

**THE COMMUNICATIVE PROCESSES OF MUSICIANS ENGAGED IN
SYNCHRONOUS PLAY**

Sarah Faber
Master's Thesis
Music, Mind and Technology
Department of Music
9 June 2014
University of Jyväskylä

JYVÄSKYLÄN YLIOPISTO

Tiedekunta – Faculty Humanities	Laitos – Department Music Department
Tekijä – Author Sarah Faber	
Työn nimi – Title The Communicative Processes of Musicians Engaged in Synchronous Play	
Oppiaine – Subject Music, Mind & Technology	Työn laji – Level Master’s Thesis
Aika – Month and year May, 2014	Sivumäärä – Number of pages 30
Tiivistelmä – Abstract Music is a sophisticated cognitive behaviour that employs extensive bilateral neural networks. Recent research investigating the brain engaged in active music-making, both pre-composed and improvised, has localized this network, and made comparisons to similarities and differences as they relate to the production of language. This study investigated the electroencephalographic data of musicians engaged in dyadic instrumental improvisation. Ten musicians (3 pianists, 5 guitarists, and 2 ukulelists) engaged in dyadic improvisations while data was recorded from one of the pair. Playing conditions were established by the participants, and musical features were extracted from the audio data following the experiment. EEG data showed extensive bilateral activity across the cortex of all participants. Common musical features were analyzed in the EEG data, and evidence of an overall music improvisation process was found with minor differences between instrument groups and conditions.	
Asiasanat – Keywords Music, Improvisation, EEG	
Säilytyspaikka – Depository	
Muita tietoja – Additional information	

ACKNOWLEDGEMENTS

I would like to acknowledge the support of Marc Thompson, Tommi Makkonen, Petri Toiviainen, and Jörg Fachner without whom this project would not have made it this far. Thanks also to Anna Fiveash and Emily Carlson for their input and expertise, and my clients and co-workers at Shannex for opening the door. Finally, 30 pages of thanks go out to Adam, who should get a master's in music psychology, too; Mom, Dad, Heather, Julia, Nanny, Grandad, Uncle Alec, Carol, Rick, and Scott; who kept being family from this far away and who all learned as much about the neuroscience of music as I did – whether they wanted to or not.

CONTENTS

1	Introduction.....	1
2	Literature review	3
2.1	Music and Language in Evolution	3
2.2	Musical Brain Areas vs. Language Brain Areas	3
2.3	Music-related neuro-imaging studies	4
2.4	Music and EEG studies	5
2.5	Improvisation Studies	6
2.6	Model of Brain Activity during Musical Improvisation.....	7
3	Research Methods	9
3.1	Participants.....	9
3.2	Design.....	9
3.3	Procedure	10
4	Results	11
4.1	Improvisation Analysis	11
4.2	EEG Pre-Processing.....	11
4.3	T-tests	12
4.4	ANOVA analysis.....	14
4.4.1	Between-instrument within-condition region ANOVA	14
4.4.2	Between-instrument between-condition ANOVA.....	15
4.5	Correlation Analysis	15
4.5.1	Within-instrument between-condition correlations.....	15
4.5.2	Between-instrument between-condition correlations.....	18
4.5.3	Averaged correlations.....	18
4.5.4	Individual electrode correlations	19
5	Discussion.....	21
6	Conclusion	25
7	References.....	26

TABLE OF FIGURES

1	Proposed model of musical improvisation and language.....	8
2	Music areas transposed mapped using Brodmann Areas.....	8
3	Electrode correlation relationships	20

1 INTRODUCTION

Music is a puzzling universality. It is present in every known society and is used as a tool of communication and expression both with others, and within ourselves (North, Hargreaves & Hargreaves, 2004); yet its purpose and origins in human development remain a mystery. Current theories paint music as a communicative medium that may pre-date language in human evolutionary history (see Cross & Woodruff, 2009; Mithen, 2006) - a musical innateness that can be witnessed in interactions between mother and infant, between children, in musical ensembles, and in therapeutic settings.

This thesis examines the neural processes of musicians engaged in synchronous improvisation using EEG in the hope of constructing a model of dyadic improvisation. This model will allow for further research into spontaneously created music, comparisons of music to speech, and study of the neural processes of individuals with cognitive impairments engaging in musical improvisation.

The research questions are as follows:

- What neural processes occur when two musicians are engaged in synchronous play as captured via EEG?
- Which processes are similar between instrument groups and playing conditions?
- Which processes are unique?
- Can these processes be considered communicative?
- Is there evidence for an observable improvisation process in the brain?
- How does this process differ or relate to linguistic communication?

Current music research has focused on music's proposed origins (see Levitin, 2006; Mithen, 2006; Cross, 2009) and cites, among other things, music's universality as what defines its necessity in human existence (Levitin, 2006). Music is also gaining popularity as a tool of therapy, yet the existing research on shared music-making is limited to pre-composed music (see Lindenberger, Li, Gruber, & Mueller, 2009; Sanger, Muller, & Lindenberger, 2012). Playing pre-composed music requires extensive training, but the act of improvisation, like spontaneous conversation, requires an ongoing system of high-level cognitive processes (Limb & Braun,

2008; Friederici, 2002; Brown, Martinez & Parsons, 2006) that pre-dates the technology of written notation.

The broad academic rationale for this study is to add to the current literature on music as a uniquely evolved cognitive process. Citing both the overlap and divergence with linguistic development, through its cultural universality and communicative ambiguity, it is argued that music has evolved to fulfill a specific aspect of human behaviour unique from language (Mithen, 2006), and should be studied as a unique cognitive process (Besson & Schön, 2001).

Practically, the results may offer avenues into researching musically communicative behaviours in individuals with impaired communicative abilities (individuals with autism, general global delay, Alzheimer's disease, etc). This may provide additional information on treating individuals with these conditions, and benefit music therapists and allied health care workers through further understanding of intervention strategies.

2 LITERATURE REVIEW

2.1 Music and Language in Evolution

It has been proposed that humans' capacity for music, though pleasurable, is an accident of evolution – a patchwork behaviour formed by the coming together of other higher processes, such as language (the most publicised being Steven Pinker's remarks, see Levitin, 2006). This is an unpopular sentiment among music researchers (see Levitin, 2006; Mithen, 2006; Cross, 2009), for whom music is a unique process related to, but not dependent on, language. Mithen (2006) decisively challenges this idea by proposing music as a pre-cursor to language. He argues that language emerged as a more sophisticated form of communication from music, which itself developed in proto-humans as method of socio-emotional communication. He postulates that emotional expression is more central to music than to language, and fulfills a unique role as a tool of social bonding and communication – thus explaining its continued existence through tens of thousands of years of human evolution. Cross and Woodruff (2009) offer support for this idea, claiming that music can be used to manage social relationships, even during periods of social turmoil, using “floating intentionality”; the ability to present a stimulus whose interpretation of meaning will vary among listeners (Cross, 2001). Cross (2007) continues to distinguish music from language by noting that music may allow for simultaneous synchronous engagement – an impossibility in spoken language.

