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THE NEUROSCIENCE OF MUSIC; A REVIEW AND SUMMARY

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SUMMARY
Present knowledge about the neurobiology of music is discussed and summarised. Music playing, reading and listening are all complex processes requiring co-ordination of various parts of the brain in hierarchically structured sequences. The involvement of the right hemisphere of the brain in musical functions is well established, however in fact both hemispheres are involved. Plasticity is heavily involved in all functions of the brain related to music. The role of mirror neuron systems of the brain appears to be of great importance and parallels exist in the development and functioning of language and music.

Key words: *music - language – emotion – mirror neurons - right cerebral hemisphere*

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APPRECIATING MUSIC

Music performance is a natural human activity, present in all societies, and also one of the most complex and demanding cognitive challenges that the human mind can undertake (Zatorre 2007). The ability to create and enjoy music is a universal human trait and it plays an important role in the daily life of most cultures (Molnar-Szakacs 2006). In other words, music is a trait which is very clearly bound up with human expression, and so, indeed with the very essence of being human.

Music has a unique ability to trigger memories, to awaken emotions and to intensify our social experiences (Molnar-Szakacs 2006). Music has soothed the souls of human beings for centuries and it has helped people to recover from ailments since ancient times (Mula 2009). Hence it is no surprise that today, there is a widespread interest in the relationship between music, affect and mental illness (Mula 2009).

In this article, we wish to review some of these complex relationships, including examples from the neurobiology of emotions, perceptions and music language (Mula 2009). We do not expect to be fully comprehensive but instead have based our review on Jourdain's work: "Music, the brain, and ecstasy: How music captures our imagination" (Jourdain 1998).

COORDINATION OF THE BRAIN AREAS INVOLVED IN PLAYING OR LISTENING TO MUSIC

Several areas of the brain are coordinated to play or listen to music to produce a single but complex activity, and is called a hierarchically structured sequence (Jourdain 1998). The precise physical movement required by musical performances requires very accurate coordination of numerous parts of the body bolstered by detailed feedback at all levels (Jourdain1998). The different areas involved in the neuroscience of music, as discussed by Jourdain can be found in Table 1, along with updates from recent papers.

One constant finding to emerge from the studies of the effects of listening to music is the emphasis on the right hemisphere (Stewart 2006). It is possible that hemispheric specialization for musical processing may develop with age, with a study on a group of young children showing some differential specialisation for melody and rhythm processing, but to a lesser extent than previously reported in adults (Overy 2004).

THE PERCEPTION OF MUSIC

We do not only listen to music for pleasure and the attention we give to music will vary with circumstance from merely hearing music through to listening carefully (Jourdain 1998). The different aspects and corresponding processes that have been proposed by Jourdain are again best summarised in a table with updates from recent papers (Table 2). Listening to music is a human experience, which becomes an aesthetic experience when individuals immerse themselves in the music, dedicating attention to interpretation and evaluation (Reybrouck 2018). Recent neuroimaging findings indicate that music listening is traceable in terms of network connectivity and activations of target regions in the brain, in particular between the auditory cortex, the reward brain system and brain regions active during mind wandering (Reybrouck 2018).

Miles' surprise hypotheses (Miles 2007) can be illustrated by the music of Alexander Scriabin. His music has been described as a "polyphony and aesthetical experience" because his innovative use of chord structure and sequence; his creation of a chord based on fourths rather than the conventional thirds are proposed as points of departure for insight (Triarhou 2016). The underlying neuronal processes are complex and yet to be demystified despite the sophistication of our love for music.

