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The Social Neuroscience of Music: Understanding the Social Brain Through Human Song

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During the COVID-19 pandemic, we have seen that people can adapt quickly to ensure that their social needs are met after being forced to isolate and socially distance. Many individuals turned immediately to music, as evidenced by people singing from balconies, watching live concerts on social media, and group singing online. In this article, we show how these musical adaptations can be understood through the latest advances in the social neuroscience of music—an area that, to date, has been largely overlooked. By streamlining and synthesizing prior theory and research, we introduce a model of the brain that sheds light on the social functions and brain mechanisms that underlie the musical adaptations used for human connection. We highlight the role of oxytocin and the neurocircuitry associated with reward, stress, and the immune system. We show that the social brain networks implicated in music production (in contrast to music listening) overlap with the networks in the brain implicated in the social processes of human cognition—mentalization, empathy, and synchrony—all of which are components of herding; moreover, these components have evolved for social affiliation and connectedness. We conclude that the COVID-19 pandemic could be a starting point for an improved understanding of the relationship between music and the social brain, and we outline goals for future research in the social neuroscience of music. In a time when people across the globe have been unable to meet in person, they have found a way to *meet in the music*.

Public Significance Statement
This article uses individuals' musical adaptations to the COVID-19 pandemic as a launching point for a better understanding of the social neuroscience of music. The authors build on recent advances to provide a comprehensive model of the social brain regarding music and highlight the key neural and hormonal mechanisms involved in musical production.

Keywords: music, social neuroscience, social cognition, oxytocin, COVID-19

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Amid the suffering experienced during the COVID-19 pandemic, people find themselves in a quasisocial psychological experiment on a global scale[1]. Humans are intrinsically social, and feeling connected to others has profound implications for survival, health and well-being (Decety et al., 2012; Feldman, 2017; Martino et al., 2017). During the COVID-19 pandemic, we have seen that people can make quick adaptations to meet their social needs when forced to isolate to stay safe. With social distancing regulations in effect, text messaging and phone calls appear to be insufficient in meeting these social needs because people crave for face-to-face interactions. However, even solutions such as group video conferencing and Facebook Live seem to be limited in satisfying the need and desire for human connection.

What was one of the first things people did when lockdown went into effect? As first reported in Italy and then repeated in more than a dozen countries,[2] communities of people sang songs in unison from balcony to balcony (something that most in this generation have never experienced in their lifetime). However, that was only the beginning. Soon after, group singing on video conferencing platforms such as Zoom began, and digital recordings of these events went viral. Then, live concerts on social media platforms went on the airwaves, and some of the most famous musicians (who are accustomed to performing onstage for tens of thousands) began putting on living room concerts. YoYo Ma initiated #SongsofComfort; Chris Martin from Coldplay and Norah Jones took daily requests from their fans; and "One World: Together at Home" was a concert of more than 10 music legends with 270 million viewers. There have also been grassroots and small-scale community events, including neighborhood concerts (e.g., in the midwestern United States).[3] This phenomenon highlights the basic human need for social connection and bonding and the special role that participating in music plays in facilitating these bonds. At a time when people have been unable to meet in person, they appear to have found a way to *meet in the music*.

The COVID-19 pandemic is not the first crisis in which music has been used to meet the need for social connection. For example, during the 1918 Spanish flu pandemic, people participated in cultural expression by singing the blues.[4] However, the COVID-19 pandemic is occurring during a very different time period, which includes the advent of social media and increased opportunity for social connection through the Internet and virtual spaces. In this article, we argue that musical adaptations in response to the COVID-19 pandemic (even those that are not Internet-based and confined to a Western, educated, industrialized, rich, and democratic [WEIRD] audience)[5] have deep evolutionary roots and can be understood through the most recent advances in the social neuroscience of music.

This article has several objectives. First, we aim to show that the pandemic has emphasized the importance of social connection and the harmful effects of isolation and that musical adaptations during the crisis highlight the human need for social connection. Second, we aim to demonstrate that in the fields within and surrounding psychology, the pandemic is providing an opportunity to fundamentally shift the way in which we think about music and the social brain. We aim to bridge the gap between social neuroscience and the music sciences, which has yet to be formally integrated with each other. In particular, as music represents a major aspect of human connectedness with a dominant nonverbal quality, we suggest that music may introduce new insights for social neuroscience that cannot be attained purely through nonmusical paradigms. Toward that goal, we consolidate prior research from both fields to establish an initial understanding of the "social neuroscience of music." Third, we provide a working model for understanding the social brain and music, highlighting the neural networks, pathways, and hormones involved. We also outline future research goals for advancing knowledge about the social neuroscience of music. Taken together, we do not argue that the COVID-19 pandemic has produced a new human phenomenon. Rather, it has provided an opportunity to

[1] Please see Shadish et al. (2002) for details about quasi-experimental designs.