2.2 Musical Brain Areas vs. Language Brain Areas

Music and language can be experienced actively and passively, and require a wide network of neural activity in both cases. In music listening, activity patterns appear in many brain areas relating not only to the physical processing of auditory stimuli, but the semantic processing and emotional perception of higher-level musical components (Levitin, 2006). This is echoed in studies of linguistic sentence processing (see Friederici, 2002). It has been shown that if music is perceived as pleasurable, it engages the mesolimbic system and stimulates dopamine activity (Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011), whereas emotionally-charged speech can activate the amygdala within the limbic system (Wildgruber et al., 2006). As a

communicative tool, improvised music is heavily implicated (Schögler, 1998), as it requires a cognitive system of continuous self-monitoring, memory, and context to be used effectively (Limb & Braun, 2008). Spontaneous speech production likewise relies on a complex cognitive network of memory and on-line processing (Friederici, 2002; Brown, Martinez & Parsons, 2006). Communication, however, contains more than semantics. There are emotional cues in tone of voice, gesture, and inflection (Pell, 2006), and in this domain both music and language are effective (Steinbeis & Koelsch, 2008). They are linked through linguistic prosody (Pell, 2006) and musical dynamics (Van der Zwaag, Westerlink, & Van den Broek, 2011). This level of shared yet distinct cortical involvement indicates that music is a highly sophisticated and carefully organized behaviour related to, yet unique from, language (Levitin, 2006).

2.3 Music-related neuro-imaging studies

Besson and Schön (2001) offer rationale for studying music and language together from a general and shared cognitive-processing perspective. Rather than mutually exclusive cerebral centres responsible for each process, they encourage investigating the common processes that link them together, and much research has been completed on the semantic and syntactic processing of music and language (see Koelsch et. al., 2002, Koelsch et al., 2005). Koelsch and colleagues (2002) found evidence for a cortical network for the processing of music while studying the brain activity of non-musicians listening to harmonically appropriate and deviant musical phrases using fMRI. They found activity in Broca's and Wernicke's areas, which led them to conclude that the overlapping processes offer support for a syntactic and semantic division of music, and that musical elements of speech play a role in language acquisition. They also concluded that, based on the responses in the brains of non-musicians of harmonically deviant phrases (eg. an unexpected cadential resolution), music employs an innate or implicit knowledge in the human brain.

Sammler and others (2013) continue by comparing syntactically deviant musical and linguistic phrases while recording brain activity through intracranial EEG, finding support for an early error-detection system in the temporal lobe for both language and music, though with slight differences in timing and localization. Brown et al. (2004) expanded the comparison of language and music by studying individuals actively producing music. They studied the PET patterns of

student musicians' brains while replicating tones and melodies, and harmonizing to simple melodies. The results showed much bi-lateral activity, notably in Broca's area, as well as the planum polare; areas involved with the production of language and self-representation in humans respectively. Activity in the planum polare was exclusive to the repetition and harmonization of melodic stimuli, suggesting that they are more complex and highly developed behaviours than simple tonal repetition. Brown et al. continued in 2006 by studying the PET activity of participants during the spontaneous generation of completions of novel linguistic and musical phrases. The authors found an overlap of brain activity between the two processes, with slight lateralization between the conditions (left for language, right for music), and encouraged future research on the neural organization of spontaneous music and language production in the brain.

2.4 Music and EEG studies

Methodology-wise, capturing linguistic and musical phenomena using EEG has been investigated thoroughly (see Babiloni et al., 2011; Lindenberger, Li, Gruber, & Mueller, 2009; Sanger, Muller, & Lindenberger, 2012). For language, Van Berkum (2012) encouraged the use of EEG to study linguistic discourse, citing its high temporal resolution as essential in the capture of the brain's rapid electrical responses to stimuli. He proposes that speed of response is one of the more salient features of linguistic cognitive processing, and PET or fMRI studies, though highly spatially resolved, are rendered less accurate by the time it takes blood to reach the active brain areas following neuron firing. Babiloni et al (2011) captured simultaneous EEG data from a quartet of saxophonists playing a short ensemble piece. They did not analyze the data collected; rather they evaluated their method's viability and proclaimed the procedure possible for future studies of ensemble musicians. Lindenberger, Li, Gruber and Mueller (2009) collected EEG data from dyads of guitarists playing the same short melody in unison following a preparatory tempo setting using metronome. Results showed synchrony in the oscillatory waves between guitarists, the highest occurring in the fronto-central regions of the brain between 0-10Hz. Temporal and parietal regions also showed synchronization, but to a less pronounced degree. The authors concluded that oscillatory couplings were present both prior to and during the task, but were quick to state that the study did not provide a clear answer to whether these patterns were evidence of internal neural processes, or an internal response to external cues provided by the

other pair member. Sanger, Muller, and Lindenberger (2012) continued in researching neural synchronization between pairs of guitarists, but expanded the study to include melodically independent duets. Their findings were consistent with Lindenberger et al. (2009), but noticed increasing synchronization between the brains during more challenging musical phrases (requiring increased coordination between the guitarists). These findings expanded the scope of study beyond synchronized playing of identical stimuli, and provide a starting point for the study and analysis of more complex musical behaviours.

2.5 Improvisation Studies

Musical improvisation is one of such complex musical behaviours, Limb and Braun (2008) citing it as *the* quintessential creative musical behaviour. In a 2008 study, they captured fMRI data from jazz pianists reading music and improvising novel melodies based on pre-existing chord patterns. They found activation in lateral and prefrontal regions of the brain, as well as deactivations in lateral portions of the prefrontal cortex with focal activation of the medial area of the prefrontal cortex in the improvisation condition. They concluded that lateral prefrontal regions may provide a cognitive schema for goal directed actions. Berkowitz and Ansari (2008) continued by studying the fMRI readings of pianists improvising with conditions alternately defining and allowing free play of melody and rhythm. They found activity in the premotor cortex, cerebellum, frontal and temporal gyri, and the cingulate cortex in melodically and rhythmically free conditions, supporting similar findings by Bengtsson and others (2007).

Two recent studies have examined dyadic improvisation; Donnay and others (2014), and Muller and others (2013). Donnay et al. (2014) completed an fMRI study on jazz pianists “trading fours” compared with memorized play conditions. They found increased activity in Broca’s and Wernecke’s areas during the dyadic improvisation, and increased activity in the right hemisphere posterior superior temporal gyrus, across the supplementary motor area, and in the dorsolateral prefrontal cortex. There was strong deactivation in the angular gyrus and the dorsal prefrontal cortex. Positive correlations were found bilaterally in the inferior frontal gyrus, with negative correlations were present between areas in the inferior frontal gyrus, superior temporal gyrus, and angular gyrus. Muller et al. (2013) studied free-form improvisations between pairs of guitarists using EEG. They found strong inter-brain connections over the entire cortex, with

stronger connections present in guitarists who were actively playing (as opposed to listening, which was one of three conditions: individual improvisation, listening, and dyadic improvisation). They also found significant differences between pre-determined frequency bands with higher frequencies (beta) observed most in between-brain networks, and lower frequencies (delta and theta) observed in within-brain networks.

2.6 Model of Brain Activity during Musical Improvisation

These studies offer clear support for musical improvisation as a highly specialized and advanced cognitive process however, due to the constraints of capturing such spatially resolved data as in the above mentioned fMRI studies, the complexity of the musical behaviour is compromised by eliminating the musicians' ability to play an unmodified, harmonically complex acoustic instrument with normal posture and range of motion. Furthermore, while individuals can engage in music in solitude, it, like language, is an overwhelmingly social behaviour (Mithen, 2006) that is still a new area of research. Based on these studies, the work of Friederici (2002), and the work of Brown et al. (2006), it is now possible to introduce an initial model of the neural processes involved in the brains of musicians engaged in synchronous play, and how they may mirror and contrast linguistic communication (Figures 1 and 2)¹. For tables detailing the function and associated behaviour of each region please see Appendix 1.