Table 1. Parts of the brain involved in music playing/listening

Area			Function
Right hemisphere			Prosody (poetic rhythm and emotional tone of speech) *(Mula 2009)*
			Recognition of melody *(Jourdain 1998, Overy 2004)*
	Auditory cortex		Relations between simultaneous sounds *(Jourdain 1998)*
Left hemisphere			Dominant for rhythm *(Jourdain 1998)*
		Posterior Sylvian fissure at the parietal-temporal boundary (Spt)	Sensorimotor integration, part of an auditory–motor integration circuit that may play an important role in speech and musical ability development *(Hickok 2003),* and may support verbal working memory *(Zatorre 2007)*.
The cerebrum	Auditory dorsal stream		Forward and inverse models related to music listening/performance *(Rauschecker 2014).*
	Basal ganglia		Redistribution of information, initiation of movement *(Jourdain 1998)*
	Frontal cortex		Part of an auditory–motor integration circuit that may play an important role in speech and musical ability development *(Hickok 2003),* and may support verbal working memory *(Zatorre 2007).*
		Fusiform gyrus	Rhythm reading (*Stewart 2005)*
	Motor cortex		Types of basic physical movements *(Jourdain 1998)*
		Motor neurones	Direction of movement*(Jourdain 1998)*
		Medial prefrontal cortex	Representation of elapsed time between events (shown by significant trial-by-trial relation between decoded times and the timing behaviour of the monkeys) *(Merchant 2017)*
	Parietal cortex		Coordination of touch, sight and hearing *(Jourdain 1998)*
		Superior parietal cortex	Melody reading *(Stewart 2005)*
	Premotor cortex		Coordination of sequences of movements *(Jourdain 1998)*
		Dorsal premotor cortex	Integration of higher order features of music with appropriately timed and organized actions *(Zatorre 2007)*
	Somatosensory cortex		Feedback from muscle fibre spindles and fingerprints *(Jourdain 1998)*
Cerebellum			Physical balance between ballistic movements too quick for feedback *(Jourdain 1998)*

Studies have been carried out regarding mechanisms by which music is perceived. In one study, formally trained musicians compared with nonmusicians showed more efficient neural detection of tones, superior auditory sensory-memory traces for acoustic features, and revealed enhanced sensitivity to acoustic (Nikjeh 2009). These findings suggest that musical training influences central auditory function and modulates the auditory neural system.

Along with local features such as pitch, tuning, consonance/dissonance, harmony, timbre, or beat, global sonic properties could also be viewed as contributing toward creating an aesthetic musical experience (Brattico 2017). These contributing factors to beauty are hypothesized to be global, formal/non-conceptual, computational and/or statistical, and based on relatively low-level sensory properties (Brattico 2017).

MUSIC AND EMOTION

The link between music and emotion seems to be accepted for all time (Cooke 1959). Plato considered that music played in different modes would arouse different emotions (Mula 2009). Harmony can affect the emotional significance of a piece of music e.g. major chords are cheerful and minor ones are sad (Mula 2009). The tempo or movement in time is another component of this, slower music seeming less joyful than faster rhythms. Mula suggests that this reminds us that motion is an important part of emotion; "in the dance we are moving – as we are moved emotionally by music" (Mula 2009).

Meyer explored in detail the meaning of music, especially from an emotional point of view (Meyer 1956). Music, arouses feelings and associated physiological responses, and these can now be measured (Mula 2009).

Table 2. The processes underlying music listening

Aspect	Underlying process
Expectation	Episodic memory *(Jourdain 1998)*
Anticipation	Semantic memory *(Jourdain 1998)*, pattern recognition and temporal predictions combined to generate anticipation *(Salimpoor 2015)*
Attention	Perception of *"edge elements"* e.g. melodies at the peaks and troughs, and violations of metrical pattern, thus making the perception of complex harmony a listening skill that requires training *(Jourdain 1998).*
General emotion	Brain structures that are known to be crucially involved in emotion, such as the amygdala, nucleus accumbens, hypothalamus, hippocampus, insula, cingulate cortex and orbitofrontal cortex *(Koelsch 2014)*
Anger	Misattribution of anger in the music of avantgarde jazz saxophonists could be explained by the activity of mirror neurones *(Gridley 2006)*
Preference/ Enjoyment	*Absolute-Surprise Hypothesis* – unexpected events lead to pleasure *(Miles 2017)*
	Contrastive-Surprise Hypothesis – juxtaposition of unexpected and expected events leads to rewarding response *(Miles 2017)*
	Hybrid-Surprise Hypothesis – both hypotheses play roles in the enjoyment of popular music *(Miles 2017)*
	Dopaminergic reward system in the ventral striatum *(Gold 2013).* Some musical pieces may preferentially activate reward centres in the brain *(Miles 2017)*
	Integration of complex cognitive abilities with subcortical reward and motivation systems for musical pleasure *(Salimpoor 2015)*