[2] https://www.theatlantic.com/photo/2020/03/music-and-encouragement-from-balconies-around-world/608668/

[3] https://www.artsmidwest.org/news/2020/08-26/global-music-month-connects-midwest-world

[4] https://www.pbs.org/newshour/arts/how-people-turned-pandemic-pain-into-song-across-history

[5] Indeed, we acknowledge that 14 million people in the United States and many more around the world do not have Internet access, mainly due to low income and have been facing particular struggles with social isolation. (https://www.lansingstatejournal.com/story/news/2020/04/14/people-without-internet-feel-cut-off-during-coronavirus-outbreak/2970203001/)

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accelerate our understanding of music, social behavior, and brain mechanisms.

The Evolutionary Origins of Music

In 1997; Steven Pinker famously referred to music as "auditory cheesecake," suggesting that music has no more of an evolutionary quality than a fine dessert (Carroll, 1998; Pinker, 1997). This statement motivated evolutionary theorists, musicologists, psychologists, and computer scientists to conduct rigorous research about the origins of music, its impact on the brain, and how it brings people together (Levitin, 2006). Today, more than 2 decades later, there are volumes of research linking music to neurobiology, human cognition, and social psychology, the inferences from which strongly oppose the auditory cheesecake notion.

Evolutionary accounts of music have long been debated. However, they have included a consensus emphasizing the role of music in social bonding (Cross & Morley, 2008). The first evolutionary observation was made by Darwin (1871), who observed how changes in vocal pitch influenced social interactions in primates. He extended these observations to humans and theorized that music played a role in human evolution, whereby courtship songs signaled evolutionary adaptative traits to potential mates. More than a century later, Miller (2000) expanded Darwin's theory about music and specified that music can signal "sexual fitness" to potential mates by transmitting information about coordination, strength, health, and intelligence. Miller suggested that this phenomenon still exists today, as evidenced by virtuosic performances of music and dance that require the ability for well-rehearsed and well-coordinated performances. Such performances signal information to others about the performer's motor abilities and capacity for learning, which are attractive qualities for a potential mate.

A related musical phenomenon that uses rhythmic coordination is clapping. During the COVID-19 pandemic, we observed clapping as a community activity. For example, in New York City, people have stood at windows and on balconies at 7 p.m. each day to communally applaud essential front-line workers returning home from work. Clapping is a rhythmic, ritualistic, and synchronized way to connect with others and produce music (e.g., clapping along to the beat of a song). Clapping within the context of applause has been shown to mimic musically synchronous patterns; in addition, this phenomenon of self-organization is observed in nonhuman species, including Asian fireflies, and in such natural processes as chemical reactions (Néda et al., 2000). Thus, during the COVID-19 pandemic, people have sought out not only communal singing but also other shared activities with fundamental musical properties.

Multiple theories propose that music originates from communication between mothers and their infants (Roederer, 1984). When mothers hum or sing melodies to their newborns, they communicate emotional information that is perceived by the child, fostering a sense of togetherness. Interpersonal synchrony between a mother and her child emerges between 3 and 6 months of life. One of its basic components is covocalization between a mother and her infant, which marks the quality of bonding between the child and the mother, as well as a setting for brain development and outcomes later in life (Feldman, 2007a, 2007b). The stronger the sense of bonding and security felt by the child, the greater the chance the child has of surviving.

Bonding as a result of music is not restricted to parent–child dyads and can also occur in large group settings and throughout the life span. Recently, we have shown that when three nonmusicians are asked to play drums together in a synchronous manner, they later report a high sense of cohesion with the group (Gordon et al., 2020). This effect of rhythmic synchronization on the group bond is also boosted by an emergence of physiological synchronization in heart function between group members as they play drums (Gordon et al., 2020). Emotional information can be shared by many people at once when they participate in making music (Roederer, 1984); and this process of a shared emotional experience can facilitate a sense of "groupishness" and cohesion (Brown, 2000).

It has also been argued that music can transmit information beyond that of emotion. Hagen and Bryant's (2003) coalition signaling hypothesis argues that music is a group-level adaptation that transmits information about the strength of coordination and cooperation in one group to other groups. The authors suggest that this group-level signaling was pivotal during hunting and gathering times, and based upon these signals, tribes could decide whether to cooperate and share resources or engage in conflict.

Theory and research into language (another evolutionarily adaptive tool) and music has also shed light on the human

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origins of music. Brown (2000) proposed that language and music coevolved, forming a "musilanguage" rather than one preceding the other. He argued that at some point in the evolutionary timeline, musilanguage split off to become what we know and recognize as language and music, each serving different cognitive and emotional functions, with music serving primarily group-level and social functions. This theory brings us back to Darwin's hypothesis about music because Darwin argued that in addition to music playing a role in sexual selection, there was an intermediate stage in human evolution with a communication system that more closely resembled music than what we refer to today as language (Masataka, 2009). Further, research into cognitive neuroscience has shown that music activates phylogenetically older areas of the brain than language does (Levitin, 2008). Such inferences cannot prove that music predated language in the human evolutionary timeline, but it does show that music is deeply seated in the recesses of the human mind.