¹ The following figures are the author's original designs based on a combination of the previously cited studies of Friederici (2002) and Brown et al. (2006).

Figure 1: Proposed model of musical improvisation and language

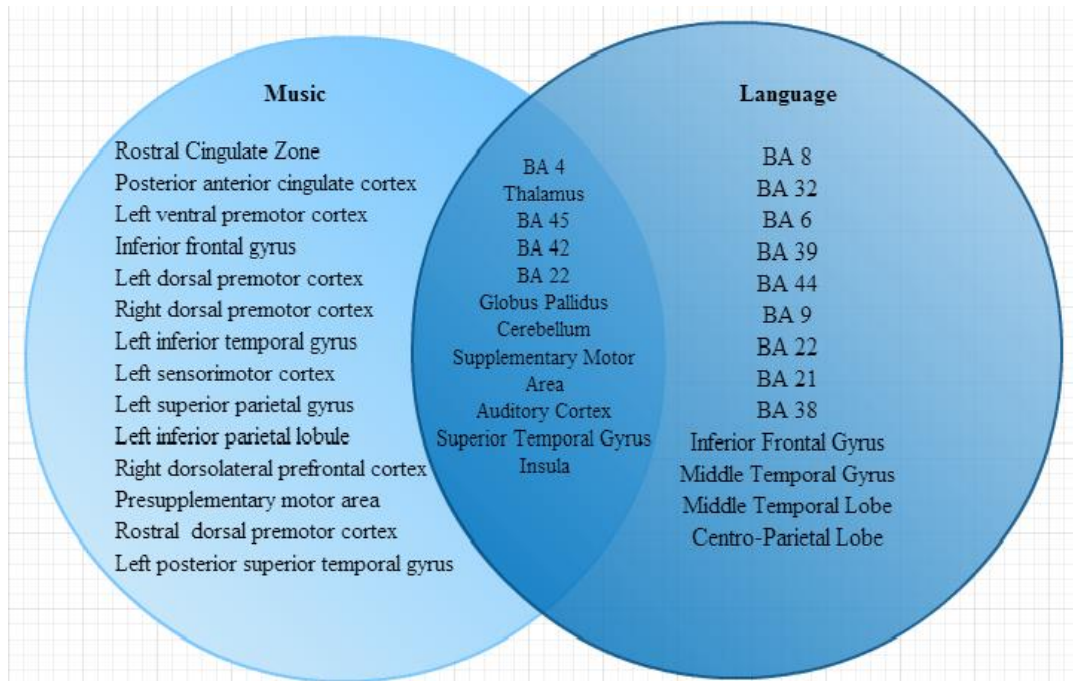
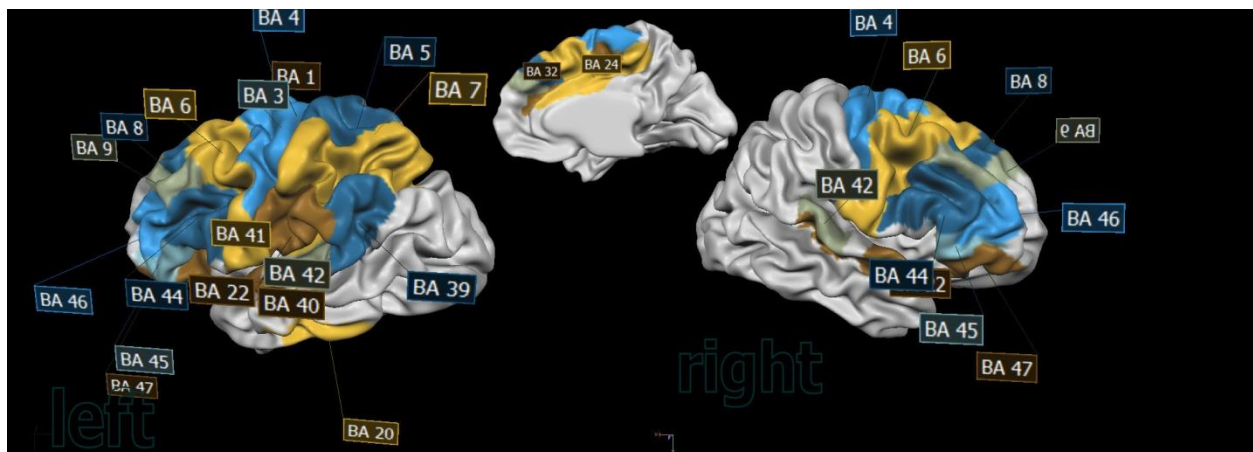


Figure 2: Music areas transposed mapped using Brodmann Areas (cortical structures only)



3 RESEARCH METHODS

3.1 Participants

Participants were 10 healthy, right-handed adults (4 males, 6 females) between the ages of 23 and 38. Five were guitarists, three were pianists, and two were ukulelists. These instruments were selected to allow maximum musical range of movement during the experiment while minimizing movement-related artefacts. All had formal musical training, either in school programs or private lessons, and all had previous experience improvising, whether formally or informally. Three participants were music therapists and had received extensive instruction in improvising in groups, and a further two were music therapy students who had clinical improvisation experience from classes and practicum placements. Participants were selected based on their skill level with their particular instrument, had the option of selecting their partner, and were aware of the experiment parameters prior to data collection. Participants were recruited through social media and signed a consent and confidentiality agreement in regards to their audio, video, and brain data. Participation was voluntary and could be withdrawn at any time without penalty.

3.2 Design

EEG data was collected using a 32-channel BioSemi ActiveTwo system (www.biosemi.com). Marker electrodes were placed on the upper and lower left eye, both earlobes, and the right and left mastoid muscles, with the average of both mastoid electrodes used as the reference. Marker electrodes were not placed on the wrists due to the amount of hand and wrist movement captured during pilot testing. Participants' EEG data was collected individually, and each pair completed two improvisations to accommodate each partner's EEG recording. Audio and video recordings of participants' improvisations were collected, and participants completed a background questionnaire detailing their level of musical training, previous experience improvising, and demographic information.

3.3 Procedure

Participants were welcomed to the lab and given a brief introduction to the EEG apparatus. Participants sat facing one another, the participant connected to the EEG facing the video camera. Participants completed a warm-up task to ensure the EEG apparatus was not restrictive and to demonstrate various artefacts (blinks, muscular tension, head movements, etc.). When the electrode connectivity had been verified and participants were comfortable, the researcher began the recording and invited the participants to start the improvisation. They were invited to set conditions prior to playing (key, mode, tempo, etc.), and there was no time limit on the improvisation. The recording ended when the participants chose to end the improvisation.

4 RESULTS

Audio and video data was used to analyze the improvisations and to synchronize the analysis to the EEG data. Specific musical features were extracted from the improvisation analysis, and isolated from the EEG data. EEG data was pre-processed in MATLAB using the EEGLab plugin (Delorme & Makeig, 2004), and was then exported as a numerical matrix to SPSS for statistical analysis. Correlation analyses were completed within and between individuals, and were then averaged into separate brain regions and instrument groups to facilitate between group comparisons.