For the ordinary listener, however, there may be no necessary relationship of the emotion to the form and content of the musical work since "the real stimulus is not the progressive unfolding of the musical structure but the subjective content of the listener's mind" (Meyer 1956).

Mirror neurones are said to have a role in emotional response.Individual mirror neurons were first seen in the macaque brain that fire both when an action is executed and when that same action is observed or heard (Overy 2009). The fact that music performance requires precise timing of several hierarchically organized actions has suggested that a mirror neuron system in humans might be important in music production. There may be two processing-levels underlying common music emotionality: 1) a widely shared core-affective process that is confined to a limbic network and mediated by temporal regularities in music and 2) an experience based process that is rooted in a left fronto-parietal network that may involve functioning of the 'mirror-neuron system (Singer 2015).

Further evidence regarding audio-motor mirror neurons was obtained from filming musicians observing piano performances (Hou 2017). In this scenario, enhanced mirror neurone activation in musicians may stem from imagining themselves actually playing the observed piece (Hou 2017). A different study similarly concluded that auditory stimuli can activate the human mirror neurone system when sounds are linked to actions (Wu 2017). Long-term training in musicians and short-term training in novices may be associated with different stages of audio-motor integration and these changes were not found for participants listening to rhythms, suggesting a degree of specificity related to training (Wu 2017).

Huron approached the emotional impact of music from an ethological perspective (Huron 2015). He raised five questions about music-related affect regarding: why music can only induce certain emotions (e.g. exuberance or tenderness) but not others (e.g. jealousy and guilt); why some induced emotions are similar to the displayed emotion whereas others aren't; why listeners often report feeling mixed emotions; why only some emotional connotations are similar across musical cultures; and finally, why musicians appear to rely on some emotion-inducing mechanisms more than others. Huron does not provide absolute answers to these questions but instead suggests that there is a potential role of ethological signals in music-related emotion. One example he gives is the use of vibrato in highly emotional string instrument playing. He suggests that vibrato correlates with the trembling frequency of an emotional voice and therefore evokes a similar emotional response.

BRAIN PLASTICITYAND MUSIC

There is much evidence that brain plasticity is caused by learning to play music. Many studies have shown grey matter differences between musicians and non-musicians in different parts of the brain. Furthermore, early exposure to music training makes a significant difference and there are critical periods of development (Joudain 1998). From the second half of the 20th century onwards, several teams of neuroscientists around the world have tried to understand the ability that our brain adapts to new experiences and the environment (neuroplasticity). In the last decade, several studies have investigated the changes that some training (such as musical practice) can elicit in the brain. Results from these investigations show that intense musical training elicits changes in sensory and motor regions, and improve the auditory discrimination and the motor synchronisation.

In one experiment, subjects listened to music from which one specific spectral frequency was removed; this led to rapid and reversible adaptation of neuronal responses in auditory cortex (Pantev 2001). Further experimental evidence demonstrated that long years of practice and training by professional musicians enable them to reach their capacity and is associated with enlarged cortical representations in the somatosensory and auditory domains (Pantev 2001). Regarding plasticity of the brain to enhance playing music, plastic changes in the somatosensory cortex proved to be specific for the fingers frequently used and stimulated and were not detected in the fingers of the hand that were not involved in playing the particular instrument (Pantev 2001).

