Evolutionary Psychology of Music: Assessing Innateness and Domain Specificity

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Evolutionary psychology often does not sufficiently document the innate constraint and domain specificity required for strong adaptationist argument. We develop these criteria within the domain of music. First, we advocate combining computational, developmental, cross-cultural, and neuroscience research to address the ways in which a domain is innately constrained. Candidate constraints in music include the importance of the octave and other simple pitch ratios, the categorization of the octave into tones, the importance of melodic contour, tonal hierarchies, and principles of grouping and meter. Second, we advocate combining psychological, neuroscience, and genetic research across cognitive domains to address the domain specificity of such constraints. Currently available evidence suggests that the innate constraints in music are not specific to that domain, making it unclear which domain(s) provided the relevant selection pressures.

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Introduction: Music, Modularity, and Adaptation

In the past two decades, the field of music cognition has proved to be an essential subdiscipline within cognitive psychology and cognitive neuroscience. Any complete theory of the human mind and brain should explain the manner in which this universal and important domain is acquired and implemented. A recent trend within the field of music cognition has been to invoke Darwinian mechanisms of natural selection (Darwin, 1859, 1871) to explain music’s origins in Homo sapiens (e.g., chapters within Wallin, Merker, & Brown, 2000; Zatorre & Peretz, 2001; Peretz & Zatorre, 2003). Pinker (1997) has offered one of the few exceptions to this trend, arguing that music is an exaptation (Gould & Vrba, 1982), having been the result of selection in other cognitive domains, including language. This idea, and particularly Pinker’s description of music as “auditory cheesecake,” has motivated many researchers within the music cognition community to respond with a renewed drive to “legitimize” music as a cognitive domain worthy of study by establishing its biological and evolutionary bases. Numerous articles, both in the popular and scientific literature, attest to the strong feelings held on this issue (e.g., Abbott, 2002; Andrade & Bhattacharya, 2003; Dorfman, 2000; Gray et al., 2001; Lewis, 2002; Levitin, 2000; Peretz & Hébert, 2000; Trainor et al., 2002; Trehub, 2001). However, despite the flurry of papers in this area, the notion that music is an evolved trait specifically shaped by natural selection is far from a foregone conclusion.

Learning and culture can still provide a robust framework from which to propose alternate scenarios for the emergence of music in Homo sapiens. Although it is possible to incorporate both biological and cultural evolution into a single theory of music’s origins, one is still left with multiple questions regarding the specific roles that each of these processes has played. Researchers may have biases in various directions in their approach to such questions, depending on the emphases of their fields. For example, evolutionary psychologists, who are primarily interested in the role that evolution played in human history, are motivated to identify cognitive traits that might have been shaped directly by natural selection. Alternatively, researchers in fields that emphasize development and culture may be wary to describe a cognitive ability as a specifically evolved trait in cases where learning and cultural transmission are thought to play an important role.

These varying approaches to evaluating evolutionary hypotheses, including the one developed in this article, are associated with specific types of error, just as an experimental paradigm involves both the error of finding an effect when one is not present, or missing an effect when one is present. The majority of the recent evolutionary treatments of music have primarily favored the approach of the evolutionary psychologist: guarding...
against the possibility that an adaptation shaped directly by natural selection might be missed. In the parlance of experimental psychology, one might say that they are guarding against a Type II error. Although we too are interested in the role of evolution in the genesis of cognitive traits, we adopt a fundamentally different perspective in the present review. This approach, rather than guarding against the possibility that an adaptation might be missed, guards against the premature acceptance of music as an evolutionary adaptation, when exaptation and culture may be sufficient to explain its emergence. One might say that we are guarding against a Type I error. This approach entails more stringent criteria for identifying a particular cognitive trait as an evolutionary adaptation, and it has at its core a fundamentally different set of concerns than those adopted by many evolutionary psychologists. We feel that such an approach could be fruitfully applied to assess music, as well as other cognitive domains, for signs of direct selection pressures. Perhaps more importantly, this approach keeps the door open to a wider array of evolutionary scenarios for complex cognitive domains, many of which may never have had direct exposure to the forces of natural selection.

In the present article, we lay out a set of criteria for determining whether a cognitive domain such as music was directly shaped by natural selection, or if it might be better accounted for by other evolutionary scenarios. We begin with a discussion of the various concepts associated with the term modularity in cognitive science, the concept of adaptation in evolutionary biology, and how we feel they interrelate. We conclude that evolutionary arguments for music and other cognitive domains would be greatly strengthened by explicitly dealing with the related issues of innate constraint and domain specificity. This is followed by a selective review of the music cognition literature, structured in an epistemological fashion to examine first the innateness and second the domain specificity of the relevant cognitive mechanisms. In doing so, we illustrate the kinds of data we feel would be the most relevant in future research concerning the evolutionary history of music.

Although the present article does focus specifically on music, we feel that the approach set forth here could be fruitfully applied to a variety of cognitive domains for which adaptationist scenarios have been, or could be, offered. The dual-criterion model that we describe in the present work could be of value to cognitive psychologists eager for more rigorous approaches to evolutionary psychology. These criteria are more stringent than those used by animal behaviorists and, to date, by most evolutionary psychologists, given the unique problems of inferring evolutionary history in a species with dual genetic and cultural inheritance and given our conservatism in accepting an argument that a cognitive domain has specifically been shaped by natural selection.

**Cognitive Science and Modularity**

Much of contemporary research in cognitive science concerns itself with the degree to which the mind is modular, an issue that has implications for which cognitive domains have undergone natural selection. In this article, we use the term cognitive domain to refer to a category of knowledge and behavior as we explicitly conceptualize it, and not the cognitive and neural resources upon which this category relies. The extent to which these explicit categories correspond to the organization of the mind is one of the main questions with which domain specificity is concerned.

Fodor’s (1983) *Modularity of Mind* (hereinafter MoM) presented a view of the mind in which some aspects of cognition are performed by mental modules: mechanisms that are (a) specific to processing only one kind of information, (b) by and large innately specified, (c) fast, automatic, and unaffected by the content of other representations, and (d) implemented by specific, localizable brain regions. We shall refer to these qualities as domain specificity, innate constraint, information encapsulation, and brain localization, respectively. In Fodor’s treatment, these qualities were argued to go hand in hand with each other. Chomsky’s arguments that language is not only innately constrained but also serviced by a domain-specific “language acquisition device” and “language organ” further contributed to the belief in a tight relationship between these qualities among some cognitive psychologists. The strength of this belief can be seen in arguments in which the demonstration of one quality in a given system, such as brain localization, is taken as evidence for the other qualities, such as innate constraint. Research in cognitive neuroscience can often provide examples of such (spurious) arguments, as when selective activation in a neuroimaging experiment or selective deficit following a lesion are sometimes

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To be precise, Fodor’s nine qualities were (1) domain specificity, (2) mandatory operation, (3) limited central access, (4) speed, (5) information encapsulation, (6) shallow output, (7) fixed neural architecture, (8) specific breakdown patterns, and (9) characteristic ontogeny. We focus on four qualities, grouping 2 through 6 under the term information encapsulation and 7 and 8 under the term brain localization for the purposes of this article.
interpreted as evidence of the “dedication” or “specialization” of that tissue for the cognitive domain in question (e.g., the fusiform face area controversy, Kanwisher, 2000; Tarr & Gauthier, 2000).