4.1 Improvisation Analysis

Improvisations were analyzed based on a framework adapted from Pelz-Sherman (1998). The adapted framework included six musical feature categories:

- Solo: primary participant is the soloist, secondary participant is the accompanist
- Accompaniment: primary participant is the accompanist, secondary participant is the soloist
- Imitation: participants are imitating one another's melodic features
- Call and Response/Melody Trading: participants are engaging in turn-taking using novel melodic features
- Polyphony: participants are using novel melodic features simultaneously
- Not Together: participants are not together musically

Each improvisation was analyzed aurally using this framework, and conditions were isolated in the EEG data. Analysis focused on the musical conditions with at least 30% prevalence across improvisations, and included: solo (80%), accompaniment (70%), polyphony (80%), and not together (50%).

4.2 EEG Pre-Processing

EEG data was exported to MATLAB and re-referenced to the average of left and right mastoid electrodes. Data was resampled to 1000 Hz and filtered between 0.5 Hz and 60 Hz. Channels

with excessive noise not attenuated by the filtering process were eliminated, and an independent component analysis was run to allow elimination of consistent non-cerebral artefacts (such as eye blinks) while preserving the time series of the data. The data was then divided into musical feature epochs based on the improvisation analysis, and artefact-free epochs were selected for further analysis. Ten-second epochs were selected for the solo, accompaniment, and polyphony conditions; and five-second epochs were selected for the not together condition due to the consistently shorter length of not together components. Sixteen electrodes (F3, F7, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, Oz) were selected based on previous EEG studies of dyadic music making (Lindenberger et al., 2009; Sanger et al., 2012), and were exported to SPSS for statistical analysis. Based on preliminary correlation analyses of individual data, electrodes were grouped into spatially related regions to compensate for missing electrodes. The regions include: Frontal Left (F3 and F7), Frontal Right (F4 and F8), Central-Temporal Left (T7 and C3), Central-Temporal Right (C4 and T8), Parietal-Occipital Left (P7 and P3), and Parietal-Occipital Right (P4 and P8). Central electrodes (Fz, Cz, Pz, and Oz) remained ungrouped to avoid uneven weighting of the lateralized regions. Data was averaged from milliseconds to centiseconds for the statistical analysis, and all units are represented in microvolts per centisecond ($\mu\text{V}/\text{cs}$).

4.3 T-tests

Paired sample t-tests were carried out between left and right grouped electrodes for each condition within instrument groups, and in averaged instrument groups. The significant differences between left, right, and central electrodes across all conditions are detailed in Table 1.

Table 1: Paired-sample t-test results between left and right regions

Condition	Instrument	Regions	N^2	M^3	SD	t	p
Solo	Guitar	Front Left	3000	-0.32	23.34	-3.22	.001
		Fz	3000	0.62	25.41		
		Front Left	3000	-0.32	23.34	-4.48	.0001
		Front Right	3000	0.82	22.51		
		Cz	2000	0.52	22.54	4.05	.0001
		CT Right	3000	0.09	21.33		

² All N values are represented in centiseconds (cs).

³ All M values are represented in microvolts per centisecond ($\mu\text{V}/\text{cs}$).

		CT Left	3000	0.80	17.08	2.22	.027
		CT Right	3000	0.09	21.33		
		Oz	1000	-0.22	14.19	-2.24	.025
		PO Right	1000	0.38	15.39		
	Ukulele	Pz	2000	0.15	13.79	2.08	.038
		PO Right	2000	-0.20	12.04		
Accompaniment	Piano	Fz	1000	0.27	32.47	-2.49	.013
		Front Left	1000	1.54	32.37		
		Fz	1000	0.27	32.47	-3.11	.002
		Front Right	1000	2.53	34.97		
	Guitar	Cz	3000	1.30	21.28	2.80	.005
		CT Left	4000	-0.15	17.61		
		Cz	3000	1.30	21.28	2.34	.011
		CT Right	4000	0.40	17.61		
		PO Left	4000	-0.62	24.54	-2.01	.044
		PO Right	4000	0.02	16.50		
		Pz	4000	0.73	24.17	4.12	.000
		Po Left	4000	-0.62	24.54		
		Pz	4000	0.73	24.17	2.82	.005
		PO Right	4000	0.02	16.50		
Polyphony	Piano	Cz	1000	-1.41	41.14	-2.24	.025
		CT Right	1000	-0.45	37.79		
	Guitar	Front Left	4000	-1.03	22.97	-2.34	.020
		Front Right	4000	-0.49	21.24		
		Oz	3000	1.02	37.95	1.97	.049
		PO Left	3000	-0.93	28.00		
Not Together	Piano	Front Right	501	-2.46	45.49	3.10	.002
		Front Left	501	-0.21	42.29		
		Fz	500	0.40	51.53	3.86	.0001
		Front Right	501	-2.46	45.49		
		CT Left	500	0.24	35.14	2.22	.027
		CT Right	500	-1.63	45.73		
		Cz	500	0.13	49.78	3.09	.002
		CT Right	500	-1.63	45.73		
		PO Left	500	1.27	27.19	2.32	.021
		PO Right	500	0.33	31.95		
	Guitar	Front Left	2001	9.08	37.85	10.27	.0001
		Front Right	2001	1.07	17.42		
		Fz	2001	0.30	26.23	-10.40	.0001
		Front Left	2001	9.08	37.85		
		CT Left	2001	2.08	18.50	6.34	.0001
		CT Right	2001	-11.87	15.08		
		Cz	2001	-0.86	21.42	-6.09	.000
		CT Left	2001	2.08	18.50		
		Cz	2001	-0.86	21.42	-2.10	.036
		CT Right	2001	-11.87	15.08		
		Oz	2001	0.54	16.58	2.24	.026
		PO Right	2001	-0.04	14.18		

All regions were significantly positively correlated ($p < .05$), and tests were subsequently conducted between the instrument groups.

4.4 ANOVA analysis

4.4.1 Between-instrument within-condition region ANOVA

A one-way analysis of variance (ANOVA) was calculated on all regions between instruments within playing conditions. In the solo condition, significant differences existed in the Central-Temporal Left region, $F(2,7997) = 3.64$, $p = .026$; and in electrode Cz, $F(2,5997) = 3.30$, $p = .037$.

In the accompaniment condition, significant differences were found between Frontal Right, $F(2,6997) = 3.96$, $p = .019$; Central-Temporal Left, $F(2,6997) = 2.52$, $p = .081$; Parietal-Occipital Left, $F(2,6997) = 2.89$, $p = .056$; Fz, $F(2,6997) = 2.04$, $p = .131$; and Cz, $F(2,6997) = 1.12$, $p = .326$. No significant differences were returned in the polyphony condition. In the not together condition, significant differences were found between instruments in both left and right Frontal regions, the left Central-Temporal region, the left Parietal-Occipital region, and in Oz. The figures can be found in Table 2.

Table 2: ANOVA results for all regions between instruments in the Not Together condition

Region	<i>df</i>	<i>F</i>	<i>p</i>
Frontal Left	2,3499	35.77	.0001
Frontal Right	2,3499	5.06	.006
Central-Temporal Left	2,3498	7.50	.001
Parietal-Occipital Left	2,3499	3.50	.030

The variance was found to be non-homogenous across all conditions as determined by Levene's test, and a Games-Howell post-hoc test was run for each condition. This test does not assume equal variances and is broadly conservative. The results of the Games-Howell test showed differences between guitar and piano, and guitar and ukulele in the solo and not together conditions; and between guitar and ukulele in the accompaniment condition (detailed in Table 3).

