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The nature of music from a biological perspective

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Abstract

Music, as language, is a universal human trait. Throughout human history and across all cultures, people have produced and enjoyed music. Despite its ubiquity, the musical capacity is rarely studied as a biological function. Music is typically viewed as a cultural invention. In this paper, the evidence bearing on the biological perspective of the musical capacity is reviewed. Related issues, such as domain-specificity, innateness, and brain localization, are addressed in an attempt to offer a unified conceptual basis for the study of music processing. This scheme should facilitate the study of the biological foundations of music by bringing together the fields of genetics, developmental and comparative research, neurosciences, and musicology.
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1. Introduction

Music is generally regarded as an exquisite art form, a refined product of human culture. Such a perspective has led many cognitive scientists to characterize music as the product of a general-purpose cognitive architecture (Bregman, 1990; Handel, 1989; Krumhansl, 1990) or as assembled from other faculties that were not originally designed for its purposes (Pinker, 1997). In a sense, contemporary composers and

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ethnomusicologists reinforce this cultural perspective on music. Modern Composers argue that musical preferences are culture-specific and can be modified by exposure alone (Schönberg, 1984). Musicologists typically study music as a social construct that varies from culture to culture, rejecting cross-cultural quests for universals underlying the diversity (Blacking, 1990). Yet, common principles may underlie the world's diverse musical cultures. These principles may also be guided by innate mechanisms. In other words, music might be in our nature. The consideration of music as a biological function rather than a cultural invention is relatively recent (Wallin, Merker, & Brown, 2000) and hence, is far from established. The objective of this special issue is to consider the different perspectives and sources of evidence regarding the biological[1] foundations of music.

Humans are, by definition, biological organisms. As a consequence, anything that the human brain creates might be considered biological. However, the human brain is also a highly flexible system that can learn and invent codes and skills that can be transmitted to others by nongenetic mechanisms. The Morse code is such an invention. The question here is whether music is such a cultural product or is in ''our genes''.

Obviously, music is not a recent product. Unlike the Morse code, music was not invented at one time and one location and then spread to others. Throughout human history and across all cultures, individuals have produced and enjoyed music (Merriam, 1964). Music has emerged spontaneously and in parallel in all known human societies. Although we do not know when music emerged because there are no fossil records of singing, archeological evidence shows a continuous record of musical instruments, dating back to at least 30,000 years (D'Errico et al., 2003). Thus, music is an ancient capacity rather than the recent creation of a single intelligence. Music appears to transcend time, place, and culture.

Paradoxically, the musical capacity appears to be fully developed in only a minority of humans who can make music. Becoming a proficient musician requires thousands of hours of practice and, in most case, explicit transmission. This is often taken as an argument against the notion that the musical capacity is innately determined. If genes were responsible for the human musical capacity, then everyone should be able to engage in musical activities. In fact, everyone does. Nearly everyone can carry a tune (Dalla Bella, Giguère, & Peretz, submitted) and move to music. The problem arises from the association of music-making with an elite of professional musicians. What is usually forgotten is that music is meant for the ears of the majority. Everyone from all walks of life and all cultures is musical to some extent. Unless they are tone-deaf, all humans exhibit a precocious inclination for music. In short, music appears as natural as language is.

Music is more mysterious than language because its *raison d'être* remains unsettled. Music has no obvious utility. Music is also difficult to define. Everyone knows what music is but cannot delimit its boundaries. The concept of music is variable, and some cultures have no separate term for music, including dance and music in

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[1] The biological-cultural distinction refers to the nature-nurture, innate-acquired distinctions. I selected the term ''cultural'' because for most people, music is part of culture like other forms of arts, and has little to do with biology.

the same category. Regardless of definitional problems, the musical capacity can be studied rigorously.

Contributions from leading scientists from the life sciences, including psychology, animal biology, cognitive neuroscience, linguistics, and musicology, are gathered in the present issue. Their positions lie between two extremes. At one extreme, the capacity for acquiring musical abilities is seen as an evolutionary adaptation, shaped by natural selection and governed by genes. At the other extreme, musical abilities are viewed as the result of general-purpose learning capacities that are shaped by the environment – the "blank slate" or the tabula rasa scenario (Pinker, 2002).

Consideration of music as arising from natural endowment or from culture is not a question for academic circles alone. These opposing views of the emergence of musicality have radically different evolutionary explanations of music. They also have a profound impact on how scientists study musical abilities, how clinicians use music and assess musical abilities, and how education policy incorporates music in the curriculum.

Let me illustrate the importance of theory with the condition of tone-deafness. Tone-deafness is a life-long inability to appreciate and engage in musical activities. For almost a century, there have been voices that have denied its existence (Kazez, 1985). Some music educators, for example, consider tone-deafness as resulting from either lack of motivation or from improper training. They believe that all individuals can learn music if given the opportunity. Yet, it is estimated that 4% of the general population might suffer from tone-deafness (Kalmus & Fry, 1980). Adherents of a biological perspective would predict such a prevalence of tone-deafness, simply on the basis of natural variation, like other developmental disorders such as specific-language-impairment and developmental prosopagnosia. This could be the cost of developing a highly modularized brain for most functions including music (see below). Ignoring the existence of tone-deafness may not only ostracize those affected but may also occlude a rich source of information about the roots of musicality as well as its neural and genetic underpinnings.

Likewise, fundamental questions regarding musical abilities have been largely neglected until recently because these were considered of limited utility. For example, there is little research on critical periods (Trainor, 2005), on universals, on animal roots (Hauser & McDermott, 2003), on genes in relation to music. Nevertheless, there have been remarkable advances in uncovering the musical abilities of infants (e.g., Trehub & Hannon, this volume) and of nonmusicians in general (e.g., Bigand & Poulin-Charronat, this volume), and in exploring the musical brain (e.g., Peretz & Zatorre, 2005) and musical emotions (e.g., Juslin & Sloboda, 2001). These sources of evidence make it possible to pose questions about the nature of music.

2. How musical are humans?

Nearly half of the English and American population has learned to play an instrument in childhood, according to a recent British survey (North, Hargreaves, & O'Neill, 2000) and the American Gallup survey. Sixty-four percent of those questioned began musical training between the ages of 5 and 11, when the brain exhibits its greatest plasticity. These children spent more time in music training and practice than in second language learning, gymnastics, arts, and other educational activities. Therefore, many have been trained musically and nearly everyone remains musically inclined and avid consumer of music in one form or another.

Thus, the ordinary adult listener is a musical expert, although s/he may be unaware of this. To reveal this expertise requires the exploitation of indirect methods, as Bigand and Poulin-Charronat (this volume) illustrate. Such indirect tests reveal that nonmusicians and proficient musicians appreciate music in a very similar manner. To take an example from our own recent work (Dalla Bella & Peretz, 2005), musicians and nonmusicians alike distinguish the styles of classical music (e.g., Baroque, Romantic). All listeners, regardless of training, rated pairs of unfamiliar musical selections as more similar when their compositional styles were closer in history. Response did not require labeling, enabling us to show that discrimination of musical styles were within the reach of the average listener. Similar findings are obtained in other musical situations that are often regarded as only accessible to the musical elite. Such situations are diverse, involving the generation of expectancies based on syntax-like relationships among tones, chords, and keys (Shepard & Jordan, 1984; Tillmann, Bharucha, & Bigand, 2000), the perception of relations between theme and variations (Bigand, 1990), perception of coherence between parts of a Haydn piano sonata, and the categorization of subtle emotional expressions in music (Bigand, Vieillard, Madurell, & Marouzeau, in press).

Interestingly, and surprisingly, musicians do not necessarily have advantages over nonmusicians in production tasks. We recently observed that professional singers (and professional musicians, in general) learned a song no more readily than nonmusicians (Racette & Peretz, in press). As can be seen in Fig. 1, musicians do not recall more words or more pitches than nonmusicians in singing, despite the fact that musicians have frequently musical lessons before the age of seven and have musical structured exposure for over 15 years. Learning a popular song appears to be a basic task that everyone can master. Mere exposure with an inclination for music is sufficient.