Adult musicians' brains show structural enlargements, but it is not known whether these are inborn or a consequence of long-term training (Norton 2005). Playing a musical instrument demands extensive procedural and motor learning that results in plastic reorganization of the human brain. These plastic changes seem to include the rapid unmasking of existing connections and the establishment of new ones. Both functional and structural changes take place in the brain of instrumentalists as they learn to cope with the demands of their activity (Pascual-Leone 2001). These structural and functional differences were found in the brains of adult instrumental musicians compared to those of matched non-musician controls, with intensity/duration of instrumental training and practice being important predictors of these differences (Schlaug 2005).

Voxel-based morphometry (VBM) studies have shown volumetric differences between musicians and non-musicians in several brain regions including the superior temporal gyrus, sensorimotor areas, and superior parietal cortex (Sato 2015). These differences are considered to be caused by neuroplasticity during long and continuous musical training periods (Sato 2015). MEG studies of the auditory cortex have demonstrated enlarged cortical representation of tones of the musical scale compared to pure tones in skilled musicians and suggested that enlargement was correlated with the age at which musicians began to practice (Pantev 2003). The corpus callosumis 15-percentlarger in adults who started playing the piano before the age of 8 than otherwise (Jourdain 1998).

In another experiment, a subset of voxels (in the the bilateral superior parietal cortex) was activated when musical notation was present, but was irrelevant for task performance. These activations suggest that music reading involves the automatic sensorimotor translation of a spatial code (written music) into a series of motor responses (keypresses) (Stewart 2003). Musical notation is automatically processed in trained pianists and visuomotor mappings are formed that generalise outside the musical context (Stewart 2004). One study found that after musical (but not painting) training, children showed enhanced reading and pitch discrimination abilities in speech (Moreno 2009). A separate study on the effect of piano or string lessons in 5- to 7-year olds found correlations between music perceptual skills and both non-verbal reasoning and phonemic awareness (Norton 2005). Interestingly, some studies have suggested important performance advantages of musical training; music training in children results in long-term enhancement of visual-spatial, verbal, and mathematical performance (Schlaug 2005).

Furthermore, plasticity also occurs when learning to read music. While reading music, the eyes embrace an area about 25mm in diameter and move every 20th of a second in a manner which reflects the structure of the music (Jourdain 1998). The presence of musical notation produces systematic effects on reaction time, demonstrating that reading of the written note, like the written word, is obligatory for those who are musically literate (Stewart 2005). The visuo-spatial mapping that occurs is present in musically naïve individuals after only a short period of training (Stewart 2003). In sight-reading in pianists, direct contrasts between music notation and verbal or numerical notation tasks were found in the right occipito-temporal junction (OTJ), superior parietal lobule and the intraparietal sulcus (Schon 2002). The difference in the right OTJ was interpreted by Schon as being due to differences at the encoding level between notes, words and numbers.

While plastic changes appear to be crucial for skilful playing, they potentially pose a risk for the development of motor control dysfunctions (Pascual-Leone 2001). Extensive musical practice is a two-edged blade that can facilitate or degrade fine motor control. However, insufficient evidence in movement organisation within the brain limits the understanding of how much music practice is optimal (Furuya 2015). The little evidence that is available suggests that motor failures in musicians develop on a continuum, "starting with subtle transient degradations, and transform into more permanent, still fluctuating motor degradations, the dynamic stereotypes, until a more irreversible condition, musician's dystonia manifests" (Altenmüller 2014).

IS MUSIC A PROTOTYPICAL LANGUAGE?

There appear to be links with emotion and music in the right brain that are analogous to language and rhythm in the left brain. Jourdain suggested that spoken language is a type of rhythm because it is devoted to mapping the flow of time (Jourdain 1998). He described how there is both meaning (definition) and intonation (feeling) in verbal language. There may be parallels between music and language based on the left hemisphere language area and corresponding right area

(Jourdain 1998). However, there are differences between language and music. For example, language tends to be externally focused and are more distinct and componetised; music tends to be internally feeling focused and more turbulent (Jourdain 1998), but the similarities outweigh the differences.

