

BEING TOGETHER IN TIME: MUSICAL EXPERIENCE AND THE MIRROR NEURON SYSTEM

KATIE OVERY
University of Edinburgh, United Kingdom

ISTVAN MOLNAR-SZAKACS
University of California, Los Angeles

THE DISCOVERY OF INDIVIDUAL “MIRROR NEURONS” in the macaque brain that fire both when an action is executed and when that same action is observed or heard, and of a homologous system in humans, is leading to an extraordinary conceptual shift in our understanding of perception-action mechanisms, human communication, and empathy. In a recent model of emotional responses to music (Molnar-Szakacs & Overy, 2006), we proposed that music is perceived not only as an auditory signal, but also as intentional, hierarchically organized sequences of expressive motor acts behind the signal; and that the human mirror neuron system allows for corepresentation and sharing of a musical experience between agent and listener. Here, we expand upon this model of Shared Affective Motion Experience (SAME) and discuss its implications for music therapy and special education. We hypothesize that imitation, synchronization, and shared experience may be key elements of successful work in these areas.

Received September 26, 2008, accepted March 15, 2009.

Key words: emotion, insula, imitation, therapy, motor

THE COMPLEX AND POWERFUL NATURE of musical experience is both mysterious and fascinating. How is it that a stream of abstract, nonreferential patterns of sound can be so enjoyable and can have such profound and varied effects in our lives? How can the simple auditory parameters of pitch, timbre, stress, and timing convey such rich information? From lullabies and work songs to advertising jingles and piano concertos, music does not appear to be limited to a particular educational, social, cultural, or even biological function. Within just a few seconds of hearing music,

we can place ourselves in a church or in a jazz bar, we can be in India or Scotland, we can remember a favorite movie or an old romance, we can feel uplifted, energized, or more relaxed. We even use music to remember the alphabet, to affect consumer spending, and to facilitate therapy. What is it about music that allows for such meaningful and varied behaviors?

Music is clearly not just a passive, auditory stimulus, it is an engaging, multisensory, social *activity*. All musical sounds are created by movements of the human body (singing, clapping, hitting, blowing, plucking)¹ and in turn seem to encourage other bodies to move (clapping, tapping, marching, dancing). Music-making usually occurs in groups (dyads, circles, ensembles), and involves the synchronization of physical actions with extraordinary temporal accuracy *and* flexibility. Such physical, social, synchronized interactions involve imitation, learning, shared understanding, and prediction, and can encourage eye contact, smiling, laughter, and relationship building, while also allowing for leadership, competition, and individual expression—all powerful social learning experiences. Even since the advent of recorded music, musical preferences are strongly linked with social groups, particularly during teenage years of social maturity and identity formation (De Nora, 2000). And yet, music is also genuinely and deeply appreciated as a solitary experience, from singing to oneself to the extraordinary cultural advent of the iPod.

Examining this rich variety of musical behavior presents experimental challenges, not least because the controlled isolation of individual variables of interest (e.g., pitch memory, beat detection, emotional response) requires the reduction or even elimination of the complexity of real-world musical experience. This is particularly true in neuroimaging research,

¹The recent advent of computer-generated music is a special case. Much electronic music emulates humanly created sounds, but not all. Interestingly, the apparent aesthetic difficulties presented by “disembodied” musical sounds are currently being discussed in the field of electro-acoustic composition (Dow, 2008).

where participants usually need to remain isolated and motionless while data are acquired (in order to avoid movement artifacts, for example). Nevertheless, the last decade has seen an explosion of scientific research into the neural basis of music, revealing that different aspects of musical processing recruit almost all regions of the brain—including prefrontal cortex, premotor cortex, motor cortex, somatosensory cortex, temporal lobes, parietal cortex, occipital cortex, cerebellum, and limbic regions including the amygdala and thalamus—unlike any other stimulus or cognitive process (for reviews see Chartrand, Peretz, & Belin, 2008; Koelsch & Siebel, 2005; Zatorre, 2005; Zatorre, Chen, & Penhune, 2007). The potential effects of music on neural plasticity are also well documented (e.g., Bangert et al., 2006; Fujioka, Ross, Kakigi, Pantev, & Trainor, 2006), as are the benefits of music as a therapeutic tool (e.g., Sarkamo et al., 2008; Thaut, 1984; Thaut, McIntosh, McIntosh, & Hoemberg, 2001), and as an educational tool (e.g., Purnell-Webb & Speelman, 2008; Schon et al., 2008). The question remains then, as to how music exerts such power—what is it that makes these abstract sound patterns so engaging and effective?

Recent research into the neural underpinnings of social communication has shed some light on how simple perceptual stimuli can convey social significance and meaning (Iacoboni et al., 2005; Molnar-Szakacs, Kaplan, Greenfield, & Iacoboni, 2006; Molnar-Szakacs, Wu, Robles, & Iacoboni, 2007). Considering this research alongside music neuroimaging research, we previously have proposed that interactions between the human mirror neuron system (MNS) and the limbic system may allow the human brain to ‘understand’ complex patterns of musical signals and provide a neural substrate for the subsequent emotional response (Molnar-Szakacs & Overy, 2006). Here, we further detail our theory of emotional responses to music—the Shared Affective Motion Experience (SAME) model—and discuss the potential implications for musical communication, therapy and education, as well as our understanding of musical experience itself.

We begin with a review of research into the mirror neuron system and its potential role in human communication and empathy. We then outline our proposed model of musical experience: Shared Affective Motion Experience (SAME), with reference to a range of research literature supporting the model. Arising from this discussion, we suggest that imitation, synchronization, and shared experience may be key aspects of human musical behavior, and thus may be key to educational and therapeutic support work

using music. In order to provide specific examples, we reflect upon two previous, small-scale studies of the potential role of music in the support of language skills. We then discuss the role of music therapy in autism, and we end with some final thoughts on the nature of musical experience, with hypotheses for future work in these areas.

Macaque Mirror Neurons and the Human Mirror Neuron System

A neural system implementing a resonance mechanism exists in the primate brain, allowing for shared representations to be established between interacting agents. At the neural level, this resonance mechanism in essence ‘mirrors’ one agent to another, allowing the observer to represent the actions of another using the same neural system as s/he uses for executing those actions. In the macaque brain, neurons with mirror properties have been described in both area F5 of the premotor cortex and in parietal area PF (Rizzolatti & Craighero, 2004). These visuomotor neurons discharge both during the performance of an action, and during the observation of another individual performing a similar action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). The monkey MNS has been shown to code motor acts as belonging to an action sequence, predicting the intended goal of a complex action (Fogassi et al., 2005), to represent actions even when the final part of the action is unseen (Umiltà et al., 2001) or when hearing sounds associated with particular actions (Kohler et al., 2002). Reciprocal connections between area F5 in the premotor cortex and parietal area PF (Luppino, Murata, Govoni, & Matelli, 1999) thus form a premotor–parietal MNS critical to action understanding and intention attribution in the macaque brain (Fogassi et al., 2005; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001).

Anatomical and cytoarchitectonic evidence support a homology between monkey premotor area F5 and parietal area PF with the posterior inferior frontal gyrus (IFG) and the rostral part of the human inferior parietal lobule (IPL), respectively (Amunts et al., 1999; Petrides & Pandya, 1997; Rizzolatti & Matelli, 2003; Tomaiuolo et al., 1999; von Bonin & Bailey, 1947; von Economo & Koskinas, 1925). Furthermore, an analogous pattern of connectivity between premotor areas and inferior parietal lobule also has been demonstrated in humans (Rushworth, Behrens, & Johansen-Berg, 2006).

While no direct evidence of mirror neurons (at the single neuron level) has yet been reported in the human

brain, Fadiga and colleagues (1995) provided the first demonstration of a neural system for coding the correspondence between observed and executed actions in humans using single-pulse transcranial magnetic stimulation (TMS). TMS was delivered to the scalp above the motor cortex while participants were either: (1) observing an experimenter perform various hand actions in front of them, or (2) during control conditions including arm movement observation, object observation, and dimming detection. Motor evoked potentials (MEPs) were recorded from extrinsic and intrinsic hand muscles. Results showed that during hand action observation, but not in the other conditions, there was an increase in the amplitude of the MEPs in the same hand muscles that are recruited when the observed action is actually performed by the observer (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). These results led the researchers to conclude that in humans there is a system matching action observation and execution, resembling the one described in the monkey. Subsequent work then confirmed these findings (Strafella & Paus, 2000) and also showed that modulation of MEPs recorded during hand action observation closely resembles the time-course of the observed action (Gangitano, Mottaghy, & Pascual-Leone, 2001).