As with many research areas in the social sciences, discussion about the origins of music can be viewed as evolutionary "just-so stories" or a byproduct rather than an adaptation. However, recent theoretical efforts have been made to overcome this critique by exploring the evolution of music in relation to credible signaling (Mehr et al., 2020) and the biology of social bonding (Savage et al., 2020). As expanded on by Mehr et al. (2020), credible signaling grounds itself in comparative literature by arguing that music has roots in primate vocalizations, including contact calls and territorial advertisements that may date back 55 to 85 million years ago. Most vocalizations in nonhumans serve as signals (Maynard Smith & Harper, 2003). For example, vocalizations in songbirds serve multiple functions, including territorial advertisements (Tobias et al., 2016), which are also evident in primates and nonprimate mammals (Bates, 1970; Gustison & Townsend, 2015; Ladich & Winkler, 2017; Wich & Nunn, 2002). It has been argued that these nonhuman vocalizations are precursors to what we refer to as music in humans (Geissmann, 2000). We can also observe traces of music-like behavior in nonhuman animals. This includes drumming-like behaviors in African apes (Goodall, 1986; Hagen & Hammerstein, 2009) and duet-like songs in birds (Hall & Magrath, 2007; Mehr et al., 2020; Schruth et al., 2019). The pivotal work by Mehr et al. (2020) provides an important conceptual thread that ties vocalizations and signaling in nonhuman primates to the social structures of music in human social groups.

Ultimately, music may not be as necessary as food and water for to biological survival, but as demonstrated by research on the origins of music and its societal functions, it may be the food and water of social psychological connectedness. The value of this statement may be intensified when humans are in isolation. Indeed, a daily diary study built on the concept of "social snacking" (i.e., overcoming feelings of loneliness by seeking out activities reminiscent of social interaction; Gardner et al., 2005; Twenge et al., 2007) showed that loneliness was associated with singing to oneself and could be assessed by the frequency with which participants talked to themselves (Jonason et al., 2008). Similarly, when viewed within the context of evolutionary theory, the musical adaptations observed during the COVID-19 pandemic may be seen as attempts to bond through communicating shared emotions, experiences, and values.

Social Cognition of Music

Building on the origins of music that are largely social, the social cognition of music investigates the social process embedded in musical perceptions, preferences, and emotions and its manifestations in daily life. Music surrounds humans from prebirth, as babies are able to recognize songs that were sung to them in utero (Partanen et al., 2013). At as early as 5 months old, infants perceive that melodies serve social functions (Mehr et al., 2016). Later, throughout children's development, the social functions served by music begin to vary based on culture: Western cultures are more individualistic, and Eastern cultures are more collectivistic (Cross & Morley, 2008). During adolescence, particularly within Western cultures, musical preferences communicate group affiliation (e.g., teenagers use music to broadcast aspects of their identity to others, and adult strangers use music as one of the first topics of conversation to get to know each other; North & Hargreaves, 1999; Rentfrow & Gosling, 2006).

The social affiliative connotations of music continue into adulthood. Historically, genres have been defined by superficial labels derived by the music industry, but through their genesis, genres have become embedded in human cultures and have thus developed social connotations. Rentfrow et al. (2011) showed that musical preferences are driven not only by acoustic attributes but also by the social connotations of genre labels. Furthermore, there is consensus that the stereotypes held about the fans of each genre contain a kernel of truth (Rentfrow & Gosling, 2006). This phenomenon contributes to a homophily mechanism by which musical preferences can be transmitted through homophonous social network ties (i.e., similar people interact with each other and develop similar preferences; Mark, 1998). Furthermore, recent research has provided evidence for a *self-congruity effect of music*, whereby musical preferences are in part driven by the similarities between the personal characteristics (e.g., personality traits) of the listener and artist. This effect extends social identity (Tajfel & Turner, 1979) and interactionist theories (Buss, 1987; Swann et al., 2002) to show that music is a social mechanism that can bond people together.

The social cognition of music can be better informed by an understanding of empathy, which plays a pivotal role in human interaction and music production[6] (Greenberg, Rentfrow et al., 2015). Empathy is the ability to understand another person's mental state (cognitive empathy) and share their emotional state (affective empathy), which often prompts caring for others (Decety & Jackson, 2004). Cognitive empathy (also referred to as "theory of mind") is based on genetics (Warrier et al., 2018), prenatal hormones (Chapman et al., 2006), and social experience (Perner et al., 1994) and has been argued to be an evolutionary trait that is highly adaptive for humans (Baron-Cohen, 1995, 2012). In relationship to music, perspective taking (the cognitive aspect of empathy) is integral in musical coordination and, in particular, rhythmic coordination (Keller et al., 2014; Novembre et al., 2014, 2019; Novembre & Keller, 2014); whereas a shared emotional experience (which is linked to the affective part of empathy) is a proposed underlying mechanism in musical interaction (Juslin & Västfjäll, 2008). These processes facilitate a person's ability to step into the shoes of the artist and tune into the emotions of other musical participants and audience members (Greenberg et al., 2015; Livingstone & Thompson, 2009). Indeed, prior research has shown that differences in musical perception, preferences, and emotion are associated with variations in empathy levels across the general population (Greenberg et al., 2015; Vuoskoski et al., 2012). Accordingly, empathy may be a cornerstone to the social benefits derived from music and its impact on the brain.