Just as music making is not necessary to acquire basic musical performance, formal training is not required for music proficiency. A well-known case is Louis Amstrong (Collier & Person, 1983). Amstrong was poor and had to make a living very early on. Because he grew up in an area where music was used to attract prostitutes' clientele, he began singing at an early age, playing regularly with three other boys in a quatuor. By 17, Amstrong owned his own cornet, and at 19, he became a musician on a touring boat. When he left the boat, at 23, he was a professional musician. Amstrong represents a prototypical example of jazz musicians who played music without explicit tutoring. Genes or talent may contribute to exceptional careers. A love for music and a musically rich environment may play an equally important, perhaps even more important, role.

In summary, humans are musical. Musical abilities are widely distributed in the population, probably on a continuum of musicianship with poor abilities at one extreme and superior abilities at the other. The vast majority lies in the middle with

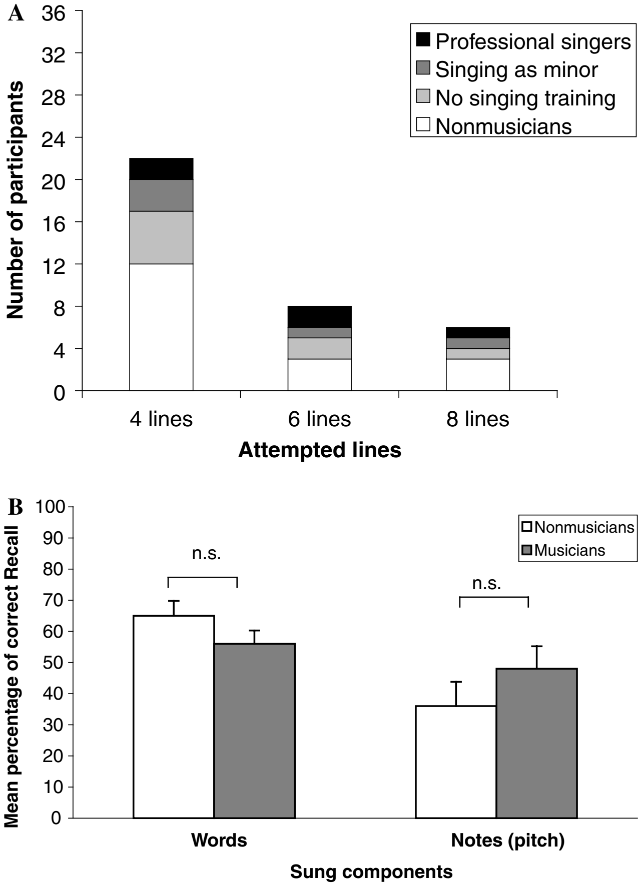

Fig. 1. (A) Proportions of nonmusicians (in white) and professional musicians (black and grey) reaching each level of song line recall; (B) mean percentage of words and notes correctly sung by nonmusicians and musicians. Note that musicians, including professional singers, did not reproduce more lines nor more correct pitches than nonmusicians (n.s.; Racette and Peretz, in press).

a common core of musical knowledge but modest production skills. For music to be appreciated, performers and listeners alike must share core processes and knowledge. Onto this core system, more elaborate knowledge and skills can be added as a result of music-making, with or without explicit tutoring. The point is that none of these would be necessary for the functionality of the core system.

Paradoxically, this is a recent discovery. Early empirical research in music focused on the musically trained individuals (Krumhansl & Kessler, 1982), and in theoretical proposals (Lerdahl & Jackendoff, 1983) on art music. Contemporary research is mostly conducted with musicians and nonmusicians. Such research uses musical material that is accessible to the majority of individuals. The focus on "functional music" is more valid psychologically and it also has cross-cultural implications.

3. What music?

By “functional” music, I endorse Nettl’s (1973) view of the kind of music that is appealing to most members of a given culture. One example is music of tribal and folk societies that engage the community as a whole. Hence, functional music can be understood by all members of the community who can participate in it as well. Such popular music, based on rock, jazz, blues, country and western, and folk music, typically has little prestige. Academic musicians often concentrate on the uniqueness of a piece of music and on its complexity of structure and texture. They may have little concern for its accessibility or approval. “Functional” or popular music incorporates very different values (see also Lerdahl, 1988; for making a similar distinction between artificial and natural compositional grammars). Uniqueness may not be important in natural or functional music. Public accessibility is the key to the survival of such music.

By studying music intended for the majority, we are closer to meeting the conditions under which people across cultures and history have interacted with music. Often the music is live, public, improvisational, spontaneous, participatory, and social (Sloboda & O’Neill, 2001). This contrasts with the prior focus on art music or contemporary music, such as serial atonal composition or quarter-tone music. Studying the music for the elite puts us at risk of focusing on a music that is ephemeral. One can make a stronger case by studying everyday music, involving lullabies (Trehub & Trainor, 1998) and adolescent music (North et al., 2000). This change in perspective is illustrated by Jackendoff and Lerdahl’s (this volume) reference to the Beatles’ songs, rather than the art or classical music that served as examples in their original publication (Lerdahl & Jackendoff, 1983).

By studying popular or functional music, we also come closer to the domain of enthnomusicologists. Ethnomusicology has contributed more than psychology to the liberation of research from “art” music, by studying any type of music in any context as worthy of interest. In principle, this discipline could provide us with a list of musical traits that are common to all known musical cultures and traits that are culture-specific. In practice, however, musicology has contributed little to the quest for universals.

3.1. Universals

Obviously, the quest for universals is seen as fruitless for those who do not consider music as biologically determined. This is the case of most ethnomusicologits who emphasize cultural diversity, in highlighting differences in historical and cultural traditions to account for the observed musical properties (Nettl, 2000). Nettl (2000), one of the leading ethnomusicologist of our time, proposes a few very basic universals: (i) vocal music; (ii) the meter or a sense of pulse, and (iii) the use of three or four pitches (usually combining major seconds and minor thirds). The only serious exception can be found in Lomax’s *Cantometric* work (Lomax, 1977, 1980). Lomax has compared the musical performance of 4000 songs from 148 geographically and culturally different world regions, on a diverse set of structural and performance properties. Lomax reduced the 148 cultures to 10 families that could be further reduced to two roots for their highly contrastive structure. One is thought to have emerged in Artic hunters and fishers and the other, among African gatherers. The first is characterized by male-dominated solos or rough unison singing, and by free or irregular rhythms. The second, in contrast, is feminized, polyvoiced, regular in rhythm, repetitious, melodically brief, cohesive, and well integrated. Clearly, the proposed universals are more tightly connected to social functions, rooted in sex role and team organization, than to melody, scale or meter. At the very least, Lomax' *cantometrics* could serve as a departure point for further study but no one has followed his lead. The scarcity of musicological research on musical universals may well arise from the resistance to consider biological determinism in music (Arom, 2000).

Psychologists were the first to point out that tonal scale systems are almost universal in the music of the world's cultures. Dowling and Harwood (1986, pp. 90–91) found only a handful of cultures in which the pitches used in singing did not provide evidence of scale steps. The overwhelming majority of cultures use stable musical scales that share several general properties: (1) discrete pitch levels, (2) octave equivalence, (3) a moderate number (usually 5–7) pitches within the octave, which are repeated through different octaves, (4) a tonal hierarchy in which certain pitches function as stable points of melodic resolution and others as contrasting unstable points (Dowling & Harwood, 1986; Dowling, 1999, 2001). Carterette and Kendall (1999) propose that the wide spectrum of musical cultures arises from the choices and elaborations of six universals. Two of these overlap with Dowling and Harwood's proposal, namely the division of the octave in scale steps and the use of a stable reference pitch. They add: (1) the notion of a deep-structural idea; (2) elementary auditory grouping; (3) reference pulses; (4) the induction of rhythmic patterns by the asymmetrical subdivision of time pulses. Similarly, but based on the remarkable similarity between infants and adults in music processing, Trehub (2000) proposes relational pitch and time features (e.g., contour); small integer frequency ratios (2:1, 3:2, 4:3); unequal scale steps; and the existence of a special genre of music for infants (e.g., lullabies) as musical universals.