Functional magnetic resonance imaging (fMRI) was used to show brain regions involved in action observation/execution matching by employing an imitation paradigm. Basing their predictions on neural firing rates in the monkey (Gallese et al., 1996), Iacoboni and colleagues (1999) hypothesized that areas of the human brain that show mirror properties would have a BOLD signal (blood-oxygen level dependent; indirect measure of brain activity in fMRI) increase during action observation that is approximately half that measured during action execution in the same area. In turn, imitation, which contains both an observation and execution component, would lead to a BOLD signal increase greater than either action observation or execution alone. This study found two cortical areas that showed this predicted pattern of activity, the posterior IFG and the rostral sector of the IPL (Iacoboni et al., 1999). Taken together, these TMS and fMRI data support the notion of a MNS in humans localized to premotor and inferior parietal regions of the brain, coupling action execution and action observation both in terms of the muscles involved and the temporal sequence of the action (for reviews see Iacoboni, 2009; Pineda, 2008; Rizzolatti & Craighero, 2004;).

Although still in its early stages of study, the MNS in humans already has been associated with a wide variety of higher-level functions in addition to action

representation, including imitation and imitation learning (Buccino et al., 2004; Iacoboni et al., 1999; Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005), intention understanding (Gallese & Goldman, 1998; Iacoboni et al., 2005), empathy, and theory of mind (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Leslie, Johnson-Frey, & Grafton, 2004; Williams, Whiten, Suddendorf, & Perrett, 2001), self-recognition (Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005; Uddin, Molnar-Szakacs, Zaidel, & Iacoboni, 2006), and the evolution of language (Arbib, 2005; Rizzolatti & Arbib, 1998). Furthermore, dysfunction of the MNS has been proposed as a possible cause of autism (Williams et al., 2001). Notably, all of the proposed and investigated functions of the human MNS relate to social cognitions, including social interaction, communication, and empathy. This is perhaps not surprising, given the theory that has led to the development of many of these studies supposes that mirror neurons establish a link between individuals via a simulation mechanism, whereby one uses the same neural resources to represent and understand the actions of others as to perform one's own actions (Gallese, 2003a). In other words, the theory holds that at a basic, unconscious, and automatic level, understanding the actions, intentions, and emotions of another person does not require that we explicitly *think* about them—our brain has a built-in mechanism for *feeling* them as we feel our own intentions, actions, and emotions. This representational equivalence between perception and action at the neural level may provide the basis for shared representations between self and other, enabling social communication and intersubjectivity (Gallese, 2003b). Such a neural system allows one, in essence, to experience the mind of the other, making others “like me” (Meltzoff & Brooks, 2001).

Neuroimaging evidence has provided support for this theory mostly at the level of action understanding, but there is growing evidence that emotional empathy also recruits the human MNS in creating links between self and other. Evolutionary evidence suggests that there are at least two main neural systems mediating empathy; a phylogenetically early emotional contagion system and a more advanced cognitive perspective-taking system (de Waal, 2008). The basic emotional contagion system is thought to support our ability to empathize emotionally (‘I feel how you feel’) and has been linked to the human MNS. This perception–action model posits that perception of emotion activates the neural mechanisms that are responsible for the generation of emotions, consistent with the theory of simulation: the “attempt to replicate, mimic or impersonate

the mental life of the target” (Gallese & Goldman, 1998, p. 497). Automatic activation of this motor representation in the observer, and associated autonomic and somatic responses that stem from the observed target allow responses to be prepared and executed (Preston & de Waal, 2002).

Thus, what is exciting about the discovery of mirror neurons, and a homologous system in the human brain, is the idea that the brain does not function as an isolated stimulus-response perception-action machine. Firstly, the brain’s functioning is intimately connected with the body, and secondly, the brain has evolved to interact with and to understand other brains. Properties of the human MNS thus allow us to consider social communication, and more specifically musical communication in a new light—less in terms of pitch/timbre/rhythmic patterns—and more in terms of action sequencing, goals/intentions, prediction, and shared representations.

Music, the Human Mirror Neuron System, and Shared Affective Motion Experience (SAME)

We have proposed that in its ability to integrate and represent crossmodal information, the human MNS may provide a domain-general neural mechanism for processing combinatorial rules common to language, action, and music, which in turn can communicate meaning and human affect (Molnar-Szakacs & Overy, 2006). Although it is not yet established which specific aspects of hierarchical processing of linguistic, musical, or motor syntax may recruit the human MNS, the emerging picture from the literature suggests that the MNS may provide a neural substrate for generating infinite possible combinations of hierarchical structures—intentions, goals, kinematics, and motor acts (Kilner, Friston, & Frith, 2007a)—a computation that may underlie more general cognitive abilities (Tettamanti & Weniger, 2006). Based on the integration of results from behavioral studies, neuroimaging, and primate physiology, it has been proposed that the encoding of pertinent rules in the prefrontal cortex may “guide the flow of activity along neural pathways that establish the proper mappings between inputs, internal states, and outputs needed to perform a given task” (Miller & Cohen, 2001, p. 167). Thus, the essential role of the MNS to both representing and executing intentions and actions makes it a critical link in the ‘flow of activity’ from inputs to internal states and consequent outputs. Due to its functional situation at the confluence of sensory information, top-down cognitive control, affective information,

and motor output, the human MNS seems the ideal starting point for a model that aims to explain musical sound—a stimulus that activates all of these neural systems in concert.

The Shared Affective Motion Experience (SAME) model suggests that musical sound is perceived not only in terms of the auditory signal, but also in terms of the intentional, hierarchically organized sequences of expressive motor acts behind the signal. Within a neural network involving the temporal cortex, the frontoparietal MNS, and the limbic system, auditory features of the musical signal are processed primarily in the superior temporal gyrus and are combined with structural features of the expressive *motion* information within the MNS. The anterior insula forms a neural conduit between the MNS and the limbic system (Carr et al., 2003), allowing incoming information to be evaluated in relation to the perceiver’s autonomic and emotional state, thus leading to a complex *affective* or emotional response to the music (Molnar-Szakacs & Overy, 2006). The recruitment of these neural systems in both the agent and the listener allows for a *shared affective motion experience* (SAME). Thus, the expressive dynamics of heard sound gestures can be interpreted in terms of the expressive dynamics of personal vocal and physical gestures. Below, we discuss this model further with reference to the role of the anterior insula, the hierarchical organization of motor behavior, neuroimaging evidence, the concept of music as minimized prediction error, and the implied sense of agency in music.

The Anterior Insula as a Neural Conduit

A key aspect of the SAME model is the proposed role of the anterior insula as a neural conduit between the limbic system and the MNS (Carr et al., 2003). Functional neuroimaging studies have shown recruitment of the anterior insula when an individual feels disgusted and when they see someone else expressing disgust (Wicker et al., 2003). Several studies using pinpricks, electrical shock, and thermal stimulation have examined neural activity associated with experiencing pain directly and perceiving someone else experiencing pain. All of these studies have identified recruitment of the anterior insula, supporting the notion of overlapping patterns of activation during perception *and* experience of pain, and lending support to the theory of *shared representations* during perception of emotional stimuli (Botvinick et al., 2005; Jackson, Rainville, & Decety, 2006; Lamm, Batson, & Decety, 2007; Morrison, Lloyd, di Pellegrino, & Roberts, 2004;

Morrison, Peelen, & Downing, 2007; Ochsner et al., 2008; Singer et al., 2004; Singer et al., 2006). Thus, the anterior insula may be part of the emotional contagion system (de Waal, 2008), supporting our ability to empathize emotionally—to understand human behavior using our own experiences.

Hierarchical Organization

Another key aspect of the model is its emphasis on the hierarchical organization of motor control. There is some evidence that the premotor cortex may be the source of predictive models of upcoming events in sequential processing, a feature common to language and music—but also a more general principle that underlies hierarchical processes of cognitive control and action selection associated with the frontal lobes (Molnar-Szakacs et al., 2005; Zatorre, 2005). In this hierarchy, actions are subordinate to the rules that govern them. Based on a series of repetition suppression experiments, Grafton and Hamilton (2007) proposed a motor hierarchy consisting of three principal levels: (1) outcome, (2) goal-object and (3) kinematics. This was then further developed by Kilner and colleagues (2007a, 2007b) to a four level hierarchy, including, from the highest to the lowest level of complexity: (1) The intention level that defines the long-term goal of an action; (2) The goal level that describes short-term goals that are necessary to achieve the long-term intention; (3) The kinematic level that describes the shape of the hand and the movement of the arm in space and time; (4) The muscle level that describes the pattern of muscle activity required to execute the action. Only having access to a visual representation of the kinematic level, an observer must thus be able to infer the intention behind the observed movement at either the goal level or the intention level (Kilner et al., 2007a, 2007b). They suggest that this problem is solved by the MNS using predictive coding on the basis of a statistical approach known as empirical Bayesian inference. This means that the most likely cause of an observed movement can be inferred by *minimizing the prediction error* at all cortical levels that are engaged during movement observation (Kilner et al., 2007b).