It is also important to mention the related topic of dancing, which is a coordinated physiological and motor response to auditory stimuli. Music and dance are so interconnected that there are more than 100 languages and dialects, largely in African cultures, that use the same word for both, suggesting that when there is music, there is dance, and when there is dance, there is music (Stone, 2017). Indeed, research has shown that there are individual differences in sensory-motor responses to music (as there are in dance; Martínez-Molina et al., 2019; Mas-Herrero et al., 2013) and that dance-movement therapy can improve symptoms of depression and loneliness in both individual and group settings (Koch et al., 2007; Mala et al., 2012; Meekums et al., 2015). Recently, Zoom dance classes and virtual at-home dance parties have emerged in response to the COVID-19 pandemic.[7] These online activities bring the social qualities of dancing to the forefront. The social and affiliative underpinnings of dance have been supported by previous research anchored in social network analysis to show that dancing in the classroom can promote a sense of belonging and increased acceptance of others (Kreutzmann et al., 2018).

One limitation of prior research on the social cognition of music has been its reliance on Western music and culture. Recent research has moved beyond that of the Western world to grasp the pervasiveness of musical elements across all genres. Although it is well established from social anthropology that every recorded human culture has had music (Blacking, 1995), only recently has there been empirical evidence for its universal features and variations. Recent investigations have shown that human song has cultural universal characteristics of form and function (Mehr et al., 2018, 2019). Research has also shown cultural universal characteristics and variations in pitch perception (Jacoby et al., 2019), perceptual fusion (McPherson et al., 2020), and musical emotions (Cowen et al., 2020). Together, these studies emphasized the social–cognitive basis of music in group formation, laying the foundation for future work in social neuroscience to shed light on musical adaptations in response to the current COVID-19 pandemic.

The Social Neuroscience of Music

The social musical behaviors that have been observed during the COVID-19 pandemic can be understood in part through human biology. The need to cooperate in groups has arguably fostered a uniquely human biobehavioral circuitry dedicated to being interconnected (Cacioppo & Decety, 2011; Tomasello et al., 2012). This need is evident in the stress we experience when we are isolated and the harmful consequences of loneliness (Cacioppo et al., 2009). Increasing stress due to the isolation of the COVID-19 pandemic can manifest in the brain and peripheral nervous system (e.g., cortisol levels and vagal tone). There is rapidly emerging evidence across societies and populations that the COVID-19 pandemic is detrimental to mental health—loneliness during quarantine is a prime risk factor, with specific consequences

[6] In this article, we use the terms "music production" and "music-making" interchangeably.

[7] https://www.ctvnews.ca/health/coronavirus/at-home-dance-parties-are-helping-people-shake-off-the-self-isolation-jitters-1.4860419 and https://www.latimes.com/entertainment-arts/story/2020-05-11/coronavirus-los-angeles-dance-companies-virtual-shows-online-classes-zoom

including increased stress and depressive symptoms (Barzilay et al., 2020; Brooks et al., 2020; Gao et al., 2020; Groarke et al., 2020; Gur et al., 2020; Hertz-Palmor et al., 2020; Horesh et al., 2020; Loades et al., 2020; Wang et al., 2020). Stress also drives us to bond (Norman et al., 2012; Taylor, 2006). When an infant is distressed, the caregiver's response is to provide consolation through physical proximity, touch, affect matching, and the sing-song vocalizations known as "motherese" (Gordon & Feldman, 2015). Furthermore, there is convergent evidence from randomized controlled trials (RCTs) and case-control studies showing that musical interventions (e.g., clinical music therapy) have a positive impact on reducing depressive symptoms, stress, and loneliness (Aalbers et al., 2017; Bensimon et al., 2008; Fancourt et al., 2016; Gold et al., 2009; Hole et al., 2015; Windle et al., 2020; Zhao et al., 2016). One RCT even showed that music therapy was more effective in reducing depressive symptoms than psychotherapy (Castillo-Pérez et al., 2010).

Joining together in groups is part of our neurobiological makeup. Herding in humans is considered a conserved phenomenon that has an evolutionary basis and allows us to survive and thrive. This coming together, which is often accompanied by spontaneous forms of synchronized behavior, is known to impact the brain and behavior. Synchronized behavior, which has been suggested to have evolutionarily adaptive qualities (Duranton & Gaunet, 2016), has prosocial effects linked to bonding, trust, cooperation, and the threshold for pain (Bernieri & Rosenthal, 1991; Gordon & Feldman, 2015; Hove & Risen, 2009; Rennung & Göritz, 2016). Synchrony often occurs spontaneously and has recently been proposed to be associated with predictive coding in the brain (Koban et al., 2019). Synchrony also impacts rapport and a sense of shared emotional experience and closeness (Au & Lo, 2020; Lakens & Stel, 2011; Mogan et al., 2017) and therefore is a bedrock of herding behavior. As such, several neural substrates have been suggested to comprise the herding brain, and they are thought to be linked to various behavioral manifestations of social convergence, including crowd behavior, conformity, "group mind," emotional contagion, and motor synchrony (Raafat et al., 2009; Shamay-Tsoory et al., 2019). Traditionally, the ideal setting for the social brain to thrive is during face-to-face and real-life interactions (Gordon et al., 2014). Thus, one might wonder how our herding instincts and social needs can be met with current social distancing. The solution is simple: with a tool that has been around for at least 40,000 years (Conard et al., 2009)—music.