Table 3: between-instrument differences as per the Games-Howell post hoc test

Condition	Region	Instrument	<i>M</i>	<i>SD</i>	Instrument	<i>M</i>	<i>SD</i>
Solo	Central-Temporal Left	Guitar	0.80	17.08	Piano	-0.51	23.91
		Guitar	1.52	22.54	Piano	-0.26	28.82
	Cz	1.52	22.54	Ukulele	0.03	8.39	
Accompaniment	Parietal-Occipital Left	Ukulele	0.76	13.89	Guitar	-0.62	24.54
	Fz	Ukulele	0.73	11.61	Guitar	-0.38	20.31

	Cz	Guitar	1.30	21.28	Ukulele	0.10	7.79
Not Together	Frontal Left	Guitar	9.08	37.85	Piano	-0.21	42.29
	Frontal Left				Ukulele	-1.39	22.89
	Frontal Right	Guitar	1.07	17.42	Ukulele	-0.94	22.28
	Central-Temporal Left	Guitar	2.08	18.50	Ukulele	-1.26	22.14

4.4.2 Between-instrument between-condition ANOVA

Based on the positive correlations returned in the t-test analysis and the lack of inter-regional differences in the initial ANOVA, regions were further combined into three average region variables for each condition: Frontal (Frontal Left and Right and Fz), Central-Temporal (Central-Temporal Left and Right and Cz), and Parietal-Occipital (Parietal-Occipital Left and Right, Pz, and Oz). A one-way within-region ANOVA returned no significant differences between the instrument groups.

A one-way ANOVA was completed between-instrument between-condition. Significance was reported in Frontal ($F(8,22001) = 2.47, p = .011$), and Central-Temporal ($F(8,22001) = 2.24, p = .022$) regions. Post hoc tests revealed significant differences between ukulele accompaniment and guitar polyphony in both regions (see Table 4).

Table 4: between-instrument between-condition differences as per the Games-Howell post hoc test

Region	Condition	<i>M</i>	<i>SD</i>	Condition	<i>M</i>	<i>SD</i>
Frontal	Ukulele	0.70	10.43	Guitar	-0.83	20.25
	Accompaniment			Polyphony		
Central-Temporal	Ukulele	0.71	10.20	Guitar	-0.48	16.85
	Accompaniment			Polyphony		

4.5 Correlation Analysis

4.5.1 Within-instrument between-condition correlations

Data was averaged from microvolts per centisecond to microvolts per second for the correlation analysis to show large-scale relationships during the course of the experiment. Values were converted to standardised z-scores and combined into master instrument groups. Bivariate

correlation analyses were then completed on region variables within instruments between the conditions. Average region and condition variables are coded as such: F = Frontal; CT = Central-Temporal; PO = Parietal-Occipital; Acc = Accompaniment; Poly = Polyphony; NT = Not Together.

In the piano instrument group, solo, accompaniment, and polyphony were highly positively correlated between the regions within the playing conditions. Not together was significantly positively correlated only between central-temporal and parietal-occipital regions. Between the conditions, solo regions were negatively correlated with accompaniment regions (though only significantly between the solo central-temporal region and accompaniment frontal, central-temporal and parietal-occipital regions). Solo and polyphony were positively, though non-significantly correlated, and polyphony was negatively correlated, again non-significantly, with accompaniment. The not together condition proved less homogenous in correlation directionality. Solo and accompaniment were almost perfectly opposed in their correlations with not together (the not together central-temporal region was negatively correlated with parietal-occipital regions in both solo and accompaniment conditions), and polyphony was negatively correlated throughout with the exception of the central-temporal region positively correlated with the frontal region in the not together condition (see Table 5).

Table 5: between-condition correlations for averaged piano regions

	Solo F	Solo CT	Solo PO	Acc F	Acc CT	Acc PO	Poly F	Poly CT	Poly PO	NT F	NT CT	NT PO
Solo F	-											
Solo CT	.96***	-										
Solo PO	.90***	.94***	-									
Acc F	-.59	-.64*	-.53	-								
Acc CT	-.58	-.64*	-.54	1.0***	-							
Acc PO	-.62	-.68*	-.58	.99***	1.0***	-						
Poly F	.44	.41	.38	-.41	-.42	-.37	-					
Poly CT	.37	.35	.27	-.43	-.44	-.38	.95***	-				
Poly PO	.26	.27	.21	-.52	-.51	-.45	.92***	.88***	-			
NT F	-.29	-.33	-.56	.15	.18	.20	-.03	.20	-.02	-		
NT CT	.23	.22	-.03	-.28	-.24	-.30	-.41	-.20	-.40	.59	-	
NT PO	.30	.30	.10	-.37	-.34	-.42	-.57	-.44	-.54	.26	.92*	-

* $p < .05$

** $p < .01$

*** $p < .001$

In the guitar instrument group, solo, accompaniment, and polyphony were highly correlated between the regions within the playing conditions. Not together regions were positively correlated within condition, but were non-significant. Similar to the piano group, the solo

condition central-temporal region was significantly correlated with accompaniment condition central-temporal and parietal-occipital regions, but the correlations were positive. All other correlations between the conditions were non-significant with mixed directionality present in polyphony and not together conditions (see Table 6).

Table 6: between-condition correlations for averaged guitar regions

	Solo F	Solo CT	Solo PO	Acc F	Acc CT	Acc PO	Poly F	Poly CT	Poly PO	NT F	NT CT	NT PO
Solo F	-											
Solo CT	.98***	-										
Solo PO	.64*	.67*	-									
Acc F	.32	.47	.45	-								
Acc CT	.46	.62*	.56	.80**	-							
Acc PO	.51	.65*	.43	.78**	.78**	-						
Poly F	.01	.00	.47	.31	.23	.29	-					
Poly CT	-.55	-.55	.03	-.05	-.14	-.10	.68*	-				
Poly PO	-.42	-.44	-.04	.05	-.08	-.02	.66*	.93***	-			
NT F	-.10	-.24	-.13	.04	-.58	-.56	.19	-.06	.33	-		
NT CT	.51	.39	.44	.49	-.05	.00	.58	-.19	.30	.80	-	
NT PO	.87	.83	.81	.87	.54	.61	.62	-.19	.31	.31	.80	-

* $p < .05$

** $p < .01$

*** $p < .001$

In the ukulele group, regions were significantly positively correlated within the accompaniment, polyphony, and not together conditions, and positively, though non-significantly, correlated in the solo condition. Between the conditions, the central-temporal region in the solo condition was significantly negatively correlated with all regions in the accompaniment condition. The frontal region in the solo condition was significantly positively correlated with frontal and central-temporal regions in the polyphony condition, and the parietal-occipital region in the solo condition was significantly correlated with all regions in the polyphony condition. All other between-condition correlations were non-significant (see Table 7).