According to Kilner and colleagues (2007a):

For the MNS this means that anatomically the areas engaged by movement observation are arranged hierarchically and the anatomical connections between these areas are reciprocal. In terms of functional anatomy it means that the prediction error encoding higher-level

attributes will be expressed as evoked responses in higher cortical levels of the MNS. For action observation the essence of this approach is that, given a prior expectation about the goal of the person we are observing, we can predict their motor commands. Given their motor commands we can predict the kinematics on the basis of our own action system. The comparison of this predicted kinematics with the observed kinematics generates a prediction error. This prediction error is used to update our representation of the person's motor commands. Similarly, the inferred goals are updated by minimizing the prediction error between the predicted and inferred motor commands. By minimizing the prediction error at all the levels of the MNS, the most likely cause of the action will be inferred at all levels (intention, goal, motor and kinematic). (pp. 161-162)

According to the SAME model of affective musical experience, we predict that depending on a listener's level and kind of music training, they are able to extract information at different levels of the motor hierarchy: (1) the intention level, (2) the goal level, (3) the kinematic level, and even 4) the muscle level. For example, at one extreme, a professional musician listening to music which they know how to perform (e.g., a saxophonist listening to a saxophone piece they know well) is able to access precise information at all levels of the hierarchy, from imagined emotional intentions to specific finger movements and embouchure. At the other extreme, a musical novice listening to unfamiliar music from an unknown sound source (e.g., someone who has no knowledge of the existence of saxophones) is not able to access precise information at any level, but may feel the beat, sub-vocalize, and interpret emotional intention accordingly (e.g., fast, loud, and high in pitch might be considered emotionally charged). Thus, the resonance or simulation mechanism implemented by the human MNS matching perceived and executed actions allows a listener to reconstruct various elements of a piece of music in their own mind (bringing together auditory, motion, and emotion information), and the richness of that reconstruction depends on the individual's musical experience.

Neuroimaging Evidence for SAME

Neuroimaging support for the SAME model of musical experience can be found in a range of studies of musical processing, including evidence suggesting that the neural basis of music listening involves the outlined fronto-parietal network (Haslinger et al., 2005), the

anterior insula (Koelsch, Fritz, Muller, & Friederici, 2006) and the limbic system (Blood & Zatorre, 2001; Blood, Zatorre, Bermudez, & Evans, 1999), and that this neural network demonstrates experience-dependent plasticity and activity. In an elegant fMRI experiment, Lahav and colleagues (2007) trained nonmusicians to play a simple piano melody by ear and found that when participants simply listened to the melody without performing any movements, regions consistent with the fronto-parietal MNS were activated. Presentation of the notes of the melody in a different order activated the network to a much lesser degree, whereas listening to equally familiar but motorically unknown music did not activate this network. These findings complement previous work in the area suggesting that expert musicians activate the appropriate motor network when listening to piano music, while nonmusicians activate it to a much lesser extent (Bangert & Altenmüller, 2003; Bangert et al., 2006; Haslinger et al., 2005), but also highlights the tremendous plasticity within this system during imitative learning (Lahav et al., 2007). We can predict that nonmusicians will activate the MNS during music listening when mapping the stimulus onto basic, nonexpert musical behaviors that they are able to perform such as singing, clapping and tapping. Indeed, Koelsch and colleagues (2006) have shown that listening to pleasant music activates premotor representations for vocal sound production. However, the study by Lahav and colleagues (2007) indicates that acquiring new actions associated with sounds via imitative learning can quickly generate a functional neural link between the sound of those actions and the corresponding motor representations—opening the door to sound and music-based training and therapies.

Synchronization and ‘Minimized Prediction Error’

The role of synchronization is also clearly important in shared musical experience. It has been proposed that the evolutionary origins and motivation for the capacity to entrain to an isochronous pulse lies in the possibilities of group synchronization, signal amplification and a resulting reproductive advantage (Merker et al., 2009). The ability of humans to synchronize with a steady pulse has been demonstrated extensively under a variety of complex conditions (e.g., Large et al., 2002; Repp, 2005), with motor regions of the brain strongly implicated in the detection of pulse and metre (e.g., Grahm & Brett, 2007; Phillips-Silver & Trainor, 2007; Chen et al., 2008), and the concept of ‘prediction’ emerging as a key mechanism, from neural oscillation

and dynamic attending theories (see Large, 2008, for a review) to neural predictive coding theories (see Bengtsson et al., 2009; Vuust, Østergaard, Pallesen, Bailey, & Roepstorff, 2009). Considering these ideas and research findings within the framework of SAME, we propose that a central feature of music’s potential to create shared, affective experiences and subsequent prosocial behavior, above even the potential of speech, may be its capacity for *minimized prediction error*. At a basic level, this is evident in the simple pulse that underlies most musical behaviors, which is highly predictable and allows for spontaneous, enjoyable synchronization (e.g., group clapping, dancing). At a higher level, it is evident in our strong emotional responses to, and preferences for, extremely familiar music (e.g., Peretz et al., 1998), a phenomenon that seems to appear in early childhood and continue throughout adulthood. It might appear that this proposal contradicts the classic theory of musical expectancy, which suggests that emotional responses occur to *unexpected* features in music (Juslin, 2001; Steinbeis, Koelsch, & Sloboda, 2006; Meyer, 1956). Rather, we suggest that the capacity for music to create such a strong environment for *minimized prediction error* (and resultant affect) provides the very basis for a strong emotional response to an *unpredicted* event. While familiar, predictable music can be enjoyed to its fullest, the violation of expectancies can be more emotionally dramatic, as evidenced, for example, in the Romantic era of classical music, when composers and performers generally aimed to expand musical norms and boundaries and be as individually expressive as possible. The SAME model thus describes affective musical experience at what has been called the ‘emotional contagion’ level of emotional response, rather than, for example, ‘musical expectancy’ or ‘episodic memory’ responses (Juslin & Västfjäll, 2008), and we propose that this level may be the most effective for use in special education and therapeutic work.

Sense of Agency

A final, key aspect of the SAME model is the idea that music can convey a sense of agency—a sense of the presence of another person, their actions and their affective state. This in fact may be at the core of musical experience—not the nature of the acoustic signal per se, or the ability to perform complex motor skills, but the sense of human interaction. Some recent behavioural work supports this idea, for example, it has been shown that adults tend to synchronize more accurately with a human partner than with a recording (Himberg,

2006), while young children are more accurate when tapping along with a human partner than with a drumming machine, or a drum sound coming from a speaker (Kirschner & Tomasello, 2009a). Further indication of the social nature of musical experience comes from evidence that four-year-old children who have recently shared a musical experience (versus a story-telling experience) show more cooperative, helpful and empathetic behavior (Kirschner & Tomasello, 2009b). Similarly, it has been demonstrated that adults are significantly more cooperative in group economic exercises (to the advantage of the group), when they previously have been engaged in synchronized singing and/or moving activities, as compared to unsynchronized singing and/or moving activities (Wiltermuth & Heath, 2009). The fact that shared music-making has the power to engage neural systems supporting such strong social drives and shared, affective processes, has tremendous implications for musical communication in therapy and education.

SAME, Special Education and Therapy: Examples from Dyslexia, Aphasia and Autism

The conception of musical experience as Shared Affective Motion Experience presents an interesting and useful way in which to consider the potential role of music in therapeutic and educational work. Essentially, the model suggests that when we hear music, we hear the presence (or agency) of another person, whose actions we can interpret, imitate, and predict. We may hear a representation of their emotional state (loud/quiet, high/low, tense/relaxed), physical state (slow/fast, moving/still), technical expertise (basic, skilled, virtuosic), social status (leader, follower, sharer) and importantly, intentions (greeting, supporting, attacking). We can share a narrative of call and response, synchronization, prediction, interruption, and imitation. We can use this musical, social, playful, and imitative environment to learn to take turns, learn to listen, learn to lead, learn to count, learn songs in a new language, or simply learn to be together in a group. We can even simply listen to music and understand that this creates the feeling of being socially interactive.

When group music-making reaches a certain level of cooperation and coordination, the sense of shared purpose and togetherness can be extraordinarily powerful and even threatening (consider war songs or football fans). Whether making entirely different musical contributions to weave a musical texture, or all producing exactly the same sounds, the whole is much greater than the individual parts, from a choir to a drum circle

to the stadium bleachers. The emerging sound is a group sound, almost “larger than life,” created by a sense of shared purpose. The intentional gestures and actions are simply a means to an end: coordinated activity and the affective experience that results from the sound. The experience of being synchronized together in time, and yet with a musical, human flexibility and variety creates a powerful sense of togetherness, and demonstrates to listeners the cooperation and strength of a social group. It thus seems likely that imitation, synchronization, and affective, shared experience are key elements of musical behavior, which may be crucial or at least important in music education and music therapy. In order to discuss these ideas in context, the work of two previous, small-scale studies of the role of music in the support of language skills are presented as examples.