In our view, these different facets of modularity are dissociable. Research since MoM in the cognitive psychology and neuroscience of language provides many appropriate examples. The idea that innateness and domain specificity are dissociable, for instance, is supported by the possibility that many of the innately constrained mechanisms that we use for word learning are not specific to language, resulting largely from more domain-general constraints on conceptual representation (Bloom, 2000). These two facets of modularity also each dissociate from brain localization, i.e., a predictable and highly localized region of tissue serving as the locus of a representation. The dissociation of brain localization and innateness has been shown with specific cortical areas that come to process information in learned domains such as reading (e.g., orthography-specific visual cortex, Farah, 1999; Polk et al., 2002). Similarly, brain localization and domain specificity often dissociate, as shown by the participation of specific cortical and subcortical regions in multiple domains (e.g., the basal ganglia and their participation in multiple domains requiring sequential/syntactic representations, Lieberman, 2000). Brain localization, innateness, and particularly domain specificity can also dissociate from information encapsulation. Language may make use of cortical organization that is modular in the sense of information encapsulation, resulting in separate processing for some aspects of syntax and semantics (e.g., Friederici, 1995, 2000). However, neither this cortex nor its encapsulated structure is necessarily domain-specific for language; the syntax-semantics distinction might be better explained as the result of distinct neural systems for procedural and declarative knowledge (Ullman, 2001). As the result of such dissociations, Dick et al. (2001) introduced the term *distributivity* as an alternative to modularity/localization and its traditional alternative, equipotentiality. The term *distributivity* implies that a complex cognitive domain will rely on a widespread network of cortical regions that are recruited based on the computational demands of the domain but are not necessarily devoted exclusively to it.

Most currently available arguments about music and modularity have not considered the separateness of these issues. For example, Peretz and Morais (1989) have argued that the representation of pitch in terms of a tonal system is a module. Music does utilize predictable regions of cortex, as suggested by neuropsychological work on pitch perception in particular (see Peretz, 2001b, for review). This cortex is also organized such that different subdomains within music, such as pitch and rhythm, may dissociate in neuropsychological patients (Peretz, 1990; Liégeois-Chauvel et al., 1998; Peretz & Coltheart, 2003). Similarly, much of music processing occurs implicitly and automatically, being impervious to changes in attention or conscious strategies (Justus & Bharucha, 2001; Trainor et al., 2002), suggesting another kind of information encapsulation (Fodor’s “limited central access”; see Raffman, 1993). However, given that brain localization and information encapsulation each can dissociate from the other facets of modularity, we feel that it is incorrect to conclude that the relevant cortex is domain-specific for music or that any domain-specific cortex that might emerge during development is genetically determined.

**Evolutionary Biology and Adaptation**

For some researchers, the next step in many modularity arguments is to determine the adaptive value of each cognitive domain in order to ascertain how it evolved in *Homo sapiens* (e.g., Tooby & Cosmides, 1992), a movement that Fodor himself regards with skepticism (Fodor, 2000). The extreme form of such adaptationism found in much of contemporary psychology is a problem that has already been faced in evolutionary biology, where much of the discussion was framed in terms of original functions and modern uses (Williams, 1966; Gould & Lewontin, 1979; Jamieson, 1986). A function of a given structure is a purpose for which it was selected, whereas a use is a purpose that this structure allows but was not one for which it was selected. Consequently, Gould and Vrba (1982) argued that the term adaptation should be reserved for structures whose modern functions of interest are the same purposes for which they were selected, and they introduced the term exaptation for structures whose original functions and modern uses differ. According to these authors, exaptations can arise by recruiting other structures that were either selected themselves as adaptations or were by-products of other adaptations (i.e., spandrels).

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2For the purposes of this article, we use the terms *tone* and *tonal* primarily in the musical sense of pitches or notes relative to a scale, as opposed to the psychoacoustic sense of a periodic sound with a beginning and an end.
We feel that the distinction between adaptation and exaptation is better understood in terms of phenotypic and genetic changes. In our view, exaptation involves a change or addition to a species’ phenotype, its observed structure and behavior, in the absence of any modification to the genotype, or genetic code. Without further genetic change, an exaptation remains an old structure with a new use. However, if the species’ genome is modified by natural selection for the new behavior, such a use becomes a new function and the exaptation becomes a “secondary” adaptation. Such secondary selection for a useful phenotype is not a given, however, because the remaining selection pressures on the already well-adapted ancestral form may constrain or prevent it entirely. As examples of adaptation and exaptation, if we assume for a moment that the genetics underlying the development of the perisylvian cortex have been modified in Homo sapiens by natural selection for speech, then speech would be an adaptation and a function of perisylvian cortex. These same areas (among others) are also used during reading in literate people (e.g., Paulesu et al., 2000). However, assuming that the genome has not been modified by natural selection for reading, then reading is an exaptation and a use of perisylvian cortex.

The evolutionary history of all higher cognitive functions must involve exaptation, by virtue of their initial dependence on simpler neural systems, and there should be little doubt that the evolution of music involved exaptation at some point during its history. However, the distinction between phenotypic and genetic change is crucial if one is going to argue that music specifically has been shaped by natural selection, and because of this the historical approach is prone to characterize traits incorrectly as nonadaptive. Instead, the identification of a trait as an adaptation is argued to depend on whether possession of the trait results in higher fitness within the modern environment (e.g., Reeve & Sherman, 1993). These two approaches seek to answer two very different questions; the first seeks to explain the origin and construction of a trait through evolutionary time, whereas the second seeks to answer questions surrounding the current existence, inclusive fitness, and maintenance of a particular phenotype. We find it appropriate to focus on the first question, given that much of evolutionary psychology has been explicitly concerned with historical origins (Tooby & Cosmides, 1992; Pinker & Bloom, 1990; Pinker, 1994; Plotkin, 1998; Wilkins & Wakefield, 1995) and, more importantly, because this approach has far greater implications for neurocognitive development and organization.

One methodology of the modern-fitness school of thought is the study of reproductive success, an approach that has also been advocated in studying human music as an adaptation (G. Miller, 2000). Even within a modern-fitness framework, however, the study of human reproductive success runs into fundamental problems related to the issues of innateness and domain specificity. First, any increased reproductive success in response to an expressed trait (selection of a phenotype) does not mean that the trait is heritable (the genotype); individual differences on a given trait may be due entirely to environmental-cultural differences (Lewontin, 1998, 2000; Howe et al., 1998). Second, even after a genetic basis for the individual differences is established, one must consider how many cognitive domains are affected by this variability. If the variability is not domain-specific, the correlation between the domain of interest and reproductive success may be spurious, connected only by relation to another domain that is the true source of the selection pressure.

Combining Cognitive Science and Evolutionary Biology in the Realm of Music

We argue that data drawn from the cognitive sciences are extremely relevant when evaluating the evolutionary history of a cognitive domain. Specifically, two questions pertaining to Fodor’s MoM seem particularly important when evaluating claims that Darwinian natural selection explains the historical origins of a cognitive domain. First, how innately constrained is the development of the domain? The cognitive domain must be the result of a developmental process involving high genetic constraint, rather than being the result of the internalization of culturally transmitted information by more general mechanisms. Second, are any of these constraints domain-specific? Some of the innately
constrained developmental processes must have been
directly shaped by natural selection in response to the
domain of interest, and not shaped in their entirety in
response to other domains.

With regard to the first question, one may argue
that a cognitive domain is based on innate con-
straints using converging evidence from computational
approaches, cognitive development, cross-cultural stud-
ies, and cognitive neuroscience. Otherwise the domain's
developmental origins may be explained alternatively
via mechanisms of learning and cultural transmission,
rather than through natural selection. With regard to the
second question, one may argue that some selection
pressures were for the domain of interest and not
other domains based on evidence of domain-specific
mechanisms that distinguish it from sister domains.
Otherwise its evolutionary origins may be explained
alternatively via mechanisms of exaptation rather than
adaptation, or in other words, as an adaptation for other
cognitive domains.

The combination of these two qualities—innateness
and domain specificity—in a cognitive domain would
be strong evidence that it was shaped by the forces of
natural selection. Cognitive scientists have the empiri-
cal tools to characterize the developmental process, the
adult brain phenotype, and its associated behavioral
phenotype (see the elements depicted in Figure 1A
through 1C). What we do not have access to are the
patterns of dual genetic and cultural inheritance that
are impacted by various behaviors over the course of
human evolution (Figure 1D). However, inferences
about evolutionary history may be made based on data
from cognitive science: Cognitive resources that are
innately constrained in domain-specific ways must be
the result of selection pressures for the domain in ques-
tion. We would argue that this is the most appropriate
way, albeit a conservative one, to apply an “argument
from design” to human cognitive abilities.