Among these musical universals, the use of fixed and discrete pitches seems to be fundamental and unique to music. These pitch sets remain intact from generation to generation, even in the absence of mechanical instruments or notation. The vocal play of 6–12 month olds that leads to singing is clearly distinguishable from the vocal play associated with incipient speech, both in its use of stable pitch levels on vowels and in its rhythmic organization in terms of a regular beat pattern (Dowling, 1984, 1999, p. 611; Dowling & Harwood, 1986, pp. 147ff.). Even a simple reduction of degrees of freedom in the pitch domain does not entail limited richness of music. The eight notes of a diatonic scale can be ordered in 40,320 different ways, considering note successions without repetition. If notes are a repeat, the set expands astronomically, even without the use of concurrent notes in the form of chords or simultaneous notes. This finite pitch set enables the generation of an infinite number of musical structures. Thus, factors related to the discriminability and learnability of fixed and discrete pitches must constrain these choices. These factors may well be innate (Dowling, 2005, personal communication), so shaping all the musics of the world.

4. How unique is music processing?

The observation that music but not speech uses fixed and discrete pitch sets raises the possibility that music processing is special in recruiting unique mechanisms. Indeed, one would expect a cognitive ability that is biologically determined, to be highly specialized in its operation. Unfortunately, the question of uniqueness has fueled unresolved debates in the domain of language (Liberman & Whalen, 2000) and of face processing (Gauthier & Curby, 2005). The seeds of this debate are also present in the music domain (e.g., Howe, Davidson, & Sloboda, 1998 and see below). Therefore, it is important to address the issue by distinguishing and clarifying some concepts that are often confused when questions of specialization, domain-specificity, brain localization, and innateness are considered. These concepts were connected explicitly in Fodor's (1983) proposal on the modularity of mind, and they have been confounded in many subsequent discussions.

Domain-specificity and localization can be separated from innateness. Neural systems that are domain-specific and localized do not have to be innate because experience-dependent learning may give rise to such systems. A well-known example is reading which depends critically on phonological awareness and on the visual word form system, a left inferior temporal region specifically devoted to the processing of letter strings (Cohen et al., 2000). Yet, reading cannot be considered innate. Literacy is a recent human invention that requires explicit tutoring. Conversely, innateness can be posited for a function or a task without invoking specialized or localized mechanisms. This position[2] is taken by Trehub and Hannon (this volume). They propose that music perception is the product of general mechanisms (i.e., not domain-specific) operating in conjunction with innate motivational disposition towards music and the perpetuation of musical behavior. Hence, the evidence for domain-specificity, innateness and brain localization must be examined separately.

In contrast, Lerdahl and Jackendoff (1983; Jackendoff, 1987), Dowling (2001, 2005, personal communication) and I (Peretz, 2001a, 2001b; Peretz & Coltheart, 2003) have proposed that music processing components, especially those involved on pitch-based computations, rely on domain-specific mechanisms and specialized neural networks. A prime example of such a music-specific module is the system concerned with *tonal encoding* of pitch (see also Jackendoff and Lerdahl, this volume).

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[2] Similarly, Mari Riess Jones and her colleagues (Drake, Jones, & Baruch, 2000; Jones, 1990, 2004; Large & Jones, 1999; McAuley, Jones, Holub, Johnson, & Miller, in press) regard music processing as the result of the fine-tuning of general-purpose brain oscillations. According to this theory, infants rely mainly on relatively fast periodicities that permit initial tuning into the rapid auditory events in our environment (e.g., phonemes, brief tone patterns), and maturation generates a gradual shift to slower oscillations. Thus, learning depends on these maturational constraints and the innate tendency to rely on certain (simple) time ratios among internal attending oscillations. According to Jones' rhythmic dynamic model, music is not special because timing and rhythmic information are used in many different domains. Although the oscillations may vary across domains, with some varying in their potential for synchronizing with the external world and for synchronizing with other brain oscillations, speech and music processing both fall out of these dynamics. Music and speech reflect different ways of exploiting and refining basic innate tendencies regarding rhythmic dynamics.

Pitch variations generate a determinate scale in music but not in speech intonation contours (Balzano, 1982). Moreover, scales are universal and have unequal-spaced pitches that are organized around 5–7 focal pitches. Scale tones are not equivalent and are organized around a central tone, called the tonic. Usually, a musical piece starts and ends on the tonic. Among the other scale tones, there is a hierarchy of importance or stability. The nonscale tones are the least related and often sound anomalous. This implicit tonal knowledge allows any individual to detect a wrong note, for example, in the musical surface. It is automatic and impenetrable to top-down influences (Justus & Bharucha, 2001; Shepard & Jordan, 1984). This tonal hierarchical organization of pitch is central because it facilitates perception, memory and performance by creating expectancies about future auditory events (Tillmann et al., 2000). This ability may be lost or compromised as a consequence of brain damage (Peretz, 1993) or a congenital neural anomaly (Peretz & Hyde, 2003). In the latter case, it seems to result from a deficient connectivity with the inferior frontal gyrus (Hyde, Zatorre, Griffiths, Lerch, & Peretz, under review), a brain region that is critically involved in working memory for musical pitch (Zatorre, Evans, & Meyer, 1994) and the perception of harmonic violations (Koelsch et al., 2002; Tillmann, Janata, & Bharucha, 2003).

Thus, encoding pitch in musical contexts appears to be a domain-specific ability that can be localized in the adult brain. Furthermore the ability appears to have genetic contribution. In a recent twin study, 136 identical (monozygotic) twins and 148 fraternal (dizygotic) twins were required to detect out-of-key notes in popular melodies. Performance was more similar between identical ($r = 0.79$) than between fraternal twins ($r = 0.46$). Genetic model-fitting indicates that the influence of shared genes is more important that shared environments, with a hereditability of 70–80% (Drayna, Manichaikul, de Lange, Snieder, & Spector, 2001). Thus, the evidence is quite compelling for considering musical pitch processing as a module in Fodor's sense (as initially proposed in Peretz & Morais, 1989) because this processing component meets the requirements for domain-specificity, brain localization, and innateness. Such a strong case for the biological thesis of music cannot be made forcefully for other processing components. Hence, there is a need to examine carefully each property separately, starting with domain-specificity.

4.1. Domain-specificity

Musical pitch processing represents only one component of the myriad of possible mechanisms that contribute to musical behavior. From this perspective, it may seem odd to refer to one of these components and to designate it as domain-specific. Domain-specificity is typically reserved for a faculty. As argued elsewhere (Coltheart, 1999), however, there is no theoretical reason for excluding the concept of domain-specificity at the level of components. A domain may be as broad and general as *auditory scene analysis* and as narrow and specific as *tonal encoding of pitch*. Both subsystems perform highly specific computations and hence are domain-specific. That is, both components deal with a particular aspect of music, and they do this either exclusively or more effectively than any other mechanisms. Yet, *auditory scene* *analysis* is supposed to intervene for all incoming sounds (Bregman, 1990), whereas *tonal encoding of pitch* is exclusive to music.

Another important aspect of domain-specificity is that it can emerge from learning. The learning may be guided by innate mechanisms. It may also use general principles, by extracting, for example, statistical regularities in the environment. This possibility has been considered for the acquisition of tonal knowledge (resulting from *tonal encoding of pitch*; Krumhansl, 1990; Tillmann et al., 2000). Although *tonal encoding of pitch* is music-specific, it may be built on ''listeners' sensitivity to pitch distribution, [which is] an instance of general perceptual strategies to exploit regularities in the physical world'' (Oram & Cuddy, 1995, p.114). Thus, the input and output of the statistical computation may be domain-specific while the learning mechanism is not (Saffran, 2001). Once acquired, the functioning of the system, say the *tonal encoding of pitch*, may be modular, by encoding musical pitch in terms of keys exclusively and automatically.

The same reasoning applies to *auditory scene analysis* and to *auditory grouping* (corresponding to a musical universal according to Carterette & Kendall, 1999). The fact that these two processing components organize incoming sounds according to general Gestalt principles, such as pitch proximity, does not entail that their functioning is general-purpose and mediated by a single processing system. They need not be. For instance, it would be very surprising if visual and auditory scene analyses were mediated by the same system. Yet, both types of analyses obey to Gestalt principles. It is likely that the visual and auditory input codes adjust these mechanisms to their processing needs. Thus, the input codes may transform general-purpose mechanisms into highly specialized ones. The existence of multiple and highly specialized micro-systems, even if they function in a very similar way, is more likely, because modularization is more efficient (Marr, 1982). Fortunately, the issue is testable, especially with neuropsychological methods.

