

boolean activePad[16] = {0,0}; // Array of flags of pad currently playing
int PinPlayTime[16] = {0,0}; // Counter since pad started to play
byte status1;
int pin = 0;
int hitavg = 0;
//*****
//*****

// Setup
//*****
//*****

void setup()
```

```

{
  Serial.begin(57600);                // SET HAIRLESS TO THE SAME BAUD RATE
  IN THE SETTINGS
}

//*****
//*****

// Main Program
//*****
//*****

void loop()
{
  for(int pin=0; pin < 16; pin++)      //
  {
    //int pin = 3;
    // for (pinRead=0; pinRead < 16, pin++){
    hitavg = analogRead(pinAssignments[pin]);
    //Serial.println(hitavg);
    // read the input pin
    if((hitavg > PadCutOff[pin]))
    {
      if((activePad[pin] == false))
      {
        if(VelocityFlag == true)
        {
          // hitavg = 127 / ((1023 - PadCutOff[pin]) / (hitavg - PadCutOff[pin])); // With
full range (Too sensitive ?)
          hitavg = (hitavg / 8) - 1 ;           // Upper range
        }
        else
        {
          hitavg = 127;
        }
        MIDI_TX(144,PadNote[pin],hitavg); //note on

```

```

    PinPlayTime[pin] = 0;
    activePad[pin] = true;
}
else
{
    PinPlayTime[pin] = PinPlayTime[pin] + 1;
}
}
else if((activePad[pin] == true))
{
    PinPlayTime[pin] = PinPlayTime[pin] + 1;
    if(PinPlayTime[pin] > MaxPlayTime[pin])
    {
        activePad[pin] = false;
        MIDI_TX(144,PadNote[pin],0);
    }
}
}
}

//*****
//*****

// Transmit MIDI Message

//*****
//*****

void MIDI_TX(byte MESSAGE, byte PITCH, byte VELOCITY)
{
    status1 = MESSAGE + midichannel;
    Serial.write(status1);
    Serial.write(PITCH);
    Serial.write(VELOCITY);
}

```

MEG Keyboard Arduino Code

```
//Xylophone
//Adapted for an ArduinoMega
//from Jenna deBoisblanc and Spiekenzie Labs initial code

//*****
//*****

// User settable variables

//*****
//*****

int pinRead;
char pinAssignments[5] = {
  'A0','A1','A2','A3','A4'};
byte PadNote[5] = {
  60,62,64,67,69};    // MIDI notes from 0 to 127 (Mid C = 60)
int PadCutOff[5] =
{
  290,500,500,215,300};    // Minimum Analog value to cause a drum hit
int MaxPlayTime[5] = {
  90,90,90,90,90};    // Cycles before a 2nd hit is allowed
#define midichannel 1;    // MIDI channel from 0 to 15 (+1 in "real world")
boolean VelocityFlag = true;    // Velocity ON (true) or OFF (false)

//*****
//*****

// Internal Use Variables

//*****
//*****

boolean activePad[5] = {
  0,0,0,0,0};    // Array of flags of pad currently playing
int PinPlayTime[5] = {
  0,0,0,0,0};    // Counter since pad started to play
byte status1;
int pin = 0;
int hitavg = 0;

//*****
//*****
```

```

// Setup
//*****
//*****

void setup()
{
  Serial.begin(57600);           // SET HAIRLESS TO THE SAME BAUD RATE IN
  THE SETTINGS
}

//*****
//*****

// Main Program
//*****
//*****

void loop()
{
  for(int pin=0; pin < 5; pin++) //
  {
    //int pin = 3;
    // for (pinRead=0; pinRead < 5, pin++){
    hitavg = analogRead(pinAssignments[pin]);
    //Serial.println(hitavg);
    // read the input pin
    if((hitavg > PadCutOff[pin]))
    {
      if((activePad[pin] == false))
      {
        if(VelocityFlag == true)
        {
          // hitavg = 127 / ((1023 - PadCutOff[pin]) / (hitavg - PadCutOff[pin])); // With full
          range (Too sensitive ?)
          hitavg = (hitavg / 8) - 1 ;           // Upper range
        }
      }
    }
    else
    {
      hitavg = 127;
    }
  }
}

```

```

MIDI_TX(144,PadNote[pin],hitavg); //note on
PinPlayTime[pin] = 0;
activePad[pin] = true;
}
else
{
PinPlayTime[pin] = PinPlayTime[pin] + 1;
}
}
else if((activePad[pin] == true))
{
PinPlayTime[pin] = PinPlayTime[pin] + 1;
if(PinPlayTime[pin] > MaxPlayTime[pin])
{
activePad[pin] = false;
MIDI_TX(144,PadNote[pin],0);
}
}
}
}

//*****
*****

// Transmit MIDI Message

//*****
*****

void MIDI_TX(byte MESSAGE, byte PITCH, byte VELOCITY)
{
status1 = MESSAGE + midichannel;
Serial.write(status1);
Serial.write(PITCH);
Serial.write(VELOCITY);
}

```