Rhythm-Based Language Support Activities for Children with Dyslexia

The first example involved working in the classroom with nine dyslexic boys aged 7-11 for a period of 15 weeks, with the aim of improving phonological and literacy skills. Since dyslexic children are known to have various perceptual and cognitive timing deficits (e.g., with rapid auditory temporal processing, rapid naming, rhythm copying; Tallal, Miller, & Fitch, 1993; Wolff, 2002) as well as difficulties with phonological processing (e.g., Bradley & Bryant, 1983), it was hypothesized that focusing on musical timing skills in a multisensory, musical activity program would have a positive effect on their language skills (Overy, 2000). A series of rhythm-based classroom musical activities were designed specifically for dyslexic children (see Overy, 2008), aimed at improving their rhythm skills, rapid temporal processing skills, and phonological skills. Compared to a control period of 15 weeks in which the children were simply visited in the classroom for individual reading sessions, the music lessons were found to be specifically effective in improving phonological skills and spelling skills, leading to a model of the potential role of *temporal processing* skills in the transfer from musical experience to language skills (Overy, 2003), supported and refined in further work (e.g., Tallal & Gaab, 2006). However, when considered in light of the SAME model, the nature of musical activities could be interpreted differently. For example, the activities were not simply listening activities and they were not conducted individually: they were based on group *synchronization* of rhythmic actions in a circle, various *imitation*

games, and playful, enjoyable, *shared experience* of the musical activity. Children were invited to copy rhythms, to play rhythms all together at the same time, to listen to each other's rhythms, to imagine rhythms, to perform actions to rhythms, and to create group performances. It seems possible that these elements of the intervention were as important and effective as the specific rhythmic content.

*The Use of Melodic Intonation Therapy (MIT)
in Aphasia*

It has been documented that aphasic patients sometimes can sing more fluently than they can speak (Gerstman, 1964; Geschwind, 1971), leading to the development of a speech therapy method based upon singing: Melodic Intonation Therapy (MIT; Albert, Sparks, & Helm, 1973). MIT employs a highly structured, repetitive technique in which short, high probability phrases are initially sung and tapped out syllabically by the therapist and patient together, and finally spoken by the patient alone. The effectiveness of MIT was demonstrated in a few early studies (e.g., Sparks, Helm, & Albert, 1974), and has been formally recognized by an Assessment Subcommittee of the American Academy of Neurology (1994). However, the method has not become widely used and the neural basis of its effectiveness has remained unclear (e.g. Belin et al., 1996). In this pilot study, MIT was conducted for eight weeks with a severely nonfluent aphasia patient and fMRI data were acquired pre, mid and post-therapy. Results showed improved speech output accompanied by functional differences in the neural basis of both speech and singing, including a general shift towards the right hemisphere—a pattern also shown in subsequent aphasic patients (Overy, Norton, Ozdemir, Helm-Estabrooks, & Schlaug, 2004; Overy, Norton, Ozdemir, Helm-Estabrooks, & Schlaug, 2005; Schlaug, Marchina, & Norton, 2008). This suggests that singing and rhythmic syllabic tapping were effective at supporting language skills, much like the previous study with dyslexic children. When considered in the light of the SAME model though, it is notable that the method is also highly *imitative*, *synchronized*, and an intensely *shared experience*. The technique uses short, high frequency phrases that initially are sung to the patient, then sung with the patient, and then imitated by the patient—all accompanied by synchronized tapping with physical hand contact and face-to-face eye contact. Once again, it seems possible that the imitative, synchronized, and shared elements of this music intervention method may be central to its effectiveness.

This idea is complemented by recent research by Racette and colleagues (2006), in which no evidence of preserved singing abilities in aphasic patients was identified until a paradigm was used which involved singing in synchrony ('in chorus') with another voice—singing alone was not effective (Racette, Bard, & Peretz, 2006).

Since numerous other larger-scale studies have investigated the potential for music training to support language skills, with varying degrees of effectiveness (e.g., Chan, Ho, & Cheung, 1998; Douglas & Willatts, 1994; Purnell-Webb & Spelman, 2008; Schon et al., 2008; Wong, Skoe, Russo, Dees, & Kraus, 2007), it would be interesting for future work to examine the similarities and differences between these musical interventions or training in detail, paying attention to elements such as rhythmic work, imitation, shared experience, and synchronization, to develop even more effective, evidence-based approaches.

Implications for Therapy in Autism

A developmental disorder that has had a long association with music, both anecdotal and scientific, is autism. Autism is a neurodevelopmental disorder that affects socialization and communication and causes repetitive and stereotyped behavior (Lord et al., 2000). A range of studies have shown severe impairments in socio-emotional functioning in autism, including difficulties in recognizing emotional expressions on faces (Bormann-Kischkel, Vilsmeier, & Baude, 1995; Hobson, 1986a, 1986b; Macdonald et al., 1989; Ozonoff, Pennington, & Rogers, 1990). These impairments in socio-emotional communication often lead to both physical and emotional isolation from peers, family, and community (Bauminger & Kasari, 2000). Given the presence of deficits in social behavior and communication in ASD, improvement of social functioning is of paramount importance. Music appears to have special significance to many children with autism, and has proven an effective method to establish an alternative means of social interaction and creative development. Clinical reports have shown that music created spontaneously and creatively through structured and flexible improvisation attracts attention and provokes engagement in children with ASD and promotes the development of reciprocal, interactive social communication, and play. Such an approach, based on the work of Vygotsky, emphasizes the co-construction of knowledge through joint action and discourse, mediated through the use of cultural tools and artifacts (Vygotsky, 1978).

This view emphasizes the mediating role of cultural tools such as language, and in this case musical instruments and music itself in enabling children's learning and development.

In his groundbreaking paper, Leo Kanner (1943) presented eleven case studies of children with autism in which he repeatedly mentioned musical abilities and musical interest in six of the children (Kanner, 1943). Since then, researchers have systematically studied the musical processing abilities of individuals with autism, and have shown that while language abilities may be deficient, individuals with ASD process music in similar ways to typically developed individuals. Moreover, individuals with ASD appear to show a spontaneous preference for musical over verbal stimuli (Blackstock, 1978), and it has been reported that approximately 40% of this population express a special interest in music (Heaton, 2003). These reports of autistic children's prevalent interest in music suggests that musical appreciation is unimpaired in the ASD population, and may even represent a particular strength (Kanner, 1943; Rimland & Hill, 1984). Applebaum and colleagues compared three musically naïve autistic children and three typically developing musically experienced children on their ability to sing back musical stimuli. They found that children with autism performed as well or better than their more intelligent and musically experienced controls (Applebaum, Egel, Koegel, & Imhoff, 1979). Furthermore, a number of studies have indicated that individuals with ASD show superior pitch abilities, for example Heaton and colleagues (1998) found that children with ASD performed better than control children on a pitch memory task, while performing equally well on a speech sound memory task. In fact, children with autism remembered more tone/picture pairs one week after initial exposure than controls did after 2.5 minutes (Heaton, Hermelin, & Pring, 1998)! More recently, Heaton found that children with high-functioning autism showed enhanced pitch memory and labeling (Heaton, 2003). In studies of pitch discrimination, individuals with high-functioning autism were superior to the comparison group, showing enhanced perception of local pitches (Mottron, Peretz, & Menard, 2000) and exhibiting an increased sensitivity to pitch on both discrimination and categorization tasks (Bonnel et al., 2003). Gomot and colleagues have assessed the neural correlates of altered pitch perception in children with autism using the mismatch negativity (MMN). They reported shorter MMN latency but longer duration in children with versus without autism, showing a neural correlate of this special musical ability (Gomot, Giard, Adrien, Barthelemy, & Bruneau, 2002).

The fact that individuals with ASD show such abilities in the domain of music suggests that communicative and affective qualities of music might also be appreciated and understood by this population. Such understanding is in marked contrast with the general difficulties in emotional communication and interpretation experienced by individuals with ASD in social communication (Kasari, Sigman, Mundy, & Yirmiya, 1990; Langdell, 1978).

To understand the meaning of a conversation, children automatically do what adults do—besides processing the meaning of words, they unconsciously “read” the expression on a person's face and listen to their tone of voice, then integrate that information with the context at hand to discern meaning, be it humor, anger, irony, or straightforwardness. Individuals with autism typically don't do this. They often miss the subtle meanings conveyed by a person's face and tone of voice, and thus have trouble determining the communicative intent of others. Neuroimaging studies have supported this, showing that individuals with ASD show reduced activity in the regions of the brain that respond to such cues. Research using fMRI has found various differences in individuals with ASD compared with typically developing controls, such as decreased activation of the amygdala and increased activation of temporal brain regions (Baron-Cohen et al., 1999; Critchley et al., 2000). More recent neuroimaging findings show that children with autism have virtually no activity within the MNS, clearly linking their social isolation to a neural system important for understanding the intentions, actions, and emotions of others (Dapretto et al., 2006). In a task of imitating emotional facial expressions, typically developing children activated a neural network similar to adults, including motor and premotor mirror regions, striate and extra-striate cortices, the insula, and amygdala. Unlike typically developing children however, the ASD group showed no activity in the mirror area of the premotor cortex and significantly reduced activations in the insular and amygdala regions as well. These data speak to the difficulty that individuals with ASD have in understanding the emotional states of others on a behavioral level and provide a link to a dysfunction of the neural network involving the human MNS and the limbic system that may contribute to these symptoms.