The social neuroscience of music[8] is an emerging area of research that studies the social processes related to music and the human brain. This new area is juxtaposed with the well-established cognitive neuroscience of music, which focuses on individual-level processes related to the brain. Given that music is a social activity and that evolutionary theories favor a social understanding of music, it is surprising that the social neuroscience of music is only now finding its footing.[9] Here, we show that group singing on social media and other forms of musical activity during the COVID-19 pandemic can be understood by synthesizing current advances in the social neuroscience of music.

Neurobiological Candidates

Several neurobiological candidates comprise our model on the neural basis for social music production (as opposed to music listening). Oxytocin is a neuropeptide that plays a central role in social behavior, including pair bonding, sexual activity, trust, affiliative preferences, and parent–infant attachment (Carter, 2014). Importantly, there are substantial anatomical overlaps between the oxytocinergic pathways and dopamine neuron populations (for a review of this relationship, see Baskerville & Douglas, 2010; Gordon et al., 2011). The role of dopamine in supporting social bonds relates to its involvement in motivation and hedonic transformation, enabling us to feel good about those with whom we are bonding and linking the reward system to the social system in ways that support the formation of selective attachments (Leckman et al., 2005). Dopamine, which is synthesized in the ventral tegmental area (VTA), projects to the nucleus accumbens (NAcc) and amygdala (Amyg), as well as the prefrontal cortex (PFC). It is also well established that dopamine—the key neuromodulator of the reward system in the brain—is increased by music (Ferreri et al., 2019; Salimpoor et al., 2011). Oxytocin is synthesized in the paraventricular nucleus (PVN) of the hypothalamus and projects to key limbic sites on the dopaminergic pathway (the VTA, NAcc, and Amyg; for a schema, see Gordon et al., 2016). Oxytocin is released from areas in the hypothalamus rich in dopaminergic receptors, highlighting the regulatory role that dopamine plays, both in oxytocin release and its subsequent impact on social engagement and bonding (Baskerville et al., 2009; Buijs et al., 1984). The great overlap between dopamine and oxytocin circuitry also points to the bidirectional interactions between the two systems, both influencing and being influenced by each other during social processes (Baskerville & Douglas, 2010). We also note that the NAcc and the PFC, which receive input from dopamine and oxytocin neuron populations, are rich in receptors for both systems; hence, they have been proposed as further integrative loci that may influence socially motivated bonding (Baskerville & Douglas, 2010; Gordon et al., 2011).

[8] The term "social neuroscience of music" is a relatively new term. A Google Scholar search results in only two publications with the term in the title or abstract, one of which is coauthored by the first author of the present article.

[9] This is the same trend that developed in the 1990s to introduce the social realm in cognitive neuroscience.

Moreover, the PFC combines complex automatic social functions with complex automatic muscular functions that can be pivotal for music production.

Oxytocin seems particularly relevant when individuals are highly synchronized with each other (Feldman, 2012). However, in the absence of physical touch and in-person interactions, how is mechanism triggered? We know that oxytocin is released when listening to music (Nilsson, 2009b; Ooishi et al., 2017), and importantly, oxytocin is increased when participating in several forms of group singing, including improvisation (Good & Russo, 2021; Keeler et al., 2015; Kreutz et al., 2004; for two exceptions, see Fancourt et al., 2016, and Schladt et al., 2017) and also group drumming (Yuhi et al., 2017). In fact, entire social brain networks are implicated in music production. These very same networks are highly implicated in the social processes that are most evolved in human cognition—mentalization, empathy, and synchrony—all components of the herding brain, which is pivotal for social connection (Feldman, 2015; Shamay-Tsoory et al., 2019). If we use this knowledge to understand the brain mechanisms underlying the musical adaptations that we have seen in response to the COVID-19 pandemic, we may conclude that the group singing sessions on video conferencing may be activating oxytocin and dopaminergic pathways in the brain. Therefore, these singing sessions are likely to produce a sense of social bonding and comfort, even though the participants are physically isolated from one another.