Table 7: between-condition correlations for averaged ukulele regions

	Solo F	Solo CT	Solo PO	Acc F	Acc CT	Acc PO	Poly F	Poly CT	Poly PO	NT F	NT CT	NT PO
Solo F	-											
Solo CT	.18	-										
Solo PO	.56	.05	-									
Acc F	-.00	-.84***	.29	-								
Acc CT	.03	-.69*	.19	.83**	-							
Acc PO	-.00	-.65*	.16	.82**	.98***	-						
Poly F	.73*	-.10	.86***	.46	.37	.31	-					
Poly CT	.61*	.20	.92***	.18	.12	.09	.87***	-				
Poly PO	.59	.35	.86***	.01	-.06	-.10	.80**	.97***	-			

NT F	-.46	-.24	.27	.45	.09	.14	.05	.15	.09	-		
NT CT	-.51	-.14	.22	.36	.00	.05	-.01	.10	.06	.98***	-	
NT PO	-.44	-.02	.33	.27	.01	.07	.00	.17	.12	.91***	.95***	-

* $p < .05$ ** $p < .01$ *** $p < .001$

4.5.2 Between-instrument between-condition correlations

Due to the consistent within-condition positive correlations, region variables were combined into master condition. A bivariate correlation analysis showed very little significant correlations between the conditions with the exception of ukulele solo and piano solo, $r(10) = .66, p < .05$; guitar polyphony and piano accompaniment, $r(10) = .70, p < .05$; and ukulele solo and ukulele polyphony, $r(10) = .82, p < .01$. The remaining correlations were non-significant, though directionality remained consistent (piano solo positively correlated with piano polyphony, negatively with accompaniment, etc., see Table 8).

Table 8: Master condition correlations between instrument groups

	Piano Solo	Piano Acc	Piano Poly	Piano NT	Guitar Solo	Guitar Acc	Guitar Poly	Guitar NT	Ukulele Solo	Ukulele Acc	Ukulele Poly	Ukulele NT
P Solo	-											
P Acc	-.61	-										
P Poly	.33	-.46	-									
P NT	.03	-.21	-.37	-								
G Solo	-.47	.36	.04	-.68	-							
G Acc	-.50	.07	-.12	-.22	.58	-						
G Poly	-.30	.70*	-.61	-.16	-.19	.07	-					
G NT	-.63	.86	-.38	.10	.34	.08	.32	-				
U Solo	.66*	-.26	.25	-.56	-.22	-.31	.22	-.64	-			
U Acc	-.32	.28	.23	-.83	.58	.23	-.58	.44	-.25	-		
U Poly	.48	-.01	.24	-.62	-.08	-.20	.22	-.52	.82**	.16	-	
U NT	.18	.28	-.33	.33	.01	.23	.11	.27	-.16	.18	.09	-

* $p < .05$ ** $p < .01$

4.5.3 Averaged correlations

The instrument variables were further combined into a master score between regions and, when significant positive correlations were again observed between regions within playing condition, the regions were combined into master condition scores (Table 9).

Table 9: master condition correlations

	Solo	Accompaniment	Polyphony	Not Together
Solo	-			
Accompaniment	.30	-		

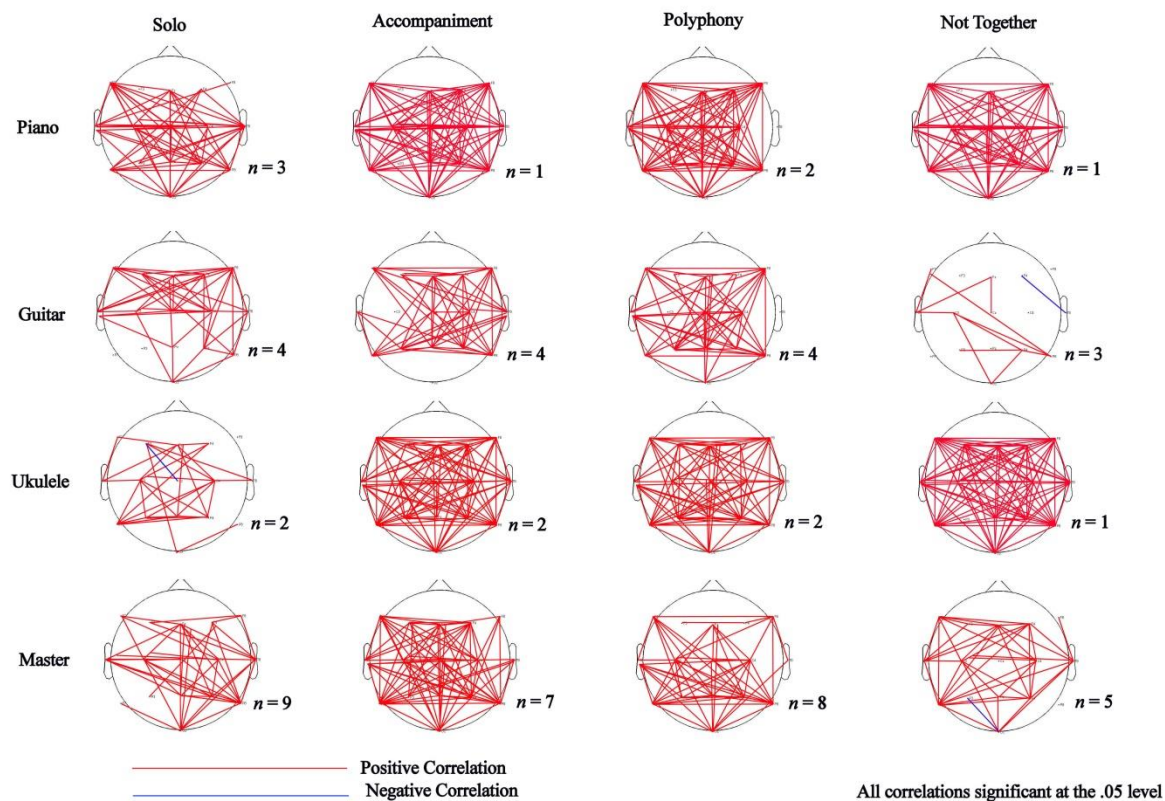
Polyphony	.44	.06	-	
Not Together	-.30	.16	.16	-

The correlation scores became non-significant when regions were combined, possibly indicating an overall between-condition functional independence in large-scale networks. The correlation directionalities were positive, with the exception of solo and not together, which was negatively correlated.

4.5.4 Individual electrode correlations

Individual electrodes were correlated at the second level to create a visual representation of averaged electrode relationships within instrument groups (solo, accompaniment, and polyphony conditions consisting of ten-second epochs, not together consisting of five-second epochs), and further combined into a master group (Figure 3). The figures show strong bilateral relationships and an almost symmetrical connectivity structure in accompaniment and polyphony, however, differences are present in the solo and not together conditions, possibly corresponding to the higher number of participants.

Figure 3: Electrode correlation relationships



5 DISCUSSION

This study investigated the electrical neural activity of one of a pair of musicians engaging in dyadic improvisation in an effort to create a model of dyadic improvisation. Musical analysis produced a set of consistent elements present in dyadic improvisation, and the features were extracted from the EEG data for statistical analysis. Initial t-tests revealed mean differences between left- and right-side electrodes, but positive correlations between the hemispheres and central electrodes indicate an overall similarity of activity. Between-instrument mean differences may indicate instrument group specificity in processing location, but could be related to electrode absences and the differences in combined scores among instrument groups and conditions. The correlation visualisation in Figure 1 shows fewer within-instrument connections as sample size increases, which could indicate overall commonalities across conditions with smaller patterns visible only in individual analysis.

Sparse significant differences between conditions in the between-instrument between-condition ANOVA offers support for a homogenous and observable improvisation process in the brain with the correlation analysis offering a generalized view of instrument group differences in electrode relationship directionality. This difference could be explained by the highly individualized nature of spontaneous music-making: each improvisation is different, and the participants were not required to include specific elements to retain as natural an environment as possible. The instruments themselves may also account for some of the differences. While all instruments are capable of melody and harmony, guitar and ukulele are most often employed as one or the other, whereas piano is capable of simultaneous solo and accompaniment. In the correlation analysis, piano data displayed more significant correlations, but it is unclear whether this points to more intensive cerebral involvement, or whether higher sample sizes would have reduced connectivity as seen in the guitar conditions. All three instruments require coordinated action between left and right sides of the body, represented in the data through bilateral correlations and mean similarities. More individual networks may emerge with the study of single-sided instrument play, such as playing melody or chords only on piano, or drumming with only one hand.