The other two qualities that we discussed in regard
to modularity, namely information encapsulation and
brain localization, are of less direct relevance to infer-
ing selection pressures (Figure 1B in isolation). By
themselves, these two issues do not aid us in disentan-
gling genetic and cultural inheritance. This is because
virtually any cognitive domain will take advantage of
cortical resources that show some degree of informa-
tion encapsulation from each other (e.g., processing
might be unaffected by an attentional manipulation)
and will be implemented by predictable regions of
cortex, depending on the computational requirements
of the domain. (We shall return to this issue in the
“Cognitive Neuroscience” sections.)

In what follows, we expand on our requirements and
apply them to the domain of music, examining the kinds
of evidence that have been and could be collected to
address these issues. We find that the currently available
evidence suggests that many aspects of music do not
meet the requirement of a sufficient degree of innate
constraint, and those that do often do not meet the
requirement of domain specificity. Our review reflects
the field's emphasis on perception over production, an
imbalance that would need to be corrected for our dual-
criterion model to be fully applied. Our review is selec-
tive, and the reader is referred to more thorough reviews
by Sloboda (1985), Dowling and Harwood (1986),
Krumhansl (1990, 2000a), McAdams and Bigand (1993),
Deutsch (1999b), and Justus and Bharucha (2002).

Determining the Degree of Innate Constraint
in Music

A major cause for uncertainty when discussing the
evolutionary forces shaping Homo sapiens is the
phenomenon of cultural transmission, a term that
“covers a series of activities, all essential to culture,
which it is useful to subdivide into the capacity to learn,
the capacity to teach, and the capacity to embody
knowledge in forms which make it transmissible at a
distance in time or space” (Mead, 1964). It typically
evokes a transformational or Lamarckian framework
in which cultural knowledge changes by accumulation
over time, whereas memetic transmission (Dawkins,
1976; Blackmore, 1999) adds a variational or Darwinian
component in which units of cultural knowledge, or
memes, are selected.

Gjerdingen’s (1988) historical study of the 1-7-4-3
idiom in Western tonal-harmonic music provides a
simple yet compelling example of cultural transmission
in music (Figure 2). The numbers “1-7-4-3” refer to the
scale degree of each note of the idiom; in E-flat major
it would be Eb-D-Ab-G, with a down-up-down direction
of motion (Figure 2A). In the music of the early eigh-
teenth century, this melodic pattern can be found in a
handful of works from composers such as Scarlatti. Its
use in Europe dramatically increased to a peak in the
heart of the classical period, the late eighteenth century,
by composers such as Haydn. By the nineteenth century,
however, its use had declined dramatically in favor of
other conventions. An anthropologist who only had
access to music from the 1770s might come to the incor-
crect conclusion that this idiom was the result of innate
constraints that would have required melodies to follow
this rule. Our understanding of human music may
be similarly limited; our database of well-documented
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FIG 1. Our conceptualization of how innate constraint and domain specificity can allow for the inference of evolutionary selection pressures.

(A) The developmental process involves an interplay between the genome, which can be thought of as a set of innate constraints, and environmental information, which for humans includes both the set of long-standing environmental regularities that are independent of human activity (e.g., the physical properties of light and sound) and the vast set of culturally transmitted information that we receive via the enculturation process.

(B) The adult brain phenotype contains structural and functional specialization for different kinds of representations and information processing. The amount of information transfer between these representations during cognitive processing varies, some exchanging freely and automatically and others being somewhat encapsulated from each other. Such representations may or may not be predictably localized to a small region of cortex.

(C) These cognitive resources allow us to process information in different kinds of cognitive domains, such as music or language. However, there is not a one-to-one correspondence between representation and domain. (D) Cognitive domains may impact the genome of subsequent generations of the species, via natural selection, as well as contribute to the body of cultural information with which those generations are enculturated. Here, Domain 3 alters the species only via cultural transmission and not natural selection. Because it alters the phenotype but not the genotype, Domain 3 is an exaptation.
music is only on the order of centuries and is highly focused on the traditions of western Europe and those regions of the world with which it has had a high degree of cultural exchange. (We discuss the importance of cross-cultural comparisons in the “Cross-Cultural Musicology” section.)

Although the terms cultural and biological are often used in opposition to each other, cultural knowledge must be biological; the cultural achievements of a society are stored in a distributed manner in the structure of the brains of its members, in combination with the vast systems of external information storage that humanity has devised (Donald, 1991). A more useful pair of terms may be cultural and evolved. There is a meaningful sense in which to be cultural is not to be evolved, because cultural transmission can create
Qualitatively new kinds of human cognition and behavior (phenotypic change) without necessarily changing the genome upon which it relies (genetic change). Granted, given the interactive nature of development, it is not logical to expect a clear separation between the developmental processes regulated by the genome and the environmental information with which that genome evolved. However, there is some independence between evolved developmental outcomes and culturally achieved outcomes for which the genome is not specifically prepared. The explosion of industry, technology, and widespread literacy of the last dozen human generations attests to the power of our species to alter itself via cultural transmission on a time scale that is virtually insignificant from the perspective of natural selection (also see Tomasello, 1999; Ehrlich, 2000; Donald, 2001).

While much of what we consider to be music is a product of culture, some aspects of it may have been programmed into the human genome by natural selection, or in other words may be “innate.” These innate constraints interact with environmental-cultural information and result in the mental representations or knowledge\(^3\) that humans apply when creating or perceiving music. A useful treatment of the concept of innateness was offered by Elman et al. (1996), who argued that innate constraints may manifest themselves in at least three ways during development: representational constraints, architectural constraints, and chronotropic constraints. Representational constraints are predetermined patterns of synaptic connectivity, such as the microcircuitry of the cortex or the strength of the connections in a neural network. Architectural constraints exist on increasingly macroscopic scales and include differences in the kinds of neurons found in different areas of cortex and the ways in which the different regions of the brain connect with inputs and outputs. Chronotropic constraints manifest themselves during development and control the relative timing of the onsets and offsets of different developmental processes (see also Gould, 1977).

Although we maintain that a distinction between the evolved and the cultural can be useful, they are not completely separable. Some long-standing cultural practices can themselves create selection pressures and alter the genome, as for example when the cultural practice of dairying may have created a selection pressure for adult lactose tolerance (Durham, 1991). Such coevolution is a specific instance of an exaptation (in this case, the cultural practice) becoming a secondary adaptation. If a cognitive domain such as music is old enough, the possibility exists that coevolution between culture and genetics occurred, and indeed, archaeological evidence suggests that musical artifacts such as flutes may have been made by humans as early as 50,000 years ago (e.g., Kunej & Turk, 2000). Such findings suggest that a significant portion of the cognitive abilities underlying music were present in *Homo sapiens* by this time. One might argue that, given the relative long age of music, such artifacts imply that the opportunity was present for natural selection to operate on this cultural practice, further modifying the genome in response to this new selection pressure. Although the age of music makes it possible that cultural practices after music’s appearance introduced selection pressures that altered the species genetically, it does not imply it. Any natural selection for music would have acted on an already well-adapted ancestral form, and such selection may have been constrained or prevented altogether by continuing selection pressures for all that preceded music.

In the remainder of this section we review a selection of the music cognition literature from four areas: computational approaches, cognitive development, cross-cultural musicology, and cognitive neuroscience. The emphasis is on the research within these areas that we feel is of assistance in identifying those aspects of music that may be innately constrained. As we consider the evidence, we ask the reader to keep in mind that it is the innate constraints and not the milieu of cultural information that can act upon them which may be explained by natural selection. Establishing innate bases is only the first step in evaluating a cognitive domain for adaptation; in all cases, caution must be used in determining how domain-general or domain-specific such innate constraints may be (which we shall address in the second portion of the article).