Thus, domain-specificity does not necessarily imply music-specificity. Rather music-specificity should be examined for each subsystem or processing component. In addition, domain-specificity does not necessarily require special-purpose learning mechanisms. Domain-specificity may either emerge from general learning processes or result from the nature of the input code.

The question now is to what extent music processing relies on dedicated mechanisms. We already have one plausible candidate: *tonal encoding of pitch*. Is this the only music-specific component? I will start with the evidence regarding the capacity for music as a whole. If we can find support for music-specificity at the level of whole functions, this will guide our search for its sources. Alternatively, if there is no hint of such specialization for music, then it would question the relevance of searching for distinctive roots of musicality in general, and of *tonal encoding of pitch* in music processing in particular.

4.1.1. Musical modules

What counts as music or as nonmusical is not always clear. For example, rap music may be heard as speech, and highly dissonant music as noise. Conversely, some speech streams, such as the typical auction speech, may not be considered as musical and yet this form of chanting might be processed as music. Such ambiguous signals are not problematic for the auditory system, which does not need some kind of gatekeeper to decide which part of the auditory pattern is sent to music processors and which part to the language system. All information in the auditory input, including the text and the melody of an auction chant, would be sent to all music and language processors. The intervention of music- or language-specific components is determined by the aspect of the input for which the processing component is specialized.

For example, the bids in the auction chant reach the processors concerned with encoding of speech and music. The pitch and time dynamics guide listeners' attention to the critical words that carry the bids, and the language modules are actively engaged to derive the meaning (i.e., the price). In contrast, music-specific processors, like the module for tonality, may not be very active because the chanted pitches are not fixed and hence, fail to activate a determinate key.

More critical is the possibility that music has no domain-specific component other than the module for tonality. As Pinker (1997) suggests, the music processing system might be assembled from processors that are not specialized for music, but for something else. In other words, music may act as a parasite. For example, the cognitive system may track musical pitch contour by engaging the mechanisms for speech intonation. Music may aim at the language system just as artistic masks target the face recognition system. We can stretch this argument further and envisage that music owes its efficacy in relying on the natural disposition for speech. Music may exaggerate particular speech features such as intonation and affective tone, that are so effective for bonding. In this perspective, the actual domain of the language modules is invaded (Sperber & Hirschfeld, 2004). Music could have stabilized in all cultures because music is so effective at co-opting one or several evolved modules. Multiple anchoring in several modules may even contribute to the ubiquity and power of music.

Presently, there is little support for this parasitic view because it is difficult to identify directionality. Language or music may have come first. It also requires identification of all music processing components as shared with other functions. Nevertheless, cases of isolated sparing or impairment of musical abilities suggest that some processing components must be both essential and music-specific. Otherwise, co-occurrence of disorders (co-morbidity) should be the rule. In many cases of autism, musical abilities develop spontaneously despite deficits in cognitive and affective systems. Autistic individuals are generally more apt in music than in other cognitive domains (Heaton, Hermelin, & Pring, 1998). Conversely, there are cases of musically inept individuals who have normal language and intelligence. As noted, these individuals exist and are commonly called *tone-deaf* (Grant-Allen, 1878).

The selectivity of the musical disability is remarkable. These tone-deaf individuals can have above average language skills, and may speak several languages without accent (Geschwind, 1984). However, they are unable to sing, dance or recognize music, despite formal training. This condition is termed *congenital amusia* (Peretz, 2001c). Their condition is the reverse of the musical-savant syndrome (Miller, 1989), illustrating exceptional isolation of musical modules in the developing brain.

Thus, co-morbidity between musical disorders and other deficiencies seems to be negligible, which argues against the view that *all* of music processing components are the result of general abilities or language abilities.

The best-known evidence for the autonomy of music processing comes from the study of the effects of brain accidents in adults. Brain lesions can selectively interfere with musical abilities while the rest of the cognitive system remains essentially intact (e.g., Steinke, Cuddy, & Holden, 1997). Conversely, brain damage can impair musical abilities exclusively. Patients may no longer recognize melodies (presented without words) that were highly familiar to them prior the onset of their brain damage. In contrast, they are normal at recognizing spoken lyrics (and words, in general), familiar voices and other environmental sounds (such as animal cries, traffic noises, and human vocal sounds). The deficit can be remarkably selective. For example, C.N. was unable to recognize hummed melodies from familiar songs. Yet, she could recognize the lyrics accompanying these melodies (Peretz, 1996). Moreover, C.N. could recognize the intonation patterns of speech (Patel, Peretz, Tramo, & Labrecque, 1998). The existence of a specific problem with music alongside normal functioning of other auditory abilities, including speech comprehension, is consistent with damage to processing components that are both essential to the normal process of music recognition and specific to the musical domain. This condition is termed *acquired amusia* (see Table 1, left panel).

A typical objection to this argument is that most people are amateurs at music but experts at speech. Hence, music may suffer more than speech in the case of brain insult. Thus, there would be no modules but a general auditory recognition system. When damaged, amateur abilities (e.g., music) would be more impaired than expert abilities (e.g., speech). This account predicts that it should not be possible to find brain-damaged patients who are able to recognize music whilst being unable to recognize spoken words. However, such cases exist. Nonmusicians may lose their ability to recognize spoken words while remaining able to recognize music (see Table 1, left panel).

Similar findings are obtained in production studies. Brain-damaged patients may lose the ability to sing familiar songs but retain the ability to recite the lyrics and speak with normal prosody (Peretz et al., 1994). The selectivity of the vocal deficit is not limited to amateurs. Schön, Lorber, Spacal, and Semenza (2004) recently reported the case of an opera singer who was no longer able to sing pitch intervals but who spoke with the correct intonation and expression. The reverse condition (i.e., impaired speech with intact vocal production) is more common or reported more often. Aphasic patients may remain able to sing familiar tunes and learn novel tunes; in contrast, they fail to produce intelligible lyrics in both singing and speaking (Hébert, Racette, Gagnon, & Peretz, 2003; Peretz, Gagnon, Macoir, & Hébert, 2004). The results (see Table 1, right panel) indicate that verbal production, whether sung or spoken, is mediated by the same (impaired) language output system, and that this speech route is distinct from both the (spared) musical and prosodic route. In sum, the autonomy of music and language processing extends to production tasks.

Such neuropsychological cases are the best evidence in favor of musical modules. The double dissociation implies the existence of anatomically and functionally segregated systems for music and speech in which one system can function relatively

Table 1
Case reports of selective impairment and selective sparing in the auditory recognition of words, tunes, and other meaningful sounds (left panel) and in the production of notes, words, and intonation (right panel)

Reports	Input domains			Reports	Output domains			
	Tunes	Words	Other familiar sounds		Singing		Speaking	
					Notes	Words	Intonation	Words
Peretz et al. (1994) C.N. and G.L.	–	+	+	C.N. and G.L.	–	+	(+)	+
Peretz et al. (1997). I.R.	–	+	+	I.R.	–	+	(+)	+
Griffiths et al. (1997). H.V.	–	+	+	Schön et al. (2004). 1 case	–	+	(+)	+
Wilson and Pressing (1999). H.J.	–	+	+	Murayama et al. (2004) 1 case	–	+	(+)	+
Piccirilli et al. (2000). 1 case	–	+	+					
Steinke et al. (2001). K.B.	–	+	+					
Ayotte et al. (2002). 11 cases of congenital amusia	–	+	+ (+ voices)	11 cases of congenital amusia	–	+	(+)	+
Satoh et al. (2005). 1 case	–	+	+					
Laignel-Lavastine and Alajouanine (1921). 1 case	+	–	+	Hébert et al. (2003) CC	+	–		–
Godefroy et al. (1995). 1 case, during recovery	+	–	+	Peretz et al. (2004) GD	+	–		–
Mendez (2001). N.S.	+	–	+	Racette and Peretz (in press) 8 cases	+	–		–
Metz-Lutz and Dahl (1984). G.L.	+	–	–					
Takahashi et al. (1992). 1 case	+	–	–					
Yaqub et al. (1988). 1 case	+	–	–					

+, preserved; –, impaired; (+), preserved but not formally tested.

independently of the other so that one system can be selectively impaired. Although this assumption remains unchallenged, sceptics have argued that double dissociations are not conclusive. A double dissociation can be simulated in an artificial network that is built with a unitary system. That is, lesioned connectionist systems are capable of generating double dissociations in the absence of clear separation of functions or modules (e.g., Plaut, 1995). However, there is as yet no plausible unitary explanation that can account for the pattern of selective impairment and sparing of musical abilities reported here. Thus, the evidence points to the existence of at least one distinct processing module for music.