Proposed Model

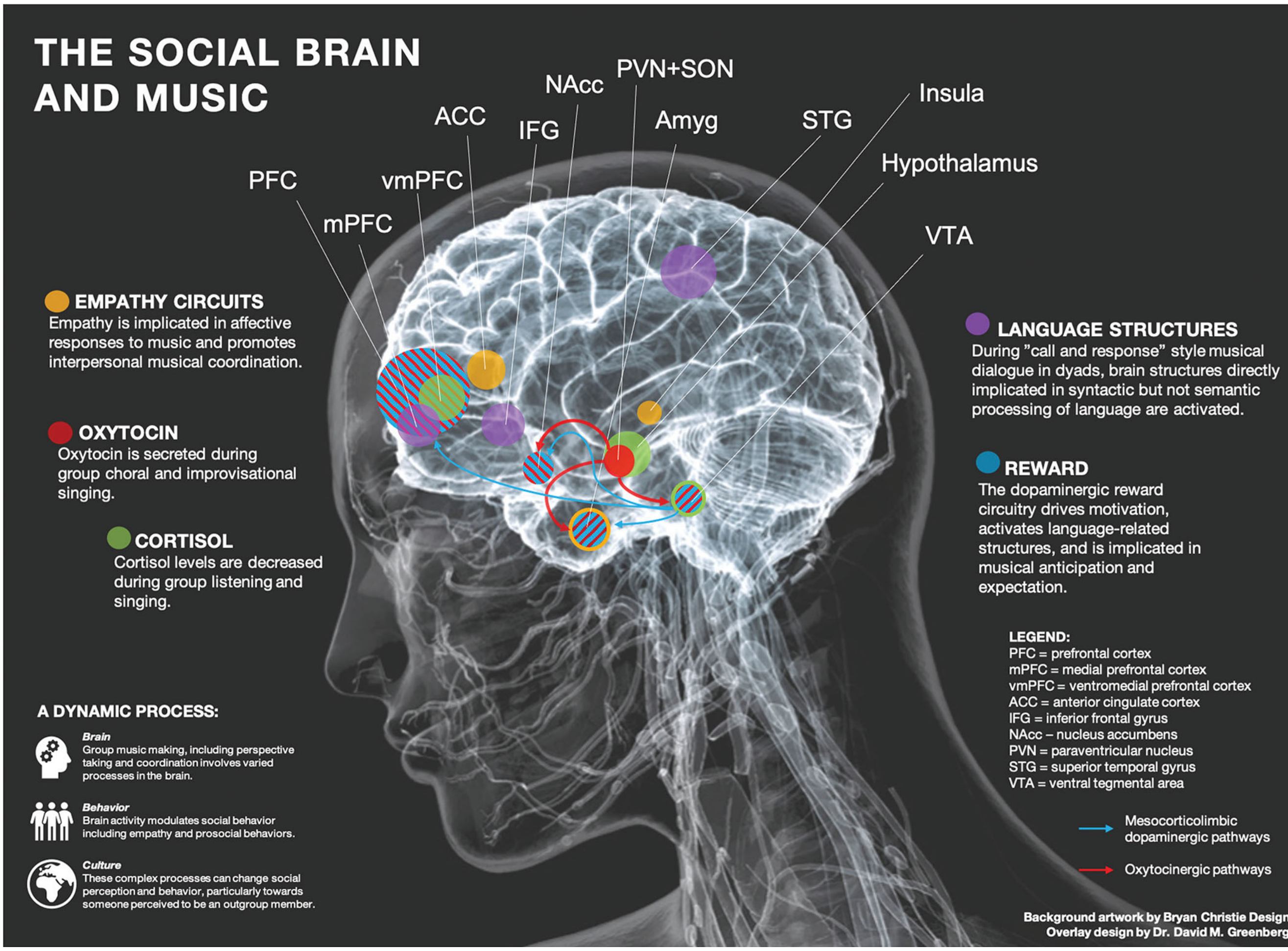
As part of the social neuroscience of music, we focused on brain networks that have been implicated in music production, as well as brain networks that are key to social functioning. Figure 1 provides a visualization of our model that illustrates the neurobiological candidates involved in the social neuroscience of music production. Empathy circuits are crucial for social understanding; they are associated with the anterior cingulate cortex (ACC), insula, and ventromedial prefrontal cortex (vmPFC). Caring for someone else (the affective part of empathy) and other prosocial behaviors can be predicted by activity in the ventral striatum (Báez-Mendoza & Schultz, 2013; Decety, 2020; Decety et al., 2009), which is also implicated in the anticipation of reward (Diekhof et al., 2012). Although there is preliminary evidence that high empathizers' enjoyment of listening to music is modulated by the supplementary motor area (SMA) and the inferior frontal gyrus (IFG; Wallmark et al., 2018), there is no such evidence for music production. Furthermore, the roles of the IFG and the mirror neuron network in empathy remain unclear (Hickok, 2014); therefore, we did not include them as part of the empathy circuit in our model.

In Figure 1, we also highlight the pathways of oxytocin and dopamine. Oxytocin can rapidly reach the PFC, which, as previously discussed, is densely interconnected with many other regions of the brain (Baskerville & Douglas, 2010; Ross & Young, 2009). Through its interaction with neural motivational factors, oxytocin can influence approach and avoidance, as well as attention to and the perception of social cues. Additionally, as previously discussed, oxytocin-dopamine interactions can enhance the feel-good aspects of connecting with others; we suggest that these interactions may explain why so many are currently looking to video platforms to sing together. There is an additional element in music that is worth noting. Similar to attachments (Gordon et al., 2011), music can induce neurochemical reactions that support the immune system and reduces stress (Chanda & Levitin, 2013). In regard to the COVID-19 pandemic, certain aspects of musical activity may be able to boost the immune system, both mitigating susceptibility to the SARS-CoV-2 virus and defending against it when contracted. Given our knowledge of the health benefits of music (e.g., postoperative recovery; Hole et al., 2015; Nilsson, 2009a), it is reasonable to suspect that music may improve physical health when used in an evidence-based, clinically informed, or medically informed way.