**Computational Approaches**

Recent computational approaches using connectionist modeling have been used to test what kinds of innate constraints are required to develop knowledge about different domains (e.g., Elman et al., 1996). Many of the original arguments for innate constraints on learning stem from Chomsky’s (e.g., 1957, 1975) work on language. Chomsky argued that in some cases, learning mechanisms may be relatively general and rely on laws of association, as argued by the behaviorists. In others, a higher degree of innate constraint must be present in order for organisms to draw the right conclusions about...
the structure of the environment. Such "poverty of the stimulus" arguments have been applied not only to language but also to other domains, especially vision (e.g., Helmholtz, 1867/1925; Marr, 1982; Palmer, 1999).4

In contrast, no well-documented cases for a problem with the learnability of musical grammar given environmental input have been made to our knowledge. This is despite the existence of a substantial literature in the development of musical knowledge (for a review see Deliège & Sloboda, 1996) and a detailed hypothesis of the grammar we have for structuring musical information in the Western tonal-harmonic tradition, the Generative Theory of Tonal Music (hereinafter GTTM; Lerdahl & Jackendoff, 1983). In fact, evidence often suggests the opposite; the development of many kinds of musical knowledge can be successfully modeled by self-organizing neural networks. Given that musical grammar appears to be highly learnable, no poverty of the stimulus argument would seem to apply for music (for reviews of neural networks and music, see Todd & Loy, 1991; Bharucha, 1999).

LOW CONSTRAINT: ACQUISITION OF TONAL-HARMONIC REPRESENTATIONS

Consider, for instance, the implicit knowledge that Western listeners have about the tones, chords, and keys of tonal-harmonic music. For a given section of a tonal-harmonic piece (including most popular music in Western cultures), seven of the twelve chromatic tones are chosen and combined such that certain tones and chords come to be regarded as more important or stable than others (Krumhansl, 1990). The intricate set of rules governing these relationships may, however, be modeled by neural networks using relatively simple principles (e.g., MUSACT, Bharucha, 1987a, 1987b). Furthermore, such models require few architectural (i.e., "innate") constraints when exposed to the structurally rich music that is characteristic of Westerners’ everyday environments. Tillmann, Bharucha, and Bigand (2000) successfully used an unsupervised learning algorithm incorporating Kohonen’s (1995) self-organizing maps to model the acquisition of knowledge of Western music. After exposure, the network developed layers representing the chords and keys of tonal-harmonic music, and furthermore it could then model the results of a large body of behavioral experiments on musical expectation (Figure 3).

Krumhansl and colleagues have also used Kohonen self-organizing maps to model the musical expectations of three different musical-cultural backgrounds: musicians of the Sami or Lapp culture, Finnish music students with some exposure to Sami music, and other European music students with no exposure to Sami music. The SOMs correctly modeled the knowledge of the three groups, depending on the kind of music with which they were trained (Krumhansl, Louhivuori, Toiviainen, Järvinen, & Eerola, 1999; Krumhansl et al., 2000; Krumhansl, 2000b). The results of Tillmann et al. and Krumhansl et al. pose a serious challenge to any argument of poverty of the stimulus with regard to tonal-harmonic regularities and, in doing so, do not support an innate mechanism for the acquisition of these aspects of Western music.

As these examples show, computational approaches using neural network models, particularly those that self-organize in the face of environmental regularities, are a useful tool for a precise characterization of the kind and degree of innate constraint needed to acquire adult knowledge in a given domain. Although the neural net tradition in music has not been as explicitly empiricist in its theoretical approach as has that of other domains (e.g., the emergence movement in language, MacWhinney, 1999), much of the currently available research does lend itself to such questions about innate constraint, suggesting that not many constraints are required.

Even though computational research may suggest that a musical regularity is learnable, this does not necessarily imply that it is indeed learned. Some regularities may be assisted by innate constraints, perhaps making their acquisition faster and more efficient than would be the case otherwise. What computational approaches can do is argue for or against the minimal amount of constraint that is required to learn a given regularity. Because of this, we must look to converging and opposing evidence from other sources that might suggest that the constraints go beyond the required minimum.

Cognitive Development

Studies of cognitive development also provide empirical data relevant to the issue of innate constraint. Those aspects of musical knowledge that appear early with minimal exposure are more likely to be the result of innately specified developmental programs. Of course,
it must be acknowledged that this trend is a soft one; many aspects of human cognition that manifest early may still be learned, and aspects of cognition appearing later may still be highly constrained. Further, developmental studies of audition must always bear in mind that, unlike vision, auditory experience begins well before birth (see Lecanuet, 1996; Abrams et al., 1998) and that knowledge apparent in the newborn may reflect this prenatal experience. We consider three areas of music cognition that emerge early and thus may be considered candidates for innate constraint in music: the special status of the octave and perfect fifth, pitch...
processing relative to scales and contours, and basic principles of grouping and meter.

**CANDIDATE CONSTRAINT: THE OCTAVE AND SIMPLE PITCH RATIOS**

One element of music that develops early is the perceived similarity of pitches separated by octaves and other simple ratios; this also appears within the first few months of life (Demany & Armand, 1984). Such octave equivalence results in the logarithmic function observed between frequency and pitch; in systems with 12 tones within each octave, each one is $2^{1/12}$ (about 1.06) times the frequency of the preceding note. Schellenberg and Trehub (1996a, 1996b; also 1994a, 1994b) have argued that the octave (2:1), perfect fifth (3:2), and other pitch intervals with simple ratios are the reflection of innate constraints, as their presence facilitates processing early in development (also see Trainor & Trehub, 1993), and they hold a privileged status historically and cross-culturally (Sloboda, 1985). This idea that intervals of simple frequency ratios are more “natural” can be traced back to the writings of Pythagoras in ancient Greece and earlier to China (Daniélou, 1943). Despite such early emergence, however, neural network models suggest that innateness arguments may not be required. For example, Bharucha and Mencl (1996; also Terhardt, 1974) suggested that only the general mechanisms of perceptual learning, along with the harmonicity regularities found ubiquitously in the acoustic environment, are required to grant these intervals such special status. Nevertheless, such early display of these perceptual abilities is consistent with the involvement of innate constraints that make some regularities easier to learn than others.

**CANDIDATE CONSTRAINT: SCALE CATEGORIES AND MELODIC CONTOUR**

There is also evidence that the specific tones of the scale beyond these special intervals may be acquired early, and in this case we know that the knowledge in question must be acquired because such information is highly culturally relative. Lynch and colleagues have shown that whereas Western infants do not show an advantage for the major scale over a Javanese pélog scale at 6 months of age (Lynch et al., 1990), they do begin to differentiate between major, augmented, and pélog scales by 12 months (Lynch & Eilers, 1992; Lynch, Short, & Chua, 1995; also see Lynch et al., 1991). Although the specifics of the scales vary, the early tendency to categorize the octave into a set of tones may be guided by constraints.

Similarly, melodic contour, the overall pattern of ups and downs in a melody, is also an important device in musical organization that appears early in development (Morrongiello et al., 1985; Trehub, Bull, & Thorpe, 1984; Trehub, Thorpe, & Morrongiello, 1987). Infants treat an original melody and either one that has been transposed to a new key or one in which the specific intervals have been changed as the same melody, so long as the melodic contour is preserved. They discriminate, however, between melodies with different contours. Both observations echo Dowling’s (1978) distinction between scale and contour in music processing, which suggested that a melody is represented in terms of the contour, a pattern of approximate up and down intervals, and somewhat separately in terms of the tonal scale on which the contour is grounded.