Could this distinct processing module for music be *tonal encoding of pitch*? Indeed, there is no need for all components that contribute to the musical capacity to be specialized for music. Only one critical component, if damaged or absent, could account for all the manifestations of music-specificity that we have seen so far. Moreover, all cases of amusia that we have studied seem to suffer from a dysfunction at this level (Ayotte, Peretz, & Hyde, 2002). Every individual who is suffering from congenital amusia fails to notice an out-of-key note that is inserted in a highly tonal melody. This difficulty in detecting pitch-related changes extends to congenital amusics' inability to perceive dissonance (Ayotte et al., 2002; Peretz, 2001a, 2001b, 2001c). Moreover, all amusic cases who suffer from a recognition or production disorder as a consequence of brain damage (see Table 1) are systematically impaired on the pitch dimension, not on the time dimension. However, the origin of the deficit need not be *tonal encoding of pitch*. An impairment in *tonal encoding of pitch* may arise as a consequence of a lower level deficiency, involving fine-grained pitch analysis (Hyde & Peretz, 2004) or pitch direction extraction (Foxton, Dean, Gee, Peretz, & Griffiths, 2004).

In principle, an impairment in rhythmic processing, particularly in rhythmic entrainment, should also be detrimental to musical activities. Rhythm appears as the essence of music. Moreover, rhythm disorders can occur independently from pitch disorders (Di Pietro, Laganaro, Leeman, & Schnider, 2004), arguing for the functional separability of rhythm and pitch-based processing of music. It remains to determine to what extend these rhythmic disorders affect musical abilities exclusively.

Thus, the current evidence points to musical capacity as being the result of a confederation of functionally isolable modules. To date, however, only abilities related to fine-grained processing of pitch appear to be uniquely engaged in music. The music-specificity of many other modules remain to be examined (see Peretz & Coltheart, 2003). Nevertheless, the current evidence, essentially based on pitch-related processes, argues against the view that the musical capacity is the result of general-purpose procedures.

4.2. Innateness

It is trivial to claim that no amount of training can make a Mozart. To be a Mozart entails to be born Mozart. But what does it mean to be born Mozart (Arshavsky, 2003)? The innateness of the musical capacity is taken for granted, at least among nonscientists. As noted, domain-specificity does not entail that musical capacity is coded in the genome. Reading the alphabet recruits whole word recognition mechanisms involving mostly the left inferior temporal area, and yet reading modules could not possibly be in the human genome. Literacy is a recent invention and is not ubiquitous. In contrast, music possesses all the properties that make its innate origins a legitimate question for research. Therefore, I will discuss here what we know (or do not yet know) about the genetic underpinnings of musical behavior.

The spur for this quest and above all, its feasibility come from the recent discovery of the FOXP2 gene, as related to speech. The discovery began with the study of the KE family of language-impaired individuals. The KE family has three generations, in which half the members suffer from a speech and language disorder (Hurst, Baraister, Auger, Graham, & Norell, 1990). Around half of the children of affected individuals have the disorder, whereas none of the children of unaffected individuals do. The pedigree points to a mutation on a dominant chromosome. This inherited disorder has been linked to a small segment of chromosome 7 (Fisher, Vargha-Khadem, Watkins, Monaco, & Pembrey, 1998; Hurst et al., 1990). The chance discovery of an unrelated individual with a similar speech deficit has allowed the narrowing down of the disorder down to a mutation of a specific gene, named FOXP2 (Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001). This gene seems to play a causal role in the development of normal brain circuitry that underlies language and speech (Marcus & Fisher, 2003).

The speech disorder experienced by the KE family is not language-specific. It also affects oral movements. Hence, we may wonder if the mutation of the FOXP2 gene also affects vocal abilities such as singing. It does. Alcock, Passingham, Watkins, and Vargha-Khadem (2000) tested nine affected members of the KE family and showed that they were impaired in rhythm production (and perception) while they performed as well as normal controls in melody (pitch-based) production (and perception). Hence, FOXP2 participates to other skills, such as rhythm. It is tempting to argue that the mutated FOXP2 may compromise a common underlying cause for the speech and rhythm deficits, such as a deficit in sequential temporal processing. Indeed, pitch-based musical abilities seem governed by distinct genetic factors.

As noted, the opposite pattern – preserved rhythm but impaired pitch – characterizes some “tone-deaf” individuals (e.g., Ayotte et al., 2002). Individuals affected with congenital amusia are impaired on all tasks that require sequential organization of pitch but do not necessarily have problems with time intervals (Hyde & Peretz, 2004). This pitch deficit is most apparent, and even diagnostic of their condition, when amusics are required to detect an anomalous (i.e., an out-of-key) note in a conventional melody (Ayotte et al., 2002; Hyde & Peretz, 2005). This musical pitch disorder seems family-based. As can be seen in Fig. 2, all our amusic subjects have at least one first-degree relative who is similarly impaired whereas only one member of the control families tested so far have such a disorder. Therefore, by observing how the musical pitch disorder is distributed in the families of our pool of amusics, we can obtain valuable information regarding its genetic origins. This study is currently under progress in our laboratory. Second, the test that allows the diagnosis of congenital amusia, the anomalous pitch test, has been shown to tap a

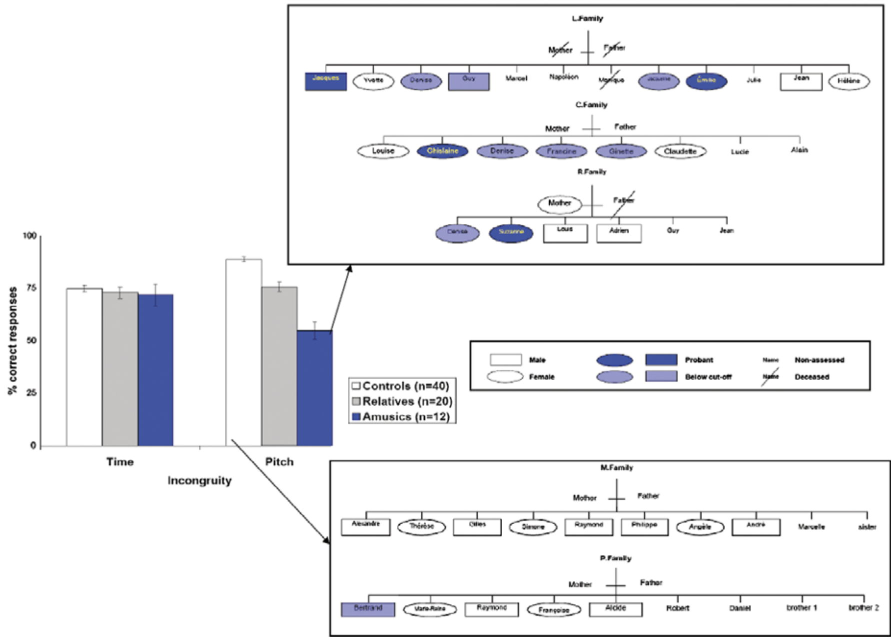

Fig. 2. Amusics and their first degree relatives were significantly impaired in the detection of a pitch anomaly in melodies as compared to their matched controls (see left graph). In contrast, all subjects performed similarly in the detection of time delays inserted in the same melodies. This pattern is supported by a significant interaction between Group and Condition ($F(2,69) = 20.45$, $p < .001$). As can be seen in the pedigree of three representative amusic (proband) families (top) and two representative control families (bottom), the presence of a musical pitch disorder runs in families; a pitch deficit corresponds to a score that lies 2 *SD* below the mean of the control group (below cut-off). Moreover, not all family members are affected, discarding an environmental factor as a plausible cause.

genetically transmitted ability (Drayna et al., 2001). Thus, the available data are compatible with the idea that there are two innate factors guiding the acquisition of the musical capacity, with one related to temporal sequencing and the other, pitch sequencing.