Language networks are also implicated in music production. For example, call-and-response-style musical dialogue (e.g., "trading fours") activates the IFG and posterior superior temporal gyrus (STG) and deactivates the angular gyrus and supramarginal gyrus (Donnay et al., 2014). This phenomenon suggests a "switch" that activates certain brain structures involved in syntactic elements in music and deactivates structures implicated in the semantic processing of language. Additionally, we highlight several brain nodes that interact with social contexts to give meaning to musical interactions. Cortisol, which is a part of the hypothalamic-pituitary-adrenal (HPA) axis regulating the stress response, is decreased during individual and group music listening and individual and group singing (Good & Russo, 2021; Ooishi et al., 2017; Wuttke-Linnemann et al., 2019). Music also decreases cortisol in the presence of stressors (Khalfa et al., 2003; Koelsch et al., 2011; Miluk-Kolasa et al., 1994). Therefore, during the COVID-19 pandemic, musical activities could improve mental health in part by decreasing cortisol in the brain, thus mitigating stress that is derived from uncertainty. Significantly, the existing evidence on cortisol suggests that both music production and listening can improve health. Therefore, listening to music during the pandemic—either on streaming platforms or by living room concerts on social media—may act as a buffer from both psychological and physiological harm.

The Amyg, in addition to its association with emotional empathy (Decety, 2010; Hurlemann et al., 2010), modulates affect and emotion regulation, and the dopaminergic reward circuitry drives motivation and learning (Arias-Carrión & Pöppel, 2007; Trifilieff et al., 2013). Interestingly, the medial prefrontal cortex (mPFC) has been associated with playing spontaneous improvisational music (as opposed to playing a

Figure 1
Neurobiological Candidates Involved in the Social Neuroscience of Music Production



Note. The neurobiological candidates involved in empathy circuits are colored orange. These include the anterior cingulate cortex (ACC), Insula, and amygdala (Amyg). Candidates involved in oxytocin signaling are colored red. These include the prefrontal cortex (PFC), nucleus accumbens (NAcc), paraventricular (PVN) and supraoptic (SON) nuclei, Amyg, and the ventral tegmental area (VTA). Candidates involved in the decrease of cortisol are colored green. These include the ventromedial prefrontal cortex (vmPFC), hypothalamus, and VTA. Candidates involved in language structures are colored purple. These include the medial prefrontal cortex (mPFC), inferior frontal gyrus (IFG), and superior temporal gyrus (STG). Candidates involved in reward are colored blue. These include the PFC, NAcc, Amyg, and VTA. Candidates that are involved in multiple processes are identified by multiple colors. The PFC, which is involved in both oxytocin signaling and reward, is identified by blue and red stripes. The NAcc, which is also involved in both oxytocin signaling and reward, is identified with blue and red stripes. The Amyg, which is involved in oxytocin signaling, reward, and empathy circuits, is identified with blue and red stripes that are surrounded by an orange circle. The VTA, which is involved in oxytocin signaling, reward, and the decrease of cortisol, is identified with blue and red stripes that are surrounded by a green circle. The three arrows that stem from the PVN identify oxytocinergic pathways and are colored red. The three arrows that stem from the VTA identify mesocorticolimbic dopaminergic pathways and are colored blue. The background artwork of the human brain was created by Bryan Christie Design. (https://bryanchristiedesign.com). The overlay design was created by Dr. David M. Greenberg. See the online article for the color version of this figure.

memorized piece; Limb & Braun, 2008). Given the associations between the mPFC and autobiographical memory, the mPFC may be an integral site in which the processing of self and group narratives may contribute to the formation of a group identity. This process may have been relevant during the COVID-19 pandemic when musicians collaborated by virtual conferencing, including on pieces that contain similar narratives and themes about the pandemic.[10] Because the act of composition involves spontaneous music production, the mPFC is likely involved, helping to fuse pandemic narratives into musical compositions. Thus, the social brain involved in music production presents a complex picture that is in need of future evaluation.

[10] The Jerusalem Youth Chorus, which includes Arab and Jewish teenagers from East and West Jerusalem, produced an online video of the song "Home" in May 2020 (https://www.timesofisrael.com/stars-join-jewish-arab-youth-chorus-to-collaborate-from-a-distance/).