Participant skill could have also played a factor in correlation differences. All participants were highly trained musicians and, while training has been shown to result in structural differences in

musicians (Wan & Schlaug, 2010), correlation images could be representative of the extensive connectivity networks present in formally trained musicians.

A loss of significance in correlations across conditions and instruments when regions were combined could indicate regional independence that is variable between conditions and instruments. In the piano and ukulele groups, the solo and polyphony conditions were positively correlated, but differed in correlation with accompaniment. In piano, polyphony was uniformly negatively correlated with accompaniment, whereas ukulele was positively correlated except in the parietal-occipital electrodes in polyphony (negatively, though not significantly, correlated with central-temporal and parietal-occipital regions in accompaniment). In the guitar group, correlations were much less uniform, possibly due to higher sample sizes. In all instrument groups, the only significant between-condition correlations was between the central-temporal region in the solo condition, and central-temporal and parietal-occipital regions in accompaniment (piano and ukulele were also significantly correlated in the frontal region of accompaniment). Central-temporal region correlations are, perhaps, unsurprising since cortical areas in this region correspond to auditory processing (including linguistic and prosodic features), motor planning, and the coordination of complex movements, which is a common element in the playing of musical instruments. When the regions were combined, the correlations became non-significant, indicating a potentially specialized and faint regional independence. More structured experiments could be conducted to establish the validity of this observation.

In the combined regions, correlations between instrument groups between conditions, piano solo and ukulele solo; and piano accompaniment and guitar polyphony were the only significant between-instrument correlations present. This could indicate independence between instrument groups, and could also be a side effect of the “none two are alike” nature of musical improvisation. When instruments were combined, between-region within-condition significance returned; and significant correlations were observed between frontal-region solo and frontal-region polyphony (positively correlated); and parietal-occipital-region solo with frontal-region polyphony (positively correlated). Where solo and polyphony conditions are characterized by generating melodic phrases, it could be that some areas in the frontal- and parietal-occipital regions of the brain are significantly engaged in both conditions. These brain areas correspond to complex cognitive functions (frontal regions), and visual and motor planning (parietal-occipital regions), and are perhaps more strongly linked in the solo and polyphony conditions due to the

cognitive and physical complexity or spontaneously generating a novel melody that complements the partner's musical activity.

When further combined, all correlations became non-significant, but the directionality remained somewhat consistent. Solo, accompaniment, and polyphony were positively correlated; and not together was negatively correlated with solo, and positively correlated with accompaniment and polyphony. This loss of significance, yet retention of directionality, indicates a similarity of relationship between instruments within conditions that, despite the numeric standardization of the scores, is still unique within the groups themselves.

When compared to the cortical model of improvisation presented in Figure 2, all areas were active in the EEG data, as well as more electrodes in the parietal-occipital region that may be related to, and confounded by, visual tracking and other processes involving the eyes. Interestingly, activity in the central parietal lobe has been linked to language comprehension (Friederici, 2002; Brown et al., 2006), but not specifically to music production, though other areas in the parietal region have been implicated in music studies (see Brown et al., *ibid*; Limb & Braun, 2008). Limb et al. (2014) observed strong deactivation of the angular gyrus, located in the inferior parietal lobe, an area implicated in semantic integration, in dyadic jazz improvisation, however, deactivation is best observed using fMRI. The high amount of complete cortical activity observed throughout the experiment and the poor spatial resolution inherent in EEG data prevents the exact cortical localization of specific electrode data, but there is a clear wealth of activity in the parietal-occipital region connected to the actions of other regions in the brain during the process of improvisation. Emerging research using spatially accurate neuroimaging equipment is beginning to investigate dyadic improvisation, and will be able to further clarify the role of the parietal-occipital region in the shared production of spontaneous music.

The activity present in the frontal and central-temporal regions between all participants and the music itself offers strong support for improvised music as a communicative medium. The nature of dyadic improvisation requires wordless communication between participants in terms of tempo setting, key and harmonic and melodic congruity. Though some participants did agree on key signature and chord progressions before the EEG recording started, no roles (such as soloist/accompanist) or melodic content were discussed. Participants were able to trade roles with no prior arrangement, and create complementary, polyphonic melodies together relying on minute musical information with only minimal bodily cues due to the restrictions of the EEG

apparatus. This, along with the previously cited improvisation studies, indicates a dynamic and cognitively sophisticated communicative behaviour.

6 CONCLUSION

Musical improvisation is a sophisticated and complex behaviour that is further complicated by the addition of a partner. This aim of this study was to investigate dyadic improvisation using EEG to create a model of dyadic improvisation. It was found that the improvisations shared common musical features which, when analyzed, were not dramatically different in the brain data indicating a functional homogeneity of improvisation as a singular, observable process in the electrical output of the brain. The amount of activity observed across the entire scalp raises questions as to the specific areas of the parietal and occipital regions implicated in the production of shared, improvised music. Further study comprising spatially accurate technology, such as fMRI, can specify and expand the intricacies of this behaviour into sub-cortical regions.

7 REFERENCES

- Babiloni, C., Vecchio, F., Infarinato, F., Buffo, P., Marzano, N., Spada, D., Perani, D. (2011). Simultaneous recording of electroencephalographic data in musicians playing in ensemble. *Cortex*, 47(9), 1082-1090. doi: 10.1016/j.cortex.2011.
- 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.
- Berkowitz, A.L., & Ansari, D. (2008). Generation of novel motor sequences: the neural correlates of musical improvisation. *NeuroImage*, 41(2), 535–543.
- Besson, M., & Schön, D. (2001). Comparison between language and music. *Annals of the New York Academy of Sciences*, 930(1), 232-258.
- Brown, S., Martinez, M., Hodges, D., & Fox, P., & Parsons, L. (2004). The song system of the human brain. *Cognitive Brain Research*, 20: 363-375.
- Brown, S., Martinez, M. J., & Parsons, L. M. (2006). Music and language side by side in the brain: A PET study of the generation of melodies and sentences. *European Journal of Neuroscience*, 23(10), 2791-2803.
- Cross, I. (2001). Music, cognition, culture and evolution. *Annals of the New York Academy of Sciences*, 930, <http://www.mus.cam.ac.uk/~ic108/crosspubs96.html>.
- Cross, I. (2007). Music, science & culture. In I. Roth (Ed.) *Imaginative Minds (Proceedings of the British Academy) 147*, pp 147-165, Oxford, Oxford University Press.
- Cross, I. (2009). The evolutionary nature of musical meaning. *Musicae Scientiae*, Special Issue: *Music and evolution*, 179-200. Retrieved from <http://www.mus.cam.ac.uk/~ic108/crosspubs96.html>.
- Cross, I. & Woodruff, G. E. (2009). Music as a communicative medium. In R. Botha & C. Knight (Eds.), *The prehistory of language* (pp113-144). Retrieved from <http://www.mus.cam.ac.uk/~ic108/crosspubs96.html>.
- Delorme, A. & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics. *Journal of Neuroscience Methods* 134:9-21.
- Donnay, G.F., Rankin S.E., 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): e88665. doi: 10.1371/journal.pone.0088665.