It is important to emphasize that twin and family aggregation studies provide an estimate of heritability but do not reveal the genetic etiology. It is a correlation, not a causal relation between genes and the musical test. The anomalous pitch detection test may be heritable in the absence of any *specific* genetic etiology. First, fine-grained pitch discrimination abilities that are recruited by this test might not be specific to music. For example, the pitch deficit might be due to slight rigidity of the basilar membrane (the part of the ear that transforms physical vibrations in electrical activity). In that case, the genetic cause may be related to cell elasticity, not musical capacity. Yet, explaining the disorder in terms of a mutated "elasticity" gene would still be valuable because it provides an entry-point into understanding the genetic factors that contribute to the capacity for music, and not speech. Indeed, the congenital amusic individuals identified to date have no speech disorder.

In sum, finding the particular gene or genes for a behavioral trait is a challenging task. All human traits (including reading) are influenced by genetic factors. The question is not so much whether there are genetic influences on behavior but rather how much influence there is and how genes work to shape this behavior (Bouchard, 2004). Hence, the goal of future research is to describe the specific molecular mechanism that explains how genes interact with the environment to produce musical capacity. The initial steps in this direction have been successfully undertaken with FOXP2 and speech, which implies that the origin of the capacity for music may be within reach.

4.2.1. Predispositions for music

Neurologically intact individuals appear to be born musical. Before one year of age, the prelinguistic infant displays remarkable musical abilities that are similar, in many respects, to those of adults (Trehub, 2001). Like mature listeners, infants display sensitivity to musical scales and to temporal regularity. Six to nine-month-old infants process consonant intervals better than dissonant intervals (Schellenberg & Trehub, 1996) and exhibit enhanced sensitivity for musical scales with unequal steps (Trehub, Schellenberg, & Kamenetsky, 1999). The latter does not seem to arise from exposure to ambient music because the bias is observed for invented musical scales, as long as these have unequal steps. Hence, infants are perceptually equipped for assimilating the pitch structure of any musical culture. On the time dimension, infants prefer music that is subject to an isochronous temporal pulse (Demany, McKenzie, & Vurpillot, 1977). They are also biased toward perceiving regularity and metricality, in exhibiting sensitivity to slight disruptions of these (Drake, 1998). The fact that all these perceptual skills appear precociously, with no obvious function in language, points to the existence of music predispositions (Trehub, 2001).

However, precocious abilities could be the result of formidable plasticity in the infant brain. The human brain is thought to be born prematurely, in the sense of being extremely plastic with little pre-wiring. There is a prolonged postnatal period during which interaction with the environment can shape the brain's circuitry (Johnson, 2001). A striking demonstration of this plasticity is the observation that congenitally blind individuals use their visual cortex for auditory localization (Röder et al., 1999). Moreover, there is little cost associated to this re-wiring of the pathways into the visual areas. Congenitally blind people have also higher auditory acuity in both pitch and time than normals (Gougoux et al., 2004). Similarly, simple exposure to music, or musical incentives, may create connections and networks that are adjusted to its needs, without reliance on inborn mechanism.

Such brain plastic responses are plausible in the case of music. Music appears to be important to infants. From birth, caregivers around the world sing to their infants, intuitively using this means to regulate the infants' state (e.g., comforting), to get their attention and to share emotions. The caregiver mirrors infants' abilities and preferences by singing more slowly, at a higher pitch level, with exaggerated rhythm, and in a more loving or emotionally engaging manner than when singing alone (Trainor, Clark, Huntley, & Adams, 1997). Responsiveness to such infant-directed singing appears inborn. Two-day-old hearing infants, born from congenitally deaf parents (who sign and do not sing or speak), prefer infant-directed to adult-directed singing (Masataka, 1999).

Caregivers also speak to infants in a sing-song manner, so-called ‘baby-talk’ or ‘motherese’. Nevertheless, infants seem to prefer (infant-directed) singing to speech. Nakata and Trehub (2004) exposed six-month-old infants to videotaped performances of their own mothers. Infants showed more sustained attention and engagement to mothers’ singing episodes than to their speaking episodes. The observation that emotional communication through singing is so powerful for infants, even for hearing newborns of deaf parents, points to biological preparedness.

As proposed by Trehub and Hannon (this volume), the propensity to listen to music may be innate. This innate “music-detector” system would direct infants’ attention toward music. This system could be coupled with a general-purpose system that acquires musical rules through learning or experience (see Morton & Johnson, 1991, for proposing a similar dual system for faces). By this view, musical abilities can emerge from the general propensity of the brain to extract regularities from the environment. Indeed, infants have powerful statistical learning capacities. Seven minutes of exposure to tones with variable sequential probabilities of occurrence is sufficient for eight-month-old babies to discover the sequential structure (Saffran, Johnson, Aslin, & Newport, 1999). Thus, infants can capitalize on the statistical regularities in their auditory environment with relatively little effort. Music acquisition can be guided by such general-purpose mechanisms. Modularization, or functional specialization of the neural circuitries that subserve music processing, might emerge later as the result of the fine-tuning of such general-purpose mechanisms through experience with ambient music.

As noted by Trehub and Hannon (this volume), such general-purpose learning mechanisms cannot easily account for the ubiquitous processing biases for consonant intervals. Octaves and perfect fifths and logarithmic pitch scales have played a structurally important role in musical systems across cultures and historical periods. A learning-oriented approach cannot easily account for these cross-cultural invariants (Saffran, 2003). Consonant intervals are not easier to sing because they are generally larger in pitch distance than dissonant intervals which may require less vocal effort. Another difficulty for a general-purpose learning approach is the definition of what is to be learned. How does the algorithm know which units of information over which correlational statistics are computed? Identification of these units, such as scale steps (the “phonology” of music) might be pre-wired. That is, plasticity might be limited at this level. Not all pitch subsets or structures would be learnable.

In sum, there is good evidence that human infants are well equipped to learn the musical regularities of their environment. What is as yet unclear is the extent this learning is constrained by innate factors or biases involving such features as unequal scale steps and isochrony. What is clear, however, is that there is an innate propensity to enjoy music.

4.2.2. A human trait

Music as a uniquely human characteristics may still build on biologically ancient precursors. Comparative studies can help reveal what they are (Hauser & McDermott, 2003). Research on the animal roots of musical behavior is just beginning (Fitch, this volume; McDermott & Hauser, 2004; Wallin et al., 2000) and distinguishing the precursors of music from those of language is challenging. Humans have both music and language whereas animals might have only one mode of auditory–vocal communication. Most compelling types of evidence come from studies that directly compare the learning and the processing abilities of primates with those of humans (either adults or children). For example, comparisons of eight-month-old human infants (Saffran, Aslin, & Newport, 1996) and cotton-top tamarins (Hauser, Newport, & Aslin, 2001) on a simple artificial language learning task using the same preferential head-turn methodology indicate that both species are capable of basic statistical learning. Similarly, Ramus, Hauser, Miller, Morris, and Mehler (2000) have conducted parallel experiments with human newborns and cotton-top tamarin monkeys, using an habituation–dishabituation procedure. They showed that human newborns and tamarins can discriminate sentences from Dutch and Japanese but not if the sentences are played backward. These results indicate that the human newborns' tuning to certain properties of speech relies on general processes of the primate auditory system. It would be interesting to exploit such comparative situations with music. Such work might allow us to clarify whether musical capacity depends on unique mechanisms or whether these mechanisms are shared with other species.

4.3. Brain localization

Domain-specificity (or modularity) is typically confounded with the notion of brain localization. The idea is that a special-purpose mechanism must be confined to a focal neural network as opposed to a vastly distributed neural network. Once again, this needs not be. Domain-specificity and brain localization are separable issues. Brain mapping of functions is extremely complex. Even in the case of the best known modules, the language modules, there is no clear correspondence in neural terms (Hickok & Poeppel, 2004). Moreover, even if the human mind contained only one music module, this module might not be neuroanatomically isolable. The neural substrate of the music module might be intermingled with networks devoted to the processing of other complex patterns, such as speech intonation.