Impact on Social Behavior

These underlying neural and hormonal mechanisms likely underpin observable social behaviors that are known to change after social music-making. Social behaviors related to music include group musical interaction, which can increase phenotypic empathy and cooperation in preschool and primary school children (Kirschner Sebastian & Tomasello, 2010; Rabinowitch et al., 2013). Listening to music with prosocial lyrics can promote prosocial behaviors and decrease aggression (Greitemeyer, 2009; 2011). Also, participating in musical education courses can decrease negative stereotypes (Bakagiannis & Tarrant, 2006). Furthermore, being exposed to music can improve one's implicit affiliation with outgroup members (Vuoskoski et al., 2017). A pivotal step for future research is to develop a systematic understanding of both the methods (e.g., musical synchrony) and biological mechanisms that bring people together, as well as their long-term effects on the brain. Research may include situation-specific effects and comparing brain-to-brain synchrony by hyperscanning during in-person versus socially distanced musical interactions.

Some of the most important contexts in which music can bring people together include circumstances involving different cultures and in the situations involving social division. Research has shown that oxytocin and empathy can change individuals' perceptions of an outgroup to be more favorable (Influs et al., 2019), and in one study, intranasal administration of oxytocin was found to increase empathy in Jewish Israelis toward the pain of Palestinians (Shamay-Tsoory et al., 2013). However, these paradigms have not yet been tested with music. A deeper understanding of the social neuroscience of music provides an opportunity for cultures, particularly those that have been historically in conflict, to come together and reach a greater cultural understanding through shared empathy. Due to biological survival mechanisms, the success of multicultural interactions depends on how the ingroup benefits, which is often at the expense of the outgroup (De Dreu & Kret, 2016). Given its universal qualities, music can be a promising tool to bind cultures and bridges divides.

Future Research and Applications

The proposed model of music and the social brain is limited because we do not yet have direct empirical data to support all of our hypotheses. Therefore, this article can be considered as a call for scientists across disciplines to work together to address these important questions, to design specific studies in reference to the social neuroscience of music, and to reanalyze preexisting data that are appropriate for these aims. Specifically, for COVID-19 research, we call on researchers to adopt a social neuroscience perspective to empirically study the social impact of musical adaptations on the pandemic. Below are three avenues that can be investigated. First, research should empirically investigate how social music applications can provide a sense of bonding and improve physical health at different levels of biological organization, including via the immune system. Such findings can provide a clinically and medically informed basis that can be applied in the present pandemic and in future pandemics. Research on this topic might address the following questions: Has the frequency of group musical activities changed during the pandemic compared with before the pandemic? Have musical engagement, preferences, and meanings changed during the pandemic compared with before the pandemic? What is the biological basis underlying individual musical activities compared with that underlying group musical activities, both during and before the pandemic? Second, research could be used to better understand the mechanisms underlying the social effects of music—for example, by exploring the role of brain-to-brain synchrony during musical activity and its impact on social perception and behavior (e.g., empathic concern for others) through hyperscanning. Third, research could investigate the neural basis of how music could be used to target biomarkers and craft clinical interventions for populations that have difficulty with social connection, such as autistic individuals.

Conclusion

In 1871, Charles Darwin described the faculty of music as one of the "most mysterious" with which humans are endowed (Darwin, 1871). Today, more than a century and a half later, during a global pandemic unprecedented in recorded history, people are relying on music for a sense of comfort and connection. It is essential that we better understand the powerful tool that is music—a tool that has accompanied our entire known journey as humans (Blacking, 1995). In this article, we have built upon our current knowledge about the evolutionary origins of music, social cognition, brain mechanisms, and behavior to establish an initial model representing the social neuroscience of music. Indeed, the musical responses to the social distancing regulations of the COVID-19 pandemic correspond with current advances in the social neuroscience of music. Music seems to provide a remarkably effective means of social connection in a time of social distancing, and in some contexts, it may allow our brains to feel connected even without traditional face-to-face interactions. Given the vast literature showing the effectiveness of music intervention, we suggest that making music together should be encouraged during periods of isolation to potentially enhance mental health, increase solidarity, and meet social needs.[11]

[11] To address the real-world applications of this article, we must note that the media has reported that face-to-face singing during the pandemic may have contributed to the spread of the virus. Though this claim has not yet been empirically proved or disproved, we highlight the fact that singing and other musical activities can still occur face-to-face while maintaining social distancing.

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Correction to Greenberg et al. (2021)

In the article "The Social Neuroscience of Music: Understanding the Social Brain Through Human Song," by David M. Greenberg, Jean Decety, and Ilanit Gordon (*American Psychologist*, 2021, Vol. 76, No. 7, pp. 1172–1185, https://doi.org/10.1037/amp0000819), the authors highlight the role of oxytocin in music listening and production. Although there are decades of social neuroscience research supporting the social implications of oxytocin secretion in nonmusical settings, the implications of oxytocin in musical settings remain emergent. For example, although there is indeed evidence that group music making increases oxytocin (e.g., Good & Russo, 2021), there are exceptions that show that oxytocin can decrease (e.g., Fancourt et al., 2016). In the second paragraph of the Neurobiological Candidates section and the third paragraph of the Proposed Model section, the authors note these exceptions and add additional citations in support of the modulation of both oxytocin and cortisol. They also correct their citation of Schladt et al. (2017), whom they had incorrectly cited as showing an increase in oxytocin when their results showed a decrease. The online version of this article has been corrected.

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