**LATE EMERGENCE: TONAL-HARMONIC KNOWLEDGE**

Such findings of early sensitivity to these aspects of pitch processing are more meaningful when they are contrasted to research suggesting that other forms of musical knowledge are apparent only later in childhood. These include a full internalization of the concept of diatonicity or key membership (Trehub et al., 1986; Trainor & Trehub, 1992) and the concept of harmony (Krumhansl & Keil, 1982; Trainor & Trehub, 1994). Although late emergence does not guarantee that the material in question is learned and not shaped by innate maturational factors, with this particular case converging evidence from computational work showing the learnability of these concepts (e.g., Tillmann et al., 2000) and particularly the fact that these aspects of music are culturally relative allow us to make a reasonably strong inference that these aspects of tonal-harmonic knowledge are heavily influenced by learned, culturally transmitted information.

**CANDIDATE CONSTRAINT: GROUPING AND METER**

Finally, developmental approaches have also begun to shed light on which temporal aspects of music emerge early. Drake (1998) has argued that there may be two basic temporal processes in music that are universal: segmentation into groups and temporal regularity extraction. These correspond roughly to the building blocks of Lerdahl and Jackendoff’s grouping and metric hierarchies in GTTM, except that Drake argued that the recursive application of the basic principles may be acquired. Evidence from infant listeners suggests that they attend to the grouping as a salient feature by at least 4.5 months (Krumhansl & Jusczyk, 1990; Jusczyk & Krumhansl, 1993) and that they are sensitive to slight tempo changes by 2 months (Baruch & Drake, 1997). The later understanding of hierarchical grouping and metric structures may be mediated in part by a
preference to attend to increasingly slower temporal intervals with age, and an increased ability to redirect attention between different hierarchical levels in time (i.e., Dynamic Attending Theory; Jones & Boltz, 1989; Drake, Jones, & Baruch, 2000). Drake and Bertrand (2001) later expanded on the idea of universal constraints in music by suggesting five candidates: (a) the grouping of similar events occurring close in time, (b) a preference for temporally regular sequences, (c) temporal organization relative to real or perceived regular pulses, (d) an optimal zone of processing around a 600 ms interonset interval, and (e) a predisposition for intervals with simple duration ratios, 2:1 or 3:1 (see also Fraisse, 1956). For each of these, Drake and Bertrand offer a summary of the evidence in favor of these five as temporal universals, as well as areas where the evidence could be improved.

In sum, the currently available developmental literature identifies several areas of music that emerge early: the special status of the octave and perfect fifth, pitch processing relative to scales and contours, and basic principles of grouping and meter. We take this early emergence as evidence suggesting that there might be innate constraints involved. Given that the relationship between early emergence and innate constraint is soft, it is important to combine developmental approaches with the computational ones discussed in the previous section, and cross-cultural approaches, discussed next.

**Cross-Cultural Musicology**

Just as the caveat was made for cognitive development that early development does not guarantee innate constraint (and vice versa), it must also be recognized that cultural universality does not guarantee it either. Some universals or near-universals may exist because of common cultural descent, as in the similarities found between certain words across Indo-European languages (Cavalli-Sforza, 2000). The converse is true as well; given that many innate constraints are soft ones, some may not manifest themselves in every culture. As a general guideline, however, aspects of music that are found in multiple systems are more likely to be shaped by innate constraints than those that are not.

**A CULTURAL RELATIVISM: VARIABLE TONAL MATERIAL AND TUNING SYSTEMS**

The ways in which the space of an octave is subdivided into tones, along with the choice of specific sets of those tones for scales, is highly variable across musical systems. Consider first the total set of pitches within an octave, what Dowling (1978) referred to as the *tonal material* (see Figure 4). The Western subdivision of the octave into 12 steps is not universal; at least two other major musical systems divide it differently, the North Indian (22 steps) and the Arabic (16–24 steps, depending on the theorist) (Ayari & McAdams, 2003; Daniélou, 1943; Jairazbhoy, 1971/1995; Malm, 1967). Even within Western music history, the practice of tuning the 12 tones such that the steps are equal in size (*equal temperament*) is a relatively recent development dating from the eighteenth century. Before this, Western tuning systems were more directly based on the frequency ratios of the tones in the scale (*Pythagorean tuning* and *just intonation*). In these systems, the simple pitch ratios were more precise within a given key, but rapid modulation between different keys was not possible (Burns, 1999).

In addition to the variability in the division of the octave, the subset of pitches chosen for scales, what Dowling (1978) referred to as the *tuning system*, varies considerably (see Figure 4). In the music of North India, one of the 10 scales, or *thāts*, is used to create a *rāg*, a melodic form based on the *thāt*. One thāt, called *bilāval*, consists of pitches approximately the equivalent of the Western major scale. The others differ in the pattern of whole steps and half steps that make up the scale (Castellano, Bharucha, & Krumhansl, 1984; Jairazbhoy, 1971/1995). In one of the musical systems of Indonesia, the Javanese and Balinese pélog scales correspond even less to the intervals found in Western scales; the size of the intervals range greatly from the range of a quarter tone to that of a minor third (Kunst, 1949; Harnish, 1998; Sutton et al., 1998; see also Perlman & Krumhansl, 1996). As before, we can also look to music history within the Western tradition to see cultural forces at work; the modern major and minor scales grew out of the Gregorian modes of the medieval church, based on those of the Greeks, which in turn were borrowed from Egypt and the Near East (Daniélou, 1943). Some of the Gregorian modes, such as the *Phrygian*, are rarely used today except in period composition and some folk traditions.

**CANDIDATE CONSTRAINT: REGULARITIES IN SCALES**

Clearly, the specifics of scale structure vary across cultures, and they are not innately specified. In spite of this variability, it has been argued that loose regularities appear, which may be interpreted as innate constraints (e.g., Dowling & Harwood, 1986). The first is the simple observation that the pitch range within the octave is divided into categories, rather than being perceived purely as a continuum, and that the number of...
categories may be limited. Burns (1999) argued that despite the fact that the music theory of the Indian and Arabic systems divides the octave into intervals smaller than the semitone, in practice the intervals are closer to the 12 Western semitones. Such arguments have been around for some time; Daniélou (1943) found them Eurocentric and argued that systems based on 22 intervals are more psychologically valid. In any case, be it the semitone or something smaller, there is likely a minimum interval size that can be handled by our systems of categorization, and beyond which a musical system would become incoherent.

Three more regularities are apparent in the structure of scales. First, most systems tend to choose five or seven pitches, forming pentatonic or heptatonic scales, respectively. Included among these are the Western major and minor scales, most Arabic maqâmât, the North Indian thâts (all heptatonic), Chinese scales,
Indonesian sléndro scales (all pentatonic), Indonesian pégólo scales, and Southeast Asian scales (heptatonic and pentatonic). Second, the majority of scales in these and other systems use tones corresponding to the perfect fourth (4:3 ratio) and perfect fifth (3:2 ratio) above the first note of the scale. The primary exceptions to this trend are some of the Indonesian scales. Third, most scales employ different interval sizes such that within the context of the scale, each pitch is unique. The primary exception to this final rule is the music of Thailand, where heptatonic scales with equal intervals are sometimes used (T. E. Miller, 1998; Burns, 1999). The issue of Thai scales is contentious, however. Although the division of the octave into seven equal intervals holds somewhat well across theory and practice, the fourth and seventh tones are often left out (T. E. Miller, 1998). This may make the seven equal tones more analogous to the 12 chromatic pitches of the Western system (the tonal material), with a pentatonic scale chosen among them such that the interval sizes are distinct (Trehub, Schellenberg, & Kamenetsky, 1999; see Figure 4). Thus, despite the large variation, musical scales may show some regularities cross-culturally in terms of the number of tones and the nature of the intervals between them.

**Candidate Constraint: Tonal Hierarchies**

Related to the phenomenon of unequal interval sizes, there is initial evidence that the phenomenon of *tonal hierarchies* may be an important aspect of musical processing cross-culturally. The term *tonal hierarchy* refers to the differentiation of the tones of the scale in the frequency of use, and consequently their perceived importance and stability. Tonal hierarchies are often studied using the probe-tone technique, in which a single tone follows a musical context and participants rate the stability of the tone (Krumhansl, 1990). Westerners rate the tonic and the perfect fifth as highly stable following major and minor contexts, with more subtle differences between the two for the other scale tones, and give low ratings to the five tones not used in the scale (Krumhansl & Kessler, 1982). Similar findings appropriate to the musical system in question have been found using listeners from India (Castellano et al., 1984), Indonesia (Kessler et al., 1984), and the Sami of northern Scandinavia (Krumhansl et al., 1999, 2000; Krumhansl, 2000b).