It might appear puzzling that children with ASD appear to have deficits in the functioning of their MNS, yet are able to experience the affective qualities of music. The very neural system that we are proposing as playing a central role in music perception appears to be

malfunctioning in children with ASD, so how is music able to affect these children? It is known that children with ASD are particularly drawn to abstract patterns, and the repetitive, predictable nature of musical sounds may fulfill such a role. It is also possible that through experience and familiarity with these patterns, or indeed through musical imitation and synchronization activities, the MNS may become sufficiently engaged for children with ASD to move from the appreciation of musical sound patterns to the appreciation of the agent making them; an agent who appears to behave in predictable, familiar ways that are comforting and companionable, rather than confusing.

Another related piece of the puzzle may be found in the two parallel auditory pathways that ascend through the brainstem to the cerebral cortices, known as the classical and the nonclassical ascending auditory pathways. While the neurons of the classical ascending auditory pathways respond distinctly to sound stimuli and are sharply tuned to the frequency of sounds, neurons in the nonclassical pathways are somewhat less sharply tuned (Aitkin, 1986; Aitkin, Tran, & Syka, 1994; Syka, Popelar, Kvasnak, & Astl, 2000) and their response to sound can be modulated by stimulation of the somatosensory system. This nonclassical pathway projects to secondary and association cortices and to regions of the brain that are not reached directly by the classical auditory pathways, such as structures of the limbic system, providing a subcortical route to the basolateral amygdala nuclei (LeDoux, 1992). This pathway also appears to be most important for hearing in childhood and less so after the age of twenty (Møller & Rollins, 2002). Thus, in addition to the cortical route—linking music processing to the limbic system through the human MNS—there is an alternate secondary route that brings sound to the limbic system through subcortical pathways. In fact, recent neuroimaging work investigating the neural underpinnings of the rewards of music listening has found that listening to music strongly modulates activity in a network of mesolimbic structures involved in reward processing, including the nucleus accumbens and the ventral tegmental area, as well as the hypothalamus and insula, which are thought to be involved in regulating autonomic and physiological responses to rewarding and emotional stimuli (Menon & Levitin, 2005). Indeed, MNS deficits in autism were demonstrated for recognition of emotion from faces, also impaired at the behavioral level, but the neural signatures of music listening in autism remain to be studied. At least at a behavioral level, evidence seems to indicate that autistic children can appreciate affective qualities of music. Indeed, Heaton and

colleagues demonstrated that while children with ASD typically show impairments in processing affective information within social and interpersonal domains, they did not differ from typically developing controls in their ability to perceive affect in musical excerpts (Heaton, Hermelin, & Pring, 1999). In a recent follow-up study, it was shown that active music listening is characteristic of children with autism, and that this listening results in the acquisition of culturally embedded knowledge about musical meaning. Furthermore, the findings suggest that emotion-processing deficits in the social domain do not generalize to music, and that understanding of affect in music is not only preserved, but is closely related to the level of language development, rather than diagnosis (Heaton, Hudry, Ludlow, & Hill, 2008).

Decades of music therapy research have indicated that autistic children respond well to music therapy (Alvin, 1975; Edgerton, 1994), since music appears to facilitate and support their desire to communicate (Thaut, 1984). Trevarthen (2000) has recommended the use of music therapy with autistic children to help them develop timing and motor skills, which he suggests may be important in the expression of emotional communication. Brownell (2002) has also found that the use of musically adapted storytelling is an effective and viable treatment option for modifying target behaviors of children with autism. A recent meta-analysis comparing music to no-music conditions in the treatment of children and adolescents with autism, found an overall effect size of $d = 0.77$, indicating a significant benefit of music intervention, including: increased appropriate social behaviors and decreased inappropriate, stereotypical, and self-stimulatory behaviors; increased verbalizations, gestures, and comprehension; and communicative acts and engagement with others, among other positive effects (Whipple, 2004). Several reviews of the literature have since reported consistent and significant improvements in communicative behavior and emotional responsiveness by means of music interventions (Kaplan & Steele, 2005; Whipple, 2004; Wigram & Gold, 2006). Thus, as the above evidence illustrates, children with ASD may benefit in particular from shared musical experience, since it offers opportunities for supporting the areas of social engagement and nonverbal communication in which they have some of their most profound difficulties (Wigram & Gold, 2006). We thus suggest that, whether the MNS is fully functioning or not in an individual with a disability, it can be stimulated via music to improve other skills involving the MNS, such as language skills and social skills.

Conclusion and Hypotheses

Within the framework of the SAME model, we have proposed that, regardless of specific style or function, music can provide an auditory representation of the presence of another person or social group, including both immediate and abstracted information about their physical and emotional state. In the case of pure music listening, the implication of the SAME model is that music provides not just a pleasant auditory signal, but a strong sense of an agent or agents—one is not alone when one listens to music. In the case of group musical performance, from a dyad to an orchestra, the SAME model suggests the potential for synchronized, affective experience and communication, with the flexibility for individual expression and variability. We propose that it is this ability of music to communicate social and affective information and to create the feeling of ‘being together’ that makes it so appealing to humans across all ages and cultures. We hypothesize that imitation, synchronization, and shared experience are all powerful components of successful therapeutic and educational music intervention activities. This hypothesis can be tested by comparing a variety of different approaches to music-making, such as listening versus playing, individual learning versus group learning, imitative versus rule-based learning, ingroup versus outgroup musical learning, and so forth.

We predict that the most naïve, ‘naturally occurring’ forms of music making, which have evolved as humans have evolved (e.g., learning a song in a group via imitation) will be the most universally effective, since they are naturally engaging and lead to prosocial behaviors. Those musical behaviors that have evolved as cultural artifacts (e.g., learning to play violin from notation) will have more limited (but perhaps highly specific) effects, with less generalized educational and therapeutic value. Finally, we suggest that we begin to conceive of music not only as “humanly organized sound” and “soundly organized humanity” (Blacking, 1974), but also as *shared affective motion experience, minimized prediction error*, and as an extraordinary case of *being together in time*.

Author Note

I.M.Sz. is grateful for support from the Tennenbaum Center for the Biology of Creativity at the Semel Institute for Neuroscience and Human Behavior at UCLA.

Correspondence concerning this article should be addressed to Katie Overy, Institute for Music in Human and Social Development, School of Arts, Culture and Environment, University of Edinburgh, 12 Nicolson Square, EH8 9DF, United Kingdom. E-MAIL: k.overy@ed.ac.uk

References

- AITKIN, L. M. (1986). *The auditory midbrain: Structure and function in the central auditory pathway*. Clifton, UK: Humana Press.
- AITKIN, L., TRAN, L., & SYKA, J. (1994). The responses of neurons in subdivisions of the inferior colliculus of cats to tonal, noise and vocal stimuli. *Experimental Brain Research*, *98*, 53-64.
- ALBERT, M. L., SPARKS, R. W., & HELM, N. A. (1973). Melodic intonation therapy for aphasia. *Archives of Neurology*, *29*, 130-131.
- ALVIN, J. (1975). *Music therapy for the autistic child*. London: Oxford University Press.
- AMUNTS, K., SCHLEICHER, A., BURGEL, U., MOHLBERG, H., UYLINGS, H. B., & ZILLES, K. (1999). Broca's region revisited: Cytoarchitecture and intersubject variability. *Journal of Comparative Neurology*, *412*, 319-341.
- APPLEBAUM, E., EGEL, A. L., KOEGEL, R. L., & IMHOFF, B. (1979). Measuring musical abilities of autistic children. *Journal of Autism and Developmental Disorders*, *9*, 279-285.
- ARBIB, M. A. (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences*, *28*, 105-124.
- Assessment Subcommittee of the American Academy of Neurology (1994). Assessment: Melodic intonation therapy. Report of the Therapeutics and Technology Assessment Subcommittee of the American Academy of Neurology. *Neurology*, *44*, 566.
- BANGERT, M., & ALTENMÜLLER, E. O. (2003). Mapping perception to action in piano practice: A longitudinal DC-EEG study. *BMC Neuroscience*, *4*, 26.
- BANGERT, M., PESCHEL, T., SCHLAUG, G., ROTTE, M., DRESCHER, D., HINRICHS, H., ET AL. (2006). Shared networks for auditory and motor processing in professional pianists: evidence from fMRI conjunction. *Neuroimage*, *30*, 917-926.
- BARON-COHEN, S., RING, H. A., WHEELWRIGHT, S., BULLMORE, E. T., BRAMMER, M. J., SIMMONS, A., ET AL. (1999). Social intelligence in the normal and autistic brain: An fMRI study. *European Journal of Neuroscience*, *11*, 1891-1898.
- BAUMINGER, N., & KASARI, C. (2000). Loneliness and friendship in high-functioning children with autism. *Child Development*, *71*, 447-456.
- BELIN, P., VAN ECKHOUT, P., ZILBOVICIUS, M., REMY, P., FRANÇOIS, C., GUILLAUME, S., ET AL. (1996). Recovery from