However, we know that music modules can be neuroanatomically isolable. Otherwise, brain damage could not affect just musical abilities whilst sparing other aspects of cognition. Thus, music modules apparently possess the property of neural separability (Peretz & Coltheart, 2003). Moreover, as argued previously, there is evidence that music processing relies on at least one module that is domain-specific and neurally separable. The best candidate we have so far concerns the system that maps pitch onto musical keys (i.e., *tonal encoding of pitch*). Current research points to the inferior frontal brain areas as critically involved (Tillmann et al., 2003; Koelsch et al., 2002; Hyde et al., submitted for publication). However, this localization mostly corresponds to the processing of harmonic structure, a culture-specific elaboration of pitch that is quite recent in music history. Moreover, *tonal encoding of pitch* is likely to recruit a vast network, because tonal encoding of pitch involves a cascade of mechanisms. For example, Jackendoff and Lerdahl (this volume) distinguish three different forms of elaboration of pitch hierarchies in a musical context, by considering different principles for pitch space, tonal reduction, and tension/relaxation. Thus, it would not be surprising to discover that more than one neural network contributes to the musical interpretation of pitch. A major breakthrough would be to localize the essential mechanism that triggers the whole cascade.

In principle, localization of such essential modules is possible. For examples, the fusiform gyrus has been associated with configural processing that is essential to face recognition (Farah, Wilson, Drain, & Tanaka, 1998) and the superior temporal sulcus, for voice processing (Belin, Fecteau, & Bédard, 2004). Presently, however, we cannot make similar claims about music (Peretz & Zatorre, 2005). Music processing recruits a vast network of regions located in both the left and right hemispheres of the brain, with an overall right-sided asymmetry for pitch-based processing. Finding such a widely distributed network of brain regions raises a number of issues that I will address in turn; first, the issue of which brain areas might share processing components with other functions, such as those involved in language and, second, the question of consistency of brain organization across individuals. Finally, the effects of musical training or of neural plasticity will be summarized.

4.3.1. Invasion of language areas

The issue of music and language specificity has a long history in neurology (Henschen, 1924). This question has been recently re-revisited by the observation that harmonic deviations activate Broca's area (Koelsch et al., 2002). This research suggests that the mechanisms underlying syntactic processing are shared between music and language (Levitin & Menon, 2003; Patel, 2003). However, there are problems with this conclusion that should be addressed. First, we should keep in mind that Broca's area is a vast brain region that can easily accommodate more than one distinct processing network (Marcus, Vouloumanos, & Sag, 2003). Second, the degree of anatomical proximity of activation maxima that should count as reactivation of the same region in another task is not straightforward, particularly when activation is not limited to Broca's area but involves the right hemisphere homologous region (Maess, Koelsch, Gunter, & Friederici, 2001) and when the cognitive domains (music and language) are studied separately in different laboratories.

Clearly, there is need for further comparison between music and language in the same experimental setting, using similar tasks that are matched (or manipulated) for attentional resources (Shallice, 2003). Indeed, it is easier to demonstrate separability than overlap. Yet, the demonstration of overlap between music and language is feasible. For example, Koelsch et al. (2004) have recently shown that semantic processing recruits the same electrical generators (e.g., underlying the N400 ERP component) in music and language. Of course, it is always possible to argue that the level of comparison is not appropriate. For instance, semantic processing is limited in music (see Bharucha et al., this volume). However, the search for commonalities is not arbitrary and depends on knowledge related to the functional organization of both music and language. As attempts for neural separability fail, we should become increasingly skeptical regarding the complete isolation of music processing from language processing.

4.3.2. Brain plasticity

Localization of the essential musical modules is not crucial for understanding the nature of music, but it provides important information regarding its biological foundations. One important neural property of a biological function is consistency across individuals. That is, one would expect a pre-wired organization to exhibit consistency in brain localization. Such a prediction is nontrivial in the case of music because there is a wide variability in experience. Depending on the moment, quality and quantity of exposure, various brain spaces may adjust to the musical needs.

This issue can be illustrated with studies of second language acquisition. The acquisition of a second language can be acquired at different moments, with varying degrees of experience. The neural consequence of this variability is that the brain areas mobilized by the second language (L2) vary capriciously from individual to individual (e.g., Dehaene et al., 1997). That is, listening to a story in L2 (i.e., English in the case of French-speakers) activates variable areas beyond the common auditory areas involved in native language processing (L1). It is only in the brain of professional translators that the two languages activate common areas, in the classical linguistic areas (Perani et al., 1998). Similarly, in bilinguals who learned their second language late in life, sentence production tasks in L1 and in L2 activate two nonoverlapping subregions of Broca's area (Kim, Relkin, Lee, & Hirsch, 1997). Only early bilinguals who received equal practice with their two languages from birth showed an activation overlap for L1 and L2. Accordingly, we may expect inter-subject variability in the cortical representation of music. At the very least, we may expect anatomical differences between musicians and nonmusicians who differ drastically in attentive exposure and practice.

Even if everyone engages in some sort of musical activity in everyday life, they do so with limited time and effort. In contrast, a few individuals become proficient musicians, through extensive practice from an early age. The fact that musical training is not uniform or systematically provided in current educational curricula introduces natural variety of musically acquired skills that could be related to brain functioning. In other words, musicians represent a unique model in which to study plastic changes in the human brain (Münte, Altenmüller, & Jäncke, 2002).

Indeed, there is increasing evidence that the brain of musicians is shaped by experience, either by expansion or reduction, depending on the stimuli and structural levels examined (see Münte et al., 2002, for a review). Hence, one would expect to find evidence of size differences in certain regions of the musician's brain compared to that of untrained individuals. The prime areas of interest are the motor areas. In a seminal study, Elbert, Pantev, Wienbruch, Rockstroh, & Taub (1995) investigated somatosensory evoked magnetic fields in string players. Source analysis revealed that the cortical representation of the digits of the left hand (the fingering hand, especially for its fifth digit) was larger in musicians than in nonmusicians. In the case of the right hand, in which no independent movements of the fingers are required in string players, no differences were found between musicians and nonmusicians. Moreover, the cortical reorganization of the representation of the fingers was more pronounced in musicians who had begun their musical training at an early age.

Training effects are not limited to motor control. Several auditory brain areas have been identified as differing between musicians and nonmusicians. For example, Pantev and colleagues, using MEG, have shown that brain responses to piano tones were 25% larger in musicians than in nonmusicians (Pantev, Hoke, Lutkenhoner, & Lehnertz, 1989). This effect appears more pronounced for tones from the practiced instrument (Pantev, Engelien, Candia, & Elbert, 2003), which implies use-dependent plasticity. However, using a similar MEG technique, Schneider, Scherg, Dosch, Specht, & Gutschalk (2002) found that both the early activity evoked by pure tones and the gray matter volume of the anteromedial portion of Heschl's gyrus was more than 100% larger in professional musicians compared to nonmusicians. Pure tones do not exist in the environment and, hence, cannot account for the observed effects. In fact, the functional and the morphological differences were related to musical aptitude, implying influence of innate determinants. These findings re-open the debate about whether the observed brain differences between musicians and nonmusicians arise from genetic or other predispositions (e.g., talent) as well as from practice and experience.

By improving our comprehension of this tuning process, research on musical expertise effects will teach us much about brain plasticity and the likelihood of finding consistent brain localization for shared musical abilities across musicians and nonmusicians. We may speculate that the brain system that underlies specialization for pitch processing is fixed (probably innate). The others might be more plastic within a time period (critical period). And finally others may be plastic over an entire lifetime. But there is a cost associated with pre-wiring. The existence of tone-deafness might correspond to the price to pay for a sophisticated machinery underlying musical sensitivity.

5. The emotional power of music

Most of us feel that music is much more than entertainment, that music can have a profound impact on listeners as well as on music-practitioners. Emotion is an integral part of the music experience. This emotional power is something of a mystery or paradox because of the abstract, nonrepresentational nature of music. Yet, music is a powerful tool for emotion and mood modulation, as further discussed in Bharucha, Curtis and Baroo (this volume). Movement is a key component of emotional reactions to music. Much music is composed with very specific action tendencies in mind-getting people to sing, to dance, march and fight, or work and play together. Up to now, the majority of studies have been concerned with the appraisal of music (Gabrielson & Juslin, 2003).