In sum, cross-cultural studies can highlight important differences and similarities across musical systems and suggest other ways in which music may and may not be innately constrained. This approach strengthens some of the candidates from the “Cognitive Development” section (a limited number of pitch categories for tonal material and scales, the special status of certain intervals) and suggests the addition of at least two more: unequal interval sizes and the tonal hierarchies that result from them.

It is essential to emphasize that, given the brevity of our cross-cultural and developmental reviews, we do not wish to make any strong statements that these are the definitive set of innately constrained universals in music. Even such a cursory approach can, however, rule out other aspects of music that are clearly products of culture, such as at least four of the seven pitches within the Western system. Although we shall use our tentative list of possible innate universals derived in the current section when we discuss domain specificity in the second half of the article, our general approach would still apply even if future research causes a rejection of the specific universals we have suggested, or the inclusion of new ones.

**Cognitive Neuroscience**

A final source of evidence that may be used in determining the innately specified aspects of music comes from neuropsychology, the study of patients with acquired brain damage, and other forms of cognitive neuroscience. Unfortunately, much of the nativist argument within cognitive neuroscience suffers from the conflation of the issues discussed in the introduction: innateness, domain specificity, information encapsulation, and brain localization.

**Difficulties in Interpreting Innate Specification from Selective Deficits**

One way in which these issues dissociate is in the form of emergent modules (see Karmiloff-Smith, 1992). Predictable regions of cortex may become informationally encapsulated and/or domain-specific at the end of the developmental process, without this outcome having been “planned” by the genome. The cortex in question is simply the best suited or situated to process the kind of information in question. For example, consider that there is evidence for orthography-specific regions of visual cortex in literate Western adults (Farah, 1999; Polk et al., 2002). Written language is clearly a cognitive phenomenon of recent invention, appearing for the first time in Mesopotamia before 3000 BCE with a second independent origin in Mexico by 600 BCE (Diamond, 1997). There has been no chance for literacy to create coevolutionary pressures; widespread literacy within a human population was not even considered an educational goal until the nineteenth century.
We disagree with this logic. Unspecified for music does not mean equipotential. Certain regions of cortex, by virtue of input sources and other architectural constraints, will consistently win the competition as the home of choice for a cognitive "squatter" with particular information processing requirements. This is why the culture-dependent orthography-specific brain region of literate Westerners mentioned earlier does not vary capriciously in its location; it is found predictably in the same regions of extrastriate cortex because the architecture of that region is best suited for the job.

**DEFICITS FROM CONGENITAL ABNORMALITIES VERSUS ACQUIRED LESIONS**

Given the multiple developmental scenarios one can hypothesize for the effects of lesions acquired in adulthood, complementary studies of congenital musical abnormalities must be documented, ones that are also domain-specific. Peretz and colleagues (2001a; Peretz et al., 2002; Ayotte et al., 2002; Peretz & Hyde, 2003) provided a useful first step in this direction by studying tone-deaf individuals, whom they identify as congenital amusics. These participants had no difficulty discriminating spoken lyrics or environmental sounds but did have difficulties with simple melodic discrimination tasks. When musical deficits are truly congenital, and not the result of impoverished experience, such results are of much more import to arguments for innate specification for music-relevant cortex than results from studies of acquired lesions, which may have disrupted a system that was more environmentally dependent in development. Again, the issue of the domain specificity of these deficits and genes remains (a topic to which we return).

The findings of Peretz and colleagues complement the converging evidence from developmental and cross-cultural work that the basics of pitch perception and relational pitch processing may be shaped by innate constraints, thus having the potential to pass the first of our requirements for labeling as an evolutionary adaptation: innate constraint in development. Although computational research shows this information to be readily learnable, these are still among the strongest candidates for innate constraints relevant to music.

**Summary**

In the first part of this article we examined the first of two issues that we feel have not been sufficiently addressed in recent discussions of the evolutionary history of human music. The first issue concerns which aspects of musicality are explained by cultural transmission and which are determined evolutionarily. Clearly, a substantial amount of music is carried by cultural transmission. We suggest that computational approaches, developmental psychology, and cross-cultural studies, together with carefully interpreted cognitive neuroscience, are the most promising tools for determining the degree to which specific aspects of music are evolved innate constraints. The currently available research in these areas suggests that the strongest candidates include the special status of the octave and perfect fifth, pitch processing relative to scales and contours, basic principles of grouping and meter, and unequal interval sizes in scales and the tonal hierarchies that result from them. Only innate constraints and not culturally transmitted information require further consideration in light of natural selection. The next question
that must be asked about these mechanisms that are believed to be innately constrained is whether they are specific to the domain of music.

Determining the Degree of Domain Specificity in Music

Although genetically determined innate constraints likely play a role in musical development, it does not necessarily follow that music was the selecting force behind their evolution. The primary reason for skepticism here is the possibility that the relevant innate constraints are not domain-specific, showing parallels in other cognitive domains. When a mechanism is not domain-specific, it becomes unclear which domain or combination of domains provided the selection pressures, making quick adaptationist arguments highly suspect. As with the first requirement of innateness, the second requirement of domain specificity has been underestimated in recent treatments of the evolution of music (e.g., Huron, 1999; G. Miller, 2000; Brown, 2000). For example:

Music making has all the hallmarks of a group adaptation and functions as a device for promoting group identity, coordination, action, cognition, and emotional expression. Ethnomusicological research cannot simply be brushed aside in making adaptationist models. ... Music making is done for the group, and the contexts of musical performance, the contents of musical works, and the performance ensembles of musical genres overwhelmingly reflect a role in group function. The straightforward evolutionary implication is that human musical capacity evolved because groups of musical hominids outsurvived groups of nonmusical hominids due to a host of factors related to group-level cooperation and coordination. (Brown, 2000, pp. 296–297)

From the perspective of cognitive science, such a statement underestimates the importance of domain specificity of musical mechanisms and therefore, from the perspective of evolutionary biology, underestimates the importance of the distinction between function and use. One needs only to replace music with any number of other human activities that are easier to accept as the products of culture and non-domain-specific mechanisms (e.g., reading, mathematics) to appreciate the fact that modern importance does not imply uniquely evolved mechanisms. Without bearing the issue of domain specificity in mind, such approaches fail to consider several alternative scenarios in which the selection pressures were for other cognitive domains.

Given the problem of assigning selection pressures to mechanisms that apply to multiple domains, we feel that the best evidence of adaptation for a cognitive domain such as music is the demonstration of innate constraints that are domain-specific. As the review in this section will illustrate, we do not feel that any compelling argument for domain specificity in musical constraints has yet been presented to meet this requirement. Although a domain-specific innate constraint is highly suggestive of adaptation in that domain’s evolutionary history, in many cases no strong evolutionary conclusion can be drawn from a lack of domain specificity. The argument then would resort to competing evolutionary scenarios between the domains that share the mechanisms in question, including scenarios in which multiple domains provided the selection pressures. This is particularly the case for overlap between two complex human domains such as music and language. For each domain, there will always be the possibility that the mechanism in question originated exclusively through selection pressures in the other. In the case of language and music, most theorists have preferred to attribute the selection pressure to language (Lerdahl & Jackendoff, 1983; Pinker, 1997; see also Rousseau, 1781). A minority has suggested that the reverse be considered as well (Langer, 1948; Brown, 2000), although in such treatments it is often debatable whether the proto-domain should be considered “language” or “music.” In order to favor one of these scenarios over the other, the most compelling argument for selection pressures in either domain would be a firm demonstration of innately constrained domain-specific mechanisms that cannot be explained by selection pressures for other types of cognition.