- nonfluent aphasia after melodic intonation therapy: A PET study. *Neurology*, 47, 1504-1511.
- BENGTSSON S. L., EHRSSON H. H., HASHIMOTO T., KITO T., ULLEN F., NAITO E., ET AL. (2009). Listening to rhythms activates motor and pre-motor cortices. *Cortex*, 45, 62-71.
- BLACKING, J. (1974). *How musical is man?* Seattle, WA: University of Washington Press.
- BLACKSTOCK, E. G. (1978). Cerebral asymmetry and the development of early infantile autism. *Journal of Autism and Childhood Schizophrenia*, 8, 339-353.
- BLOOD, A. J., & ZATORRE, R. J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences*, 98, 11818-11823.
- BLOOD, A. J., ZATORRE, R. J., BERMUDEZ, P., & EVANS, A. C. (1999). Emotional responses to pleasant and unpleasant music correlate with activity in paralimbic brain regions. *Nature Neuroscience*, 2, 382-387.
- BONNEL, A., MOTTRON, L., PERETZ, I., TRUDEL, M., GALLUN, E., & BONNEL, A. M. (2003). Enhanced pitch sensitivity in individuals with autism: A signal detection analysis. *Journal of Cognitive Neuroscience*, 15, 226-235.
- BORMANN-KISCHKE, C., VILSMEIER, M., & BAUDE, B. (1995). The development of emotional concepts in autism. *Journal of Child Psychology and Psychiatry*, 36, 1243-1259.
- BOTVINICK, M., JHA, A. P., BYLSMA, L. M., FABIAN, S. A., SOLOMON, P. E., & PRKACHIN, K. M. (2005). Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *NeuroImage*, 25, 312-319.
- BRADLEY, L., & BRYANT, P. E. (1983). Categorizing sounds and learning to read—A causal connection. *Nature*, 301, 419-421.
- BROWNELL, M. D. (2002). Musically adapted social stories to modify behaviors in students with autism: Four case studies. *Journal of Music Therapy*, 39, 117-144.
- BUCCINO, G., VOGT, S., RITZL, A., FINK, G. R., ZILLES, K., FREUND, H. J., ET AL. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron*, 42, 323-334.
- CARR, L., IACOBONI, M., DUBEAU, M. C., MAZZIOTTA, J. C., & LENZI, G. L. (2003). Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences*, 100, 5497-5502.
- CHAN, A. S., HO, Y. C., & CHEUNG, M. C. (1998). Music training improves verbal memory. *Nature*, 396, 128.
- CHEN, J. L., PENHUNE, V. B., & ZATORRE, R. J. (2008). Listening to musical rhythms recruits motor regions of the brain. *Cerebral Cortex*, 18, 2844-2854.
- CHARTRAND, J.-P., PERETZ, I., & BELIN, P. (2008). Auditory recognition expertise and domain specificity. *Brain Research*, 1220, 191-198.
- CRITCHLEY, H. D., DALY, E. M., BULLMORE, E. T., WILLIAMS, S. C., VAN AMELSVOORT, T., ROBERTSON, D. M., ET AL. (2000). The functional neuroanatomy of social behaviour: Changes in cerebral blood flow when people with autistic disorder process facial expressions. *Brain*, 123, 2203-2212.
- DAPRETTO, M., DAVIES, M. S., PFEIFER, J. H., SCOTT, A. A., SIGMAN, M., BOOKHEIMER, S. Y., ET AL. (2006). Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience*, 9, 28-30.
- DE NORA, T. (2000). *Music in everyday life*. Cambridge, UK: Cambridge University Press.
- DE WAAL, F. B. M. (2008). Putting the altruism back into altruism: The evolution of empathy. *Annual Review of Psychology*, 59, 279-300.
- DI PELLEGRINO, G., FADIGA, L., FOGASSI, L., GALLESE, V., & RIZZOLATTI, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91, 176-180.
- DOUGLAS, S., & WILLATTS, P. (1994). The relationship between musical ability and literacy skill. *Journal of Research in Reading*, 17, 99-107.
- DOW, R. (2008, June). *Musical gesture in electroacoustic music and performance*. Paper presented at the IMHSD Conference on Dance, Timing and Musical Gesture, Edinburgh, United Kingdom.
- EDGERTON, C. L. (1994). The effect of improvisational music therapy on the communicative behaviors of autistic children. *Journal of Music Therapy*, 31, 31-62.
- FADIGA, L., FOGASSI, L., PAVESI, G., & RIZZOLATTI, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, 73, 2608-2611.
- FOGASSI, L., FERRARI, P. F., GESIERICH, B., ROZZI, S., CHERSI, F., & RIZZOLATTI, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, 308, 662-667.
- FUJIOKA, T., ROSS, B., KAKIGI, R., PANTEV, C., & TRAINOR, L. J. (2006). One year of musical training affects development of auditory cortical-evoked fields in young children. *Brain*, 129, 2593-2608.
- GALLESE, V. (2003a). The manifold nature of interpersonal relations: The quest for a common mechanism. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 358, 517-528.
- GALLESE, V. (2003b). The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology*, 36, 171-180.
- GALLESE, V., FADIGA, L., FOGASSI, L., & RIZZOLATTI, G. (1996). Action recognition in the premotor cortex. *Brain*, 119, 593-609.
- GALLESE, V., & GOLDMAN, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 2, 493-501.

- GANGITANO, M., MOTTAGHY, F. M., & PASCUAL-LEONE, A. (2001). Phase-specific modulation of cortical motor output during movement observation. *Neuroreport*, *12*, 1489-1492.
- GERSTMAN, H. L. (1964). A case of aphasia. *Journal of Speech and Hearing Disorders*, *29*, 89-91.
- GESCHWIND, N. (1971). Current concepts: Aphasia. *New England Journal of Medicine*, *284*, 654-656.
- GOMOT, M., GIARD, M. H., ADRIEN, J. L., BARTHELEMY, C., & BRUNEAU, N. (2002). Hypersensitivity to acoustic change in children with autism: Electrophysiological evidence of left frontal cortex dysfunctioning. *Psychophysiology*, *39*, 577-584.
- GRAFTON, S. T., & HAMILTON, A. F. DE C. (2007). Evidence for a distributed hierarchy of action representation in the human brain. *Human Movement Science*, *26*, 590-616.
- GRAHN, J. A., & BRETT, M. (2007). Rhythm perception in motor areas of the brain. *Journal of Cognitive Neuroscience*, *19*, 893-906.
- HASLINGER, B., ERHARD, P., ALTENMÜLLER, E., SCHROEDER, U., BOECKER, H., & CEBALLOS-BAUMANN, A. O. (2005). Transmodal sensorimotor networks during action observation in professional pianists. *Journal of Cognitive Neuroscience*, *17*, 282-293.
- HEATON, P. (2003). Pitch memory, labelling and disembedding in autism. *Journal of Child Psychology and Psychiatry*, *44*, 543-551.
- HEATON, P., HERMELIN, B., & PRING, L. (1998). Autism and pitch processing: A precursor for savant musical ability? *Music Perception*, *15*, 291-305.
- HEATON, P., HERMELIN, B., & PRING, L. (1999). Can children with autistic spectrum disorders perceive affect in music? An experimental investigation. *Psychological Medicine*, *29*, 1405-1410.
- HEATON, P., HUDRY, K., LUDLOW, A., & HILL, E. (2008). Superior discrimination of speech pitch and its relationship to verbal ability in autism spectrum disorders. *Cognitive Neuropsychology*, *25*, 771-782.
- HIMBERG, T. (2006, August). *Co-operative tapping and collective time-keeping—Differences of timing accuracy in duet performance with human or computer partner*. Paper presented at the 9th International Conference on Music Perception and Cognition, Bologna, Italy.
- HOBSON, R. P. (1986a). The autistic child's appraisal of expressions of emotion. *Journal of Child Psychology and Psychiatry*, *27*, 321-342.
- HOBSON, R. P. (1986b). The autistic child's appraisal of expressions of emotion: A further study. *Journal of Child Psychology and Psychiatry*, *27*, 671-680.
- IACOBONI, M., MOLNAR-SZAKACS, I., GALLESE, V., BUCCINO, G., MAZZIOTTA, J. C., & RIZZOLATTI, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *Public Library of Science Biology*, *3*, e79.
- IACOBONI, M., WOODS, R. P., BRASS, M., BEKKER, H., MAZZIOTTA, J. C., & RIZZOLATTI, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526-2528.
- IACOBONI, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology*, *60*, 653-670.
- JACKSON, P. L., RAINVILLE, P., & DECETY, J. (2006). To what extent do we share the pain of others? Insight from the neural bases of pain empathy. *Pain*, *125*, 5-9.
- JUSLIN, P. N. (2001). *Communicating emotion in music performance: A review and a theoretical framework*. In P. N. Juslin & J. A. Sloboda (Eds.), *Music and emotion: Theory and research* (pp. 309-337). New York: Oxford University Press.
- JUSLIN, P. N., & VÄSTFJÄLL, D. (2008). Emotional responses to music: The need to consider underlying mechanisms. *Behavioral and Brain Sciences*, *31*, 559-575.
- KANNER, L. (1943). Autistic disturbances of affective contact. *Nervous Child*, *2*, 217-250.
- KAPLAN, R. S., & STEELE, A. L. (2005). An analysis of music therapy program goals and outcomes for clients with diagnoses on the autism spectrum. *Journal of Music Therapy*, *42*, 2-19.
- KASARI, C., SIGMAN, M., MUNDY, P., & YIRMIYA, N. (1990). Affective sharing in the context of joint attention interactions of normal, autistic, and mentally retarded children. *Journal of Autism and Developmental Disorders*, *20*, 87-100.
- KILNER, J. M., FRISTON, K. J., & FRITH, C. D. (2007a). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*, *8*, 159-166.
- KILNER, J. M., FRISTON, K. J., & FRITH, C. D. (2007b). The mirror-neuron system: A Bayesian perspective. *Neuroreport*, *18*, 619-623.
- KIRSCHNER, S., & TOMASELLO, M. (2009a). Joint drumming: Social context facilitates synchronization in preschool children. *Journal of Experimental Child Psychology*, *102*, 299-314.
- KIRSCHNER, S., & TOMASELLO, M. (2009b, September). Joint music making promotes prosocial behavior among four-year-olds. Paper presented at the Second European Conference on the Developmental Psychology of Music, Roehampton University, London.
- KOELSCH, S., FRITZ, T., DY, V. C., MULLER, K., & FRIEDERICI, A. D. (2006). Investigating emotion with music: An fMRI study. *Human Brain Mapping*, *27*, 239-250.
- KOELSCH, S., FRITZ, T., & SCHLAUG, G. (2008). Amygdala activity can be modulated by unexpected chord functions during music listening. *Neuroreport*, *19*, 1815-1819.
- KOELSCH, S., & SIEBEL, W. A. (2005). Towards a neural basis of music perception. *Trends in Cognitive Sciences*, *9*, 578-584.
- KOHLER, E., KEYSERS, C., UMILTA, M. A., FOGASSI, L., GALLESE, V., & RIZZOLATTI, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, *297*, 846-848.