Language and music are human universals involving perceptually discrete elements organized in hierarchically structured sequences (Jentschke 2005). Hence the question arises as to what kind of survival value could music have conferred to early hominids in comparison to propositional speech (Mula 2009). Darwin considered music to have evolved from primate sexual selection calls, and argued for a common origin of music and language (Darwin 1871). Music and language have been described as communication devices to express emotional meaning through high-registered socially accepted patterned sound (Mula 2009). Corballis remarked that given the rather diffuse yet pervasive quality of music in human society, it may well have been a precursor to language, perhaps even providing "the raw stuff out of which generative grammar was forged" (Corballis 1991). Some support for these views comes from the work of Mithen, who argued that spoken language and music evolved from a proto-language, which evolved from primate calls used by the Neanderthals: "it was emotional but without words as we know them" (Mithen 2005).

If there is an overlap between music and language centres, shared resources are needed to hold a harmonic key in some form of unification workspace related to the integration of chords and words (Kunert 2016). In one study, event-related potentials were found for the violation of expectancies in both musical regularities and syntax (Jentschke 2005). There is evidence to suggest that these potentials are generated in the same brain regions and it therefore seems plausible that there are shared processing resources for music and language. In addition, Jentschke found heightened musical expectancies in musicians compared to non-musicians, and in linguistically non-impaired children but not in age-matched children with an impairment (Jentschke 2005). In a different study, musicians with dyslexia did not perform significantly different to typical musicians and performed better than non-musicians with dyslexia for auditory sequencing and the discrimination of spectral cues, but typical musicians were better at discriminating amplitude information (Zuk 2017).

Current research suggests that Broca's area (inferior frontal gyrus and ventral premotor cortex) are activated for tasks other than language production (Fadiga 2009). A growing number of studies report the involvement of these two regions in language comprehension, action execution and observation, and music execution and listening (Fadiga 2009). Recently, the critical involvement of the same areas in representing abstract hierarchical structures has also been demonstrated (Fadiga 2009). Indeed, language, action, and music share a common syntactic-like structure. It has been proposed that these areas are tuned to detect and represent complex hierarchical dependencies, regardless of modality and use. It has consequently been speculated that this capacity evolved from motor and premotor functions associated with action execution and understanding, such as those characterising the mirror-neuron system.

MUSIC, LANGUAGE AND EMOTION - SUGGESTED FUNCTION OF MIRROR NEURONS

Recent neuroimaging evidence suggests that music, like language, involves a coupling between the perception and production of sequential information, and this structure allows the ability to communicate meaning and emotion (Molnar-Szakacs 2006). The use of fMRI to demonstrate an active mirror neurone system in pianists suggests that music is perceived not only as an auditory signal, but also as intentional sequences of expressive motor acts behind the signal, which allows for co-representation and sharing of a musical experience between agent and listener (Overy 2009). The same team expanded upon this model of Shared Affective Motion Experience (SAME) and discussed its implications for music therapy and special education (Overy 2009).

One application of the theory of mirror neurones in music production relates to autism. Individuals with autism show impairment in emotional tuning, social interaction and communication, which been attributed to a dysfunction the human mirror neuron system. Interventions using methods of music making may offer a promising approach for facilitating expressive language in otherwise nonverbal children with autism (Wan 2010).

EPILOGUE; UNDERSTANDING MUSIC (Jourdain 1998)

Over the years, a large quantity of research on the neuroscience of music has been generated. It seems fitting to summarise and end our review with a collection of Jourdain's descriptions of music:

- Music is interesting when it goes just beyond expectations.
- People almost always prefer music with too little information content rather than too much and people tend to prefer increasingly complex music as they grow older.
- People primarily use music for mood enhancement but people's personal preferences regarding genre are generally guided by their peer group.
- We listen to it for its meaning; purpose and meaning are inseparable; meaning requires context.
- There may be parallels between music and language based on the left hemisphere language area and corresponding mysterious right area.

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Contribution of individual authors:

Shentong Wang carried out the main literature search and developed the presentation on which this paper is based.

Mark Agius supervised the project, added to the literature search, and helped in developing the final text.

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