In the cases where musical constraints are even more domain-general, being shared with relatively basic perceptual or representational abilities, the argument that the selection pressure was specifically for music is even less compelling. Among other reasons, other species may demonstrate similar abilities with regard to perception and cognition, without having evolved a behavior that may be considered music, suggesting that the other uses are phylogenetically older (see Hauser & McDermott, 2003, for a more extensive review on this issue). One may object that although such basic abilities

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5We regard domain specificity and domain generality as a continuum. Many mechanisms apply to limited sets of domains that share basic computational requirements, being neither truly domain-specific nor truly domain-general. Here we use the term non-domain-specific rather than domain-general because the critical distinction for the purposes of adaptation is between mechanisms that are specific to one domain versus ones that are not.
were the building blocks for music during its evolution, music further extends these principles and applies them to new uses. The question remains of how much of this extension was mediated culturally and how much, if any, was mediated by further natural selection for music. In the case of the latter possibility, we would expect the innate constraints in music then to go beyond what can be explained by its perceptual precursors.

In the remainder of this section we consider whether any of the candidate innate constraints developed in the first half of the article can be considered domain-specific. We shall consider the octave and simple pitch ratios, scale categories and melodic contour, tonal hierarchies, and principles of grouping and meter, each in turn, in terms of the currently available evidence from cognitive science. Again, although they are the starting point for our theoretical exercise, these candidates are themselves open to substantial modification by future research. After examining the evidence from cognitive science, we shall also examine evidence concerning a subset of these candidate constraints from cognitive neuroscience. This will be followed by a brief discussion of genetic evidence as it relates to the issue of domain specificity. As we consider the evidence, we ask the reader to keep in mind that any degree of domain generality in such candidate innate constraints calls arguments about their evolutionary history into question.6

Cognitive Science
EVALUATING DOMAIN SPECIFICITY: THE OCTAVE AND SIMPLE PITCH RATIOS
A fundamental problem of auditory perception is to segregate the large set of frequency information entering the ear into categories corresponding to different environmental objects and events (i.e., auditory scene analysis, Bregman, 1990; also see Handel, 1989; McAdams & Drake, 2002). In the natural world, most sound sources produce harmonic vibration, and the auditory system exploits this regularity by making the assumption that frequencies should be organized into harmonic spectra whenever possible to discern probable environmental events.

Auditory scene analysis may be sufficient to explain the first aspect of music that appears to be innately constrained: the similarity of octaves and other simple pitch ratios and the prevalence of such intervals in musical scales across cultures (see Schwartz et al., 2003). The same harmonicity heuristics used in auditory scene analysis would also make the assumption that pitches with overlapping harmonic spectra should be categorized together, as if they were part of the harmonic vibrations emanating from a single environmental object. There is a very strong relationship between the degree of overlap of the harmonic spectra of two pitches and the ratio of their frequencies (see Burns, 1999). In other words, pitches an octave, perfect fifth, or perfect fourth apart may sound similar to each other because their harmonic spectra overlap considerably, and the auditory system attempts to fuse them as a single environmental object (Bharucha & Mencl, 1996). When spectra do not overlap, near-match frequencies interact with each other and create a sense of roughness. This is one of the reasons why pitch intervals of simple ratios are regarded as consonant, and those of complex ratios as dissonant. The importance of the octave and other simple ratios may be the results of innate constraints that are not specific to music but rather evolved in the common ancestors of humans and other species (e.g., macaques, Wright et al., 2000; Fishman et al., 2001) for nonmusical reasons.

EVALUATING DOMAIN SPECIFICITY: SCALE CATEGORIES AND MELODIC CONTOUR
The third set of candidates for innate constraint in music are the importance of scale and contour in music. The perception of categories within the octave and the age when such abilities emerge (between 6 and 12 months) exhibit similarities with language-specific phonemic categories (see Lynch et al., 1995; Handel, 1989). The parallels may potentially go far beyond language; categorization is ubiquitous to perception and cognition, and parallels may exist even with arguably more distant domains with universal category constraints (e.g., color categories, Berlin & Kay, 1969; Heider, 1972). Others have suggested that the possible constraint that scales be of five to seven tones is an example of the short-term memory limitation for categories on a continuous dimension proposed by G. A. Miller (1956) (Dowling & Harwood, 1986). Again, the similarities of these constraints across disparate cognitive domains preclude any categorical statement about which domain or set of domains drove their evolution.

Similarly, melodic contour may share many characteristics with the prosody of language. This is the

6Arguments against domain specificity in music, in and of themselves, would not undermine the legitimacy of any innate constraints established by the methods outlined in the first half of the article, as innate constraints need not be domain-specific to be legitimate as innate constraints (see Bloom, 2000; Justus, 2001, in critique of Lieberman, 2000).
information derived from the intonation of speech, such as whether a statement is being made or a question is being asked. Just as infants attend primarily to melodic contour in music, they also attend strongly to the prosodic features of speech. Further, adults cross-culturally speak to infants and children with exaggerated prosody, suggesting an important role for prosody in language acquisition (Fernald, 1992). Thus, although infants are biased to attend to melodic contour, this constraint may be shared with language. Any common basis remains to be firmly established, but preliminary neuropsychological evidence suggests that the underlying neural mechanisms overlap (see the upcoming “Cognitive Neuroscience” section).

EVALUATING DOMAIN SPECIFICITY: GROUPING AND METER
Some of the basic rhythmic constraints also seem to have parallels in other domains. Among the earliest emerging grouping principles in music are a preference for phrases ending with a drop in pitch height and longer tone duration (Krumhansl & Jusczyk, 1993; Jusczyk & Krumhansl, 1990), which may parallel early segmentation preferences in speech (e.g., Hirsh-Pasek et al., 1987). There may also be parallel grouping principles based on transition probabilities in the two domains. Saffran et al. (1999) found that adults and 8-month-old infants perceived tone sequences in groups such that tones following each other with high transition probability were grouped together and tones following each other with low transition probability signaled a group boundary, a finding that extended analogous work with speech syllables (Saffran, Aslin, & Newport, 1996).

Other grouping principles in music show parallels with the Gestalt principles (e.g., Wertheimer, 1950), which extend across many perceptual domains in vision and audition. In music, the dimensions along which the principles operate include frequency, amplitude, temporal position, spatial location, or timbre, and the principles include proximity; similarity; good continuation, and common fate, just as in vision and other aspects of audition (see Deutsch, 1999a; Handel, 1989; Temperley, 2001; Narmour, 1990, 1999; Schellenberg, 1996, 1997; Krumhansl, 1995).

EVALUATING DOMAIN SPECIFICITY: TONAL HIERARCHIES
A final set of candidates for innate constraints discussed in the previous section is the tendency for unequal interval sizes in scales and the tonal hierarchies that result from them. These organizational principles, as well as the related one of harmonic hierarchies, in which certain chords are regarded as more important or stable than others, are of extreme importance in the organization of Western tonal-harmonic music (Bharucha & Krumhansl, 1983; Krumhansl, 1990). Both Gestalt psychology and Rosch’s work on concepts, prototypes, and cognitive reference points (e.g., Heider, 1972; Rosch, 1973, 1975) are also of relevance here. Individual tones within tonal contexts are not perceived in an atomistic manner, but rather in terms of their relation to the whole. Three contextual principles summarize the findings of such top-down processing on the relationship between tones (and chords): contextual identity, contextual distance, and contextual asymmetry (also see Tversky, 1977; Krumhansl, 1978). Such findings have parallels in other domains, such as color perception (Heider, 1972) or number concepts. Even the tonal-harmonic concept of key distance (e.g., C major is closely related or similar to G major), which at first may seem complex enough to require domain-specific mechanisms, can be interpreted as the recursive application of these relatively domain-general principles of cognitive organization.