- KOSKI, L., IACOBONI, M., DUBEAU, M. C., WOODS, R. P., & MAZZIOTTA, J. C. (2003). Modulation of cortical activity during different imitative behaviors. *Journal of Neurophysiology*, 89, 460-471.
- LAHAV, A., SALTZMAN, E., & SCHLAUG, G. (2007). Action representation of sound: Audiomotor recognition network while listening to newly acquired actions. *Journal of Neuroscience*, 27, 308-314.
- LAMM, C., BATSON, C. D., & DECETY, J. (2007). The neural substrate of human empathy: Effects of perspective-taking and cognitive appraisal. *Journal of Cognitive Neuroscience*, 19, 42-58.
- LANGDELL, T. (1978). Recognition of faces: An approach to the study of autism. *Journal of Child Psychology and Psychiatry*, 19, 255-268.
- LARGE, E. W., FINK, P., & KELSO, J. A. S. (2002). Tracking simple and complex sequences. *Psychological Research*, 66, 3-17.
- LEDoux, J. E. (1992). Brain mechanisms of emotion and emotional learning. *Current Opinion in Neurobiology*, 2, 191-197.
- LESLIE, K. R., JOHNSON-FREY, S. H., & GRAFTON, S. T. (2004). Functional imaging of face and hand imitation: Towards a motor theory of empathy. *Neuroimage*, 21, 601-607.
- LORD, C., RISI, S., LAMBRECHT, L., COOK, E. H., JR., LEVENTHAL, B. L., DILAVORE, P. C., ET AL. (2000). The autism diagnostic observation schedule-generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders*, 30, 205-223.
- LUPPINO, G., MURATA, A., GOVONI, P., & MATELLI, M. (1999). Largely segregated parietofrontal connections linking rostral intraparietal cortex (areas AIP and VIP) and the ventral premotor cortex (areas F5 and F4). *Experimental Brain Research*, 128, 181-187.
- MACDONALD, H., RUTTER, M., HOWLIN, P., RIOS, P., LE CONTEUR, A., EVERED, C., ET AL. (1989). Recognition and expression of emotional cues by autistic and normal adults. *Journal of Child Psychology and Psychiatry*, 30, 865-877.
- MELTZOFF, A., & BROOKS, R. (2001). "Like Me" as a building block for understanding other minds: Bodily acts, attention and intention. In B. Malle, L. Moses, & D. Baldwin (Eds.), *Intentions and intentionality: Foundations of social cognition* (pp. 171-191). Cambridge, MA: MIT Press.
- MENON, V., & LEVITIN, D. J. (2005). The rewards of music listening: Response and physiological connectivity of the mesolimbic system. *Neuroimage*, 28, 175-184.
- MERKER, B., MADISON, G., & ECKERDAL, P. (2009). On the role and origin of isochrony in human rhythmic entrainment. *Cortex*, 45, 1-17.
- MEYER L. (1956). *Emotion and meaning in music*. Chicago, IL: University of Chicago Press.
- MILLER, E. K., & COHEN, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, 24, 167-202.
- MØLLER, A. R., & ROLLINS, P. R. (2002). The non-classical auditory pathways are involved in hearing in children but not in adults. *Neuroscience Letters*, 319, 41-44.
- MOLNAR-SZAKACS, I., IACOBONI, M., KOSKI, L., & MAZZIOTTA, J. C. (2005). Functional segregation within pars opercularis of the inferior frontal gyrus: Evidence from fMRI studies of imitation and action observation. *Cerebral Cortex*, 15, 986-994.
- MOLNAR-SZAKACS, I., KAPLAN, J., GREENFIELD, P. M., & IACOBONI, M. (2006). Observing complex action sequences: The role of the fronto-parietal mirror neuron system. *NeuroImage*, 33, 923-935.
- MOLNAR-SZAKACS, I., & OVERY, K. (2006). Music and mirror neurons: From motion to 'e'motion. *Social Cognitive and Affective Neuroscience*, 1, 235-241.
- MOLNAR-SZAKACS, I., WU, A. D., ROBLES, F. J., & IACOBONI, M. (2007). Do you see what I mean? Corticospinal excitability during observation of culture-specific gestures. *Public Library of Science ONE*, 2, e626.
- MORRISON, I., LLOYD, D., DI PELLEGRINO, G., & ROBERTS, N. (2004). Vicarious responses to pain in anterior cingulate cortex: is empathy a multisensory issue? *Cognitive, Affective, and Behavioral Neuroscience*, 4, 270-278.
- MORRISON, I., PEELEN, M. V., & DOWNING, P. E. (2007). The sight of others' pain modulates motor processing in human cingulate cortex. *Cerebral Cortex*, 17, 2214-2222.
- MOTTRON, L., PERETZ, I., & MENARD, E. (2000). Local and global processing of music in high-functioning persons with autism: Beyond central coherence? *Journal of Child Psychology and Psychiatry*, 41, 1057-1065.
- OCHSNER, K. N., ZAKI, J., HANELIN, J., LUDLOW, D. H., KNIERIM, K., RAMACHANDRAN, T., ET AL. (2008). Your pain or mine? Common and distinct neural systems supporting the perception of pain in self and other. *Social Cognitive and Affective Neuroscience*, 3, 144-160.
- OVERY, K. (2000). Dyslexia, temporal processing and music: The potential of music as an early learning aid for dyslexic children. *Psychology of Music*, 28, 218-229.
- OVERY, K. (2003). Dyslexia and music. From timing deficits to musical intervention. *Annals of the New York Academy of Sciences*, 999, 497-505.
- OVERY, K. (2008). Classroom rhythm games for literacy support. In T. Miles, J. Westcombe, & D. Ditchfield (Eds.), *Music and dyslexia: A positive approach* (pp. 26-44). Chichester, England: John Wiley and Sons.
- OVERY, K., NORTON, A., OZDEMIR, E., HELM-ESTABROOKS, N., & SCHLAUG, G. (2004, October). *Activation of the left anterior inferior frontal gyrus after melodic intonation therapy in a Broca's aphasia patient*. Paper presented at the Annual Meeting of the Society for Neuroscience, San Diego, California.
- OVERY, K., NORTON, A., OZDEMIR, E., HELM-ESTABROOKS, N., & SCHLAUG, G. (2005, May). *The behavioral and neural*