- Friederici, A.D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, 6, 78-84.
- Koelsch, S., Gunter, T.C., von Cramon, D.Y., Zysset, S., Lohmann, G., & Friederici, A.D. (2002): Bach speaks: a cortical 'language-network' serves the processing of music. *Neuroimage*, 17, 956-966.
- Koelsch, S., Gunter, T. C., Wittfoth, M., & Sammler, D. (2005). Interaction between syntax processing in language and in music: An ERP study. *Journal of Cognitive Neuroscience*, 17, 1565-1577.
- Levitin, D. (2006). *This is Your Brain on Music*. Toronto: Penguin Group.
- Limb, C.J., & Braun, A.R. (2008). Neural substrates of spontaneous musical performance: an fMRI study of jazz improvisation. *PLoS ONE* 3(2): e1679. doi:10.1371/journal.pone.0001679.
- Lindenberger, U., Li, S.-C., Gruber, W., & Mueller, V. (2009). Brains swinging in concert: Cortical phase synchronization while playing guitar. *BMC Neuroscience*, 10(22).
- MATLAB version 7.12.0. (2011). Natick, Massachusetts: The MathWorks Inc.
- Mithen, S. (2006). *The Singing Neanderthals*. Cambridge, Massachusetts: Harvard University Press.
- Müller, V., Sänger, J., & Lindenberger, U. (2013). Intra- and inter-brain synchronization during musical improvisation on the guitar. *Plos One*, 8(9): e73852. doi: 10.1371/journal.pone.0073852.
- North, A., Hargreaves, D., & Hargreaves, J. (2004) Uses of Music in Everyday Life. *Music Perception*, 22, 1, 41-77.
- Pell, M.D., (2006). Cerebral mechanisms for understanding emotional prosody in speech. *Brain and Language*, 97, 221–234.
- Pelz-Sherman, M., (1998). A framework for performer interactions in Western improvised contemporary art music. Ph.D. Dissertation, University of California, San Diego.
- Salimpoor, V., Benovoy, M., Larcher, K., Dagher, A., and Zatorre, R.J. (2011). Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nature Neuroscience* 14, 257–262.
- Sammler, D., Koelsch, S., Ball, T., Brandt, A., Grigutsch, M., Huppertz, H, Knösche, T.R., Wellmer, J., Widman, G., Elger, C.E., Friederici, A.D., & Schulze-Bonhage, A. (2013).

- Co-localizing linguistic and musical syntax with intracranial EEG. *Neuroimage*, *64*, 134-146.
- Schögler, B. (1998). Music as a tool in communications research. *Nordic Journal for Music Therapy*, *7*(1), 40-49.
- SPSS Inc. Released 2009. PASW Statistics for Windows, Version 18.0. Chicago: SPSS Inc.
- Steinbeis, N., & Koelsch, S. (2008). Comparing the processing of music and language meaning using EEG and fMRI provides evidence for similar and distinct neural representations. *PLoS ONE*, *3*, e2226. doi:10.1371/journal.pone.0002226
- Sänger, J., Müller, V., & Lindenberger, U. (2012). Intra- and interbrain synchronization and network properties when playing guitar in duets. *Frontiers in Human Neuroscience*, *6*, 00312.
- Van Berkum, J. J. A. (2012). The electrophysiology of discourse and conversation. In M. J. Spivey, K. McRae, & M. F. Joannisse (Eds.), *The Cambridge handbook of psycholinguistics* (pp. 589-614). New York: Cambridge University Press.
- Van der Zwaag, M. D., Westerink, J. H. D. M., & van den Broek, E. L. (2011). Emotional and psychophysiological responses to tempo, mode, and percussiveness. *Musicae Scientiae*, *15*(2), 250-269.
- Wan, C., & Schlaug, G. (2010). Music making as a tool for promoting brain plasticity across the life span. *Neuroscientist*, *16*(5), 566-577.
- Wildgruber, D., Ackermann, H., Kreifelts, B., & Ethofer, T. (2006) Processing of Linguistic and Emotional Prosody: fMRI Studies. *Progress in Brain Research*, *156*, 249-268.

APPENDIX 1

Brain activations as per Brown, Martinez & Parsons, 2006; Bengtesson and others, 2007; Berkowitz & Ansari, 2008, Limb and others, 2014.

Brain Area	Function	Associated Behaviour	
BA 4	Motor execution	Vocal improvisation	
Insula	Taste, emotion, sensory processing		
Thalamus	Processing and transmission of signals to the cerebral cortex		
BA 45	Language processing, emotion, personality, planning		
BA 42	Auditory processing		
BA 22	Auditory processing and language reception (prosody)		
Globus Pallidus	Coordination of voluntary movement		
Supplementary Motor Area (BA6)	Planning and coordinating complex movements		
BA 44	Language production (prosody)		
BA 38	Limbic system, self-representation (autobiographical)		
Putamen	Coordinates activity related to movement between the cerebral cortex and basal ganglia		
Cerebellum	Movement coordination, motor learning, sequencing (possibly emotion)		Vocal and instrumental improvisation
Left and Right Premotor Cortices (BA6)	Planning, programming, and execution of voluntary motor function		Instrumental improvisation
Frontal Gyrus (BA 44, 45, 47)	Language production		
Rostral Cingulate Zone (BA 24, 32, 33)	Emotional and Cognitive Processing		
Temporal Gyrus (BA 41, 42)	Visual Recognition		
Left Inferior Temporal Gyrus (BA20)	Visual Recognition		
Left Sensorimotor Cortex (BA 1,2,3)	Sensation processing, motor processing		
Parietal Gyrus (BA 5,7)	Sensory processing		
Left Parietal Lobule (BA 39,40)	Spatial orientation, associative functions		
Right Prefrontal cortex (dorsolateral) (BA 8,9,44,45,46,47)	Associative functions, cognitive and executive control		
Presupplementary Motor Area (BA6)	Motor planning		
Left Superior Temporal Gyrus (BA41,42)	Auditory information processing, language reception		

Brain activations as per Brown, Martinez & Parsons, 2006, Friederici, 2002.

Brain Area	Function	Associated Behaviour
BA 8	Eye movements	Language Reception and Production
BA 32	Emotional and cognitive processing	
BA 6	Motor planning and execution	
BA 39	Processing language, spatial orientation, semantic representation	
BA 44	Language production (semantics)	
BA 9	Prefrontal associational integration	
BA 22	Auditory processing and language reception (generation/understanding of words)	
BA 21	Processing visual information, other temporal associational function	
BA 38	Limbic system, self-representation (semantic)	
Inferior Frontal Gyrus	Language production	
Middle Temporal Gyrus	Morphological information	
Middle Temporal Lobe	Integration of semantic and syntactic information	
Centro-Parietal Lobe -	Language comprehension	
BA 4	Motor execution	
Thalamus	Processing and transmission of signals to the cerebral cortex	
BA 45	Language processing, emotion, personality, planning	
BA 42	Auditory processing	
BA 22	Auditory processing and language reception (prosody)	
Globus Pallidus	Coordination of voluntary movement	
Cerebellum	Movement coordination, motor learning, sequencing (possibly emotion)	
Supplementary Motor Area (SMA)	Planning and coordinating complex movements	
Auditory Cortex	Processing of auditory stimuli	
Superior Temporal Gyrus (STG)	Auditory information processing, language reception	
Insula	Taste, emotion, sensory processing	