With respect to emotional appraisal of music, it is remarkable how skilled young children are. From the age of three years, they show the ability to recognize happiness in the art music of their culture, and by the age of six they show adult-like abilities to identify sadness, fear, and anger in music (Cunningham & Sterling, 1988; Dolgin & Adelson, 1990; Terwogt & van Grinsven, 1991). More specifically, by the age of six, children show full knowledge of the rules (mode and tempo) that govern the happy–sad character of surrounding music. This ability remains generally unchanged over a lifetime (Dalla Bella, Peretz, Rousseau, & Gosselin, 2001).

This observation does not mean that emotional appraisal is predetermined. On the contrary, emotional appraisal is modulated by experience. The "mere exposure effect" on musical taste is well established. As listeners, we tend to like what we already know (see Bornstein, 1989, for a review). In music, we prefer familiar over unfamiliar music but we are unaware of this bias (Peretz, Gaudreau, & Bonnel, 1998). This unconscious effect of prior exposure to music may account for a vast array of phenomena, such as the preference for consonance over dissonance (Zentner & Kagan, 1996) and the association of the major–minor modes with happy and sad emotions (Peretz, Gagnon, & Bouchard, 1998).

Although shaped by individual experiences, musical emotions can trigger the limbic system, an evolutionary ancient brain structure. In one demonstration, Blood & Zatorre (2001) reported cerebral blood flow changes while people experienced musical "chills", in several brain areas, including the dorsal midbrain, ventral striatum (which contains the Nucleus Accumbens), insula, and orbitofrontal cortex. Some of these regions have been implicated in response to highly rewarding or motivationally important stimuli, including food (Small, Zatorre, Dagher, & Jones-Gotman, 2001) and drugs of abuse (Breiter et al., 1997). Interestingly, this physiological response – the "chill" – is related to the action of endorphins (Goldstein, 1980). Thus, under certain circumstances, music can access neural substrates that are associated with primary reinforcers, such as food and sex. This neurobiological link between music and the limbic system is not limited to hedonic mechanisms. The amygdala, another subcortical region associated to threat-related stimuli, can also be recruited by music (Gosselin et al., 2005). Thus, music appears as effective as food, drug, and facial expressions to elicit subcortically mediated affective responses.

Therefore, it seems that emotional responses to music can be aroused as readily in humans as *reflexes*. Indeed, musical emotions occur with immediacy (Peretz et al., 1998), through automatic appraisal, and with involuntary changes in physiological and behavioral responses. With limbic mediation, consistency, and precociousness, musical emotions resemble other important classes of biological stimuli, such as facial emotions (Peretz, 2001c). Hence, the study of music as an emotional medium may best explain its ubiquity and its utility.

6. Why are humans musical?

If music corresponds to an impulse that emerged early in human evolution, that is present and functional early in human development, that has an important emotional impact, and that resides, at least in part, in specialized brain areas, then the key question becomes "Why?". What adaptive function was served by music in ancestral activities so as to provide its practitioners with a survival advantage in the course of natural selection?

Two main evolutionary explanations have been offered. The initial account was provided by Darwin (Darwin, 1871) himself who proposed that music served to attract sexual partners. This view was revived by Miller (2000), who argues that the impulse to make music (and create art in general) is a way to impress prospective sexual partners with the quality of one's brain and thus, indirectly, one's genes. Musical virtuosity is unevenly distributed, demanding, hard to fake, and widely prized. Both males and females may use the tactic, with males impressing and females attracting partners (e.g., think of Ulysses who had to be chained up to resist to the chant of sirens). However, the dominant view about the adaptive value of music lies at the group level rather than at the individual level, with music helping to promote group cohesion (Wallin et al., 2000). Music is present in all kinds of gatherings – dancing, religious rituals, ceremonies – strengthening interpersonal bonds and identification with one's group. The initial step in this bonding could be the maternal vocal behavior of singing and expressive speech, generating emotional communion, through a process so-called *emotional contagion*. *Emotional contagion* is the tendency to automatically mimic and synchronize vocalization and movements with those of another person and, consequently, to converge emotionally (Hatfield, Cacioppo, & Rapson, 1994). In this way, as proposed by Blacking (1987), the power of music (and dance) is generated by the extension of individuality in community. The utilitarian value of dance and music would be to enhance co-operation and educate the emotions and the senses. It is a form of communion whose adaptive function is to generate greater sensory awareness and social cooperation.

In support of the contention that music has adaptive value, particularly for the group, is the fact that music possesses two features that affect contagion or communion. Pitch intervals or frequency ratios allow harmonious vocal blending, and regularity favors motor synchronicity or grace. These two musical features are highly effective in promoting simultaneous singing and dancing, while allowing some autonomy between voices and bodies (Brown, 2000). This design appears specific to music. It is not shared with speech, which requires individuality and nonsimultaneity for its intelligibility. These special features fit with an important criterion noted by Buss, Haselton, Shackelford, Bleske, & Wakefield (1998). For a system to qualify as adaptive, it must have a "special design" to offer effective solutions to a problem. The bonding problem in the case of music is to override individuality for the benefit of the group.

This solution might be the product of natural selection. As Fitch (this volume) notes, similarities in the vocal learning of complex songs in evolutionary distant lineages such as humans, birds, whales and seals may have arisen by convergent evolution. Nature generates similar solutions to similar problems. As Fitch also notes, we may never be able to evaluate the adaptive value of music.[3] Most of these hypotheses about the historical functions of music are untestable. Only questions about its current utility can be addressed (see Fitch, this volume, for a few promising avenues). However, evolutionary questions are not sterile; they may provide new ideas for research. For example, Mithen (2005) proposes that pitch could have preceded rhythm in evolution, and that pitch and rhythm could have independent evolutionary forces. Being in-tune could be one force behind sexual selection and being in-time could be a group cohesive force. After all, there is good evidence that pitch and time are independent, although interactive, in music processing.

7. Conclusion

Although many questions about music and music processing remain unresolved, there is evidence that musical abilities depend, in part, on specialized cerebral processes that have their root in musical predispositions, that hint at an initial specialization. Many of the arguments presented here are directed against strong claims about an exclusively cultural perspective on music. My intention is to show that such claims are neurobiologically questionable. I do not think that apes can learn to play music or acquire music-like behavior, nor do I believe that music acquisition is based actually on rote learning and the brain is equipotential. What I suggest, rather, is that music is an autonomous function, innately constrained and made up of multiple modules that overlap minimally with other functions (such as language).

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[3] One possibility that cannot be ignored is that music has no adaptive function. Gould & Lewontin (1979) have argued that many unique cognitive abilities are not directly selected but might be consequences of other selection pressures. Innate does not mean adaptive. Music could be innately transmitted by accident, or by being associated, by chance, with an adaptive trait. This is an important point to keep in mind because "by-products" are less informative as a focus of study than adaptations. Because nonadaptive abilities are consequences and not causes of the organization of the system, their functioning might be more arbitrary and may vary widely across individuals. If a system is adaptive, it must be universal. It must also develop reliably, be well engineered, and have a reproduction-promoting design. Although the evidence is compatible with the adaptive function of music, this evidence is not compelling. Much more data will be needed before conclusions can be drawn. Note that music is not special in this regard. The origins and evolution of language ability are still a matter of controversy and, above all, a relatively recent question of enquiry (Christiansen & Kirby, 2003). Although there seems to be agreement that some pre-adaptation occurred in the human lineage prior to the emergence of language, the nature of this pre-adaptation is a matter of debate. One recent proposal that is endorsed by Chomsky is that the ability for complex hierarchical learning of sequentially presented sequences (Hauser, Chomsky, & Fitch, 2002) or recursion is essential for the emergence of language. Another influential proposal has language originating from manual gestures rather than primate calls (Corballis, 2004). Thus, there are reasons to expect that questions related to language evolution will profit from the progress on the origins of music. At present, progress on evolution for music lags behind that of language, but perhaps not for long (Balter, 2004).

I also think that the potential applications of this type of research and questioning, as well as the current excitement in our field, should not be ignored. Question about the *nature of music* have implications for how caregivers raise children, how educators teach students and how clinicians diagnose and treat patients. The answers may also have a societal and financial significance, pointing to potential benefits of music. Much work remains to be done but discussing these issues is not premature but timely. We cannot improve the way our brain is built, but we can better understand its functioning and adjust teaching methods and musical practices to our biological make-up and limitations. The role of academia and of sciences in general is to be aware of all these implications. There is every reason to welcome advances in the biological foundations of musical behavior but to be cautious in interpreting the evidence.

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