- effects of Melodic Intonation Therapy—A pilot study. Poster presented at Music and Neurosciences II: From Perception to Performance, Leipzig, Germany.
- OZONOFF, S., PENNINGTON, B. F., & ROGERS, S. J. (1990). Are there emotion perception deficits in young autistic children? *Journal of Child Psychology and Psychiatry*, *31*, 343-361.
- PERETZ, I., GAUDREAU, D., & BONNEL, A.-M. (1998). Exposure effects on music preference and recognition. *Memory and Cognition*, *26*, 884-902.
- PETRIDES, M., & PANDYA, D. (1997). Comparative architectonic analysis of the human and the macaque frontal cortex. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. IX, pp. 17-58). New York: Elsevier.
- PHILLIPS-SILVER, J., & TRAINOR, L. J. (2008). Vestibular influence on auditory metrical interpretation. *Brain and Cognition*, *67*, 94-102.
- PINEDA, J. A. (2008). Sensorimotor cortex as a critical component of an 'extended' mirror neuron system: Does it solve the development, correspondence, and control problems in mirroring? *Behavioral and Brain Functions*, *4*, 47.
- PRESTON, S. D., & DE WAAL, F. B. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, *25*, 1-20.
- PURNELL-WEBB, P., & SPEELMAN, C. P. (2008). Effects of music on memory for text. *Perceptual and Motor Skills*, *106*, 927-957.
- RACETTE, A., BARD, C., & PERETZ, I. (2006). Making non-fluent aphasics speak: Sing along! *Brain*, *129*, 2571-2584.
- REPP, B. H. (2005). Sensorimotor synchronization: A review of the tapping literature. *Psychonomic Bulletin and Review*, *12*, 969-992.
- RIMLAND, B., & HILL, A. L. (1984). Idiot savants. In J. Wortis (Ed.), *Mental retardation and developmental disabilities* (Vol. 13, pp. 155-169). New York: Plenum Press.
- RIZZOLATTI, G., & ARBIB, M. (1998). Language within our grasp. *Trends in Neurosciences*, *21*, 188-194.
- RIZZOLATTI, G., & CRAIGHERO, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169-192.
- RIZZOLATTI, G., FOGASSI, L., & GALLESE, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*, 661-670.
- RIZZOLATTI, G., & MATELLI, M. (2003). Two different streams form the dorsal visual system: Anatomy and functions. *Experimental Brain Research*, *153*, 146-157.
- RUSHWORTH, M. F., BEHRENS, T. E., & JOHANSEN-BERG, H. (2006). Connection patterns distinguish 3 regions of human parietal cortex. *Cerebral Cortex*, *16*, 1418-1430.
- SARKAMO, T., TERVANIEMI, M., LAITINEN, S., FORSBLUM, A., SOINILA, S., MIKKONEN, M., ET AL. (2008). Music listening enhances cognitive recovery and mood after middle cerebral artery stroke. *Brain*, *131*, 866-876.
- SCHLAUG, G., MARCHINA, S., & NORTON, A. (2008). From singing to speaking: Why patients with Broca's aphasia can sing and how that may lead to recovery of expressive language functions. *Music Perception*, *25*, 315-323.
- SCHON, D., BOYER, M., MORENO, S., BESSON, M., PERETZ, I., & KOLINSKY, R. (2008). Songs as an aid for language acquisition. *Cognition*, *106*, 975-983.
- SINGER, T., SEYMOUR, B., O'DOHERTY, J., KAUBE, H., DOLAN, R. J., & FRITH, C. D. (2004). Empathy for pain involves the affective but not sensory components of pain. *Science*, *303*, 1157-1162.
- SINGER, T., SEYMOUR, B., O'DOHERTY, J. P., STEPHAN, K. E., DOLAN, R. J., & FRITH, C. D. (2006). Empathic neural responses are modulated by the perceived fairness of others. *Nature*, *439*, 466-469.
- SPARKS, R., HELM, N., & ALBERT, M. (1974). Aphasia rehabilitation resulting from melodic intonation therapy. *Cortex*, *10*, 303-316.
- STEINBEIS N., KOELSCH S., & SLOBODA J. A. (2006). The role of harmonic expectancy violations in musical emotions: evidence from subjective, physiological, and neural responses. *Journal of Cognitive Neuroscience*, *18*, 1380-93.
- STRAFELLA, A. P., & PAUS, T. (2000). Modulation of cortical excitability during action observation: A transcranial magnetic stimulation study. *Neuroreport*, *11*, 2289-2292.
- SYKA, J., POPELAR, J., KVASNAK, E., & ASTL, J. (2000). Response properties of neurons in the central nucleus and external and dorsal cortices of the inferior colliculus in guinea pig. *Experimental Brain Research*, *133*, 254-266.
- TALLAL, P., & GAAB, N. (2006). Dynamic auditory processing, musical experience and language development. *Trends in Neurosciences*, *29*, 382-390.
- TALLAL, P., MILLER, S., & FITCH, R. H. (1993). Neurobiological basis of speech: A case for the preeminence of temporal processing. *Annals of the New York Academy of Sciences*, *682*, 27-47.
- TETTAMANTI, M., & WENIGER, D. (2006). Broca's area: A supramodal hierarchical processor? *Cortex*, *42*, 491-494.
- THAUT, M. (1984). A music therapy treatment model for autistic children. *Music Therapy Perspectives*, *1*, 7-13.
- THAUT, M., MCINTOSH, K., MCINTOSH, G., & HOEMBERG, V. (2001). Auditory rhythmicity enhances movement and speech motor control in patients with Parkinson's disease. *Functional Neurology*, *16*, 163-172.
- TOMAIUOLO, F., MACDONALD, J. D., CARAMANOS, Z., POSNER, G., CHIAVARAS, M., EVANS, A. C., ET AL. (1999). Morphology, morphometry and probability mapping of the pars opercularis of the inferior frontal gyrus: An in vivo MRI analysis. *European Journal of Neuroscience*, *11*, 3033-3046.
- TREVARTHEN, C. (2000). Autism as a neurodevelopmental disorder affecting communication and learning in early childhood: Prenatal origins, post-natal course and effective

- educational support. *Prostaglandins, Leukotrienes and Essential Fatty Acids*, 63, 41-46.
- UDDIN, L. Q., MOLNAR-SZAKACS, I., ZAIDEL, E., & IACOBONI, M. (2006). rTMS to the right inferior parietal lobule disrupts self-other discrimination. *Social Cognitive and Affective Neuroscience* 1, 65-71.
- UDDIN, L. Q., KAPLAN, J. T., MOLNAR-SZAKACS, I., ZAIDEL, E., & IACOBONI, M. (2005). Self-face recognition activates a frontoparietal "mirror" network in the right hemisphere: An event-related fMRI study. *Neuroimage*, 25, 926-935.
- UMILTA, M. A., KOHLER, E., GALLESE, V., FOGASSI, L., FADIGA, L., KEYSERS, C., ET AL. (2001). I know what you are doing a neurophysiological study. *Neuron*, 31, 155-165.
- VON BONIN, G., & BAILEY, P. (1947). *The neocortex of macaca mulatta*. Urbana, IL: University of Illinois Press.
- VON ECONOMO, C., & KOSKINAS, G. N. (1925). *Die Cytoarchitektonik der Hirnrinde des erwachsenen Menschen [Atlas of Cytoarchitectonics of the Adult Human Cerebral Cortex]*. Berlin: Springer.
- VUUST, P., ØSTERGAARD, L., PALLESEN, K. J., BAILEY, C., & ROEPSTORFF, A. (2009). Predictive coding of music—Brain responses to rhythmic incongruity. *Cortex*, 45, 80-92.
- VYGOTSKY, L. S. (1978). *Mind and society*. Cambridge, MA: Harvard Press.
- WHIPPLE, J. (2004). Music in intervention for children and adolescents with autism: a meta-analysis. *Journal of Music Therapy*, 41, 90-106.
- WICKER, B., KEYSERS, C., PLAILLY, J., ROYET, J. P., GALLESE, V., & RIZZOLATTI, G. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron*, 40, 655-664.
- WIGRAM, T., & GOLD, C. (2006). Music therapy in the assessment and treatment of autistic spectrum disorder: Clinical application and research evidence. *Child: Care, Health and Development*, 32, 535-542.
- WILLIAMS, J. H., WHITEN, A., SUDDENDORF, T., & PERRETT, D. I. (2001). Imitation, mirror neurons and autism. *Neuroscience and Biobehavioral Reviews*, 25, 287-295.
- WILTERMUTH, S., & HEATH, C. (2009). Synchrony and cooperation. *Psychological Science*, 20, 1-5.
- WOLFF, P. H. (2002). Timing precision and rhythm in developmental dyslexia. *Reading and Writing*, 15, 179-206.
- WONG, P. C., SKOE, E., RUSSO, N. M., DEES, T., & KRAUS, N. (2007). Musical experience shapes human brainstem encoding of linguistic pitch patterns. *Nature Neuroscience*, 10, 420-422.
- ZATORRE, R. (2005). Music, the food of neuroscience? *Nature*, 434, 312-315.
- ZATORRE, R. J., CHEN, J. L., & PENHUNE, V. B. (2007). When the brain plays music: Auditory-motor interactions in music perception and production. *Nature Reviews Neuroscience*, 8, 547-558.