In summary, for all of the candidate innate constraints discussed earlier, including the importance of the octave and simple pitch ratios, scale and contour, grouping and meter, and tonal hierarchies, the currently available evidence from cognitive science suggests parallels in other cognitive domains. Next we return to cognitive neuroscience, which we also hope will continue to address questions relevant to this issue of domain specificity.

Cognitive Neuroscience
In discussing cognitive neuroscience in the first part of the article, we considered the role of evidence from this field in assessing innateness; here we consider it in terms of domain specificity. Two bodies of research are particularly worthy of comment in this regard: the previously mentioned neuropsychological work on pitch perception and more recent developments using other cognitive neuroscience techniques to study the processing of higher-order musical structure.

Neuropsychological work by Zatorre (e.g., 1988; Zatorre et al., 1992) and Peretz and colleagues (e.g., Peretz et al., 1994; Liégeois-Chauvel et al., 1998) has shown that the posterior region of the superior temporal lobe, particularly on the right, is crucial for various pitch tasks, including pitch perception and melodic discrimination. This is consistent with the idea that certain aspects of the perception and representation of pitch are among the more likely candidates for innate universals in music. However, it is unclear whether such
a specialization is best considered musical per se. These same areas are also implicated for nonmusical tasks that involve pitch-based information, including discriminating different prosodic patterns in speech (e.g., Patel, Peretz, Tramo, & Labreque, 1998; Patel & Peretz, 1997). Further, in those cases of single dissociation between impaired musical pitch but preserved prosody, it is often unclear whether the nonmusical tasks require the same precision in pitch discrimination and representation as the musical tasks do (Peretz & Hyde, 2003). Thus, the possibility exists that areas of the temporal lobe are specialized for pitch computation, but in a way that is not necessarily domain-specific for music (see also Zatorre & Belin, 2001; Zatorre et al., 2002).

Evidence from event-related potential (ERP) research is also of relevance to the issue of domain specificity in music. Initial research suggests that the mechanisms underlying syntactic processing in music may overlap considerably with those of language. One piece of evidence supporting this is the fact that analogues of two event-related potentials associated with syntactic processing, the ELAN and the P600, are observed when listening to musical sequences that deviate from expected patterns (see Figure 5; Patel, Gibson, Ratner, Besson, & Holcomb, 1998; Patel, 1998; Koelsch et al., 2000, 2003; Maess et al., 2001). In fact, MEG evidence suggests that the first of these ERP components is derived from processing in Broca’s area and its right-hemisphere homologue (Maess et al., 2001). Thus, the potentially constrained mechanisms underlying the processing of higher-order syntax in music may not be domain-specific, but instead shared with language and perhaps other domains.7

More recently, neuroimaging researchers have begun to address the brain regions involved in the processing of more complex musical structures (e.g., Janata et al., 2002; Janata, Tillmann, & Bharucha, 2002; Tillmann et al., 2003). Of particular interest is the sensitivity of the inferior frontal cortex to manipulations tapping into higher-order musical structure, for instance when

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7 The possibility that music and language overlap is also considered in GTTM by Lerdahl and Jackendoff (1983), although they emphasize the similarities between musical syntax and phonological structure, specifically the hierarchical stress structure found in English and related languages (see Liberman & Prince, 1977).
contrasting activation to harmonically related and unrelated target chords (Tillmann et al., 2003). This region is also of extreme importance to various subcomponents of language (e.g., Fiez, 1997), but it is unclear to what extent this region, along with other areas of the frontal lobe, contains regions of specialization by domain and to what extent it is recruited by virtue of computational resources that are useful for a variety of domains (e.g., adaptive neural coding, Duncan & Miller, 2002). As with ERPs, neuroimaging could be of great import to evaluating claims about the domain specificity of processing resources used for music, particularly if multiple cognitive domains were studied in the same testing sessions, using analogous paradigms.

Finally, neuropsychology also has great potential for addressing the domain specificity of the processing of higher-order musical syntax, in addition to work on pitch perception discussed earlier. Rather than relying on single, often anecdotal, case studies showing dissociations between language and music, systematic research is needed comparing the abilities of large groups of patients with damage to areas of interest (e.g., the inferior frontal cortex) on tasks tapping both language and music processing, using comparable paradigms (see Patel, 2003, for a similar call for research, and Saygin et al., 2003, who conducted this kind of neuropsychological group study, comparing language and environmental sounds).

Thus, a number of cognitive neuroscience approaches are beginning to be used to investigate issues of domain specificity in music. As discussed in the preceding “Cognitive Neuroscience” section, it must also be remembered that a cortical region may use domain-general constraints to organize in a domain-specific manner (Karmiloff-Smith, 1992). Neuropsychological deficits must show evidence of both innateness and domain specificity to be compelling for an evolutionary argument within the domain in question.

Genetics

Recent advances in genetics make this a promising area for future research in cognitive neuroscience. However, logical mistakes can easily be made when the genetic underpinnings of a cognitive ability are discovered. For example, Huron (2001) suggested that “the best evidence of an evolutionary origin [for music] would be the identification of genes whose expression leads to the behavior in question.” Such a statement does not fully address the complexities of the relationship between genes and behavior. Symons (1992) offered a much more incisive treatment of the issue. He discussed three forms of the question “Are there genes for trait X?” The ontogenetic form of the question might be, “Did genes play a role in the development of trait X?” In the ontogenetic sense, the answer is a trivial yes to any question about genes and behavior. Everything about being human is inextricably linked to numerous genetic processes, and therefore the ontogenetic question is not particularly interesting for our purposes.

The heritability form of Symons’s question might be, “Is any of the population variance in trait X caused by genetic variance?” The question of the heritability of musical ability (i.e., innate talent) has been debated by Howe, Davidson, and Sloboda (1998) and remains a contentious issue. Even if the concept of innate talent for music is legitimate, however, this could be the result of variability in non-domain-specific mechanisms that are relevant to music (e.g., pitch perception, Drayna et al., 2001; also see the earlier discussion of “congenital amusia”) and does not say anything about the cultural and evolutionary forces in music’s past. To consider an example from another domain, it is relatively well established that good readers and poor readers have statistically different genetics (e.g., Cardon et al., 1994), but that does not change the fact that written languages are a cultural invention. Likewise, differences in musical ability may be partly explained by genetic differences, but this would not imply anything about the evolutionary history of music.

Lastly, the adaptationist form of Symons’s question might be, “Was trait X per se designed by selection to serve some function; i.e., is it an adaptation?” This is the critical question if one is interested in evolution, addressing whether any genes have undergone natural selection based on the behavior in question. An experimenter interested in the adaptationist form of the “music genes” question may be easily led astray by evidence relevant to the ontogenetic or heritability forms of the question. Symons argues that in order to answer the third form of the question one must look for evidence from the design of the trait. For cognitive traits, the most useful first step in this direction is through studies of domain specificity using cognitive psychological methods. Once one has identified genes that are related to the ontology or heritability of a particular cognitive domain, such studies must be combined with psychological work examining the domain specificity of the mechanisms used by the domain to answer questions about adaptation.

Summary

Domain specificity is of extreme importance when making arguments about purported cognitive
adaptations. When a cognitive domain uses mechanisms that are not domain-specific, it is impossible to argue categorically that the domain in question underwent natural selection. This is because the possibility always will exist that the other domain(s) with which the mechanisms are shared provided the selection pressures. In the terminology of evolutionary biology, it could never be known whether the domain of interest is a function and adaptation of the mechanisms in question, or a use or exaptation of those mechanisms. In the case of music, the candidate innate constraints that we have outlined—the importance of simple pitch ratios, pitch processing relative to scales and contours, basic principles of grouping and meter, and tonal hierarchies—all show parallels in other domains. We suggest that further research in cognitive science, cognitive neuroscience, and genetics must be conducted in which music and other cognitive domains are systematically compared in terms of the psychological processes involved, the functional anatomy, and underlying genetics, in order to more fully address the issue of domain specificity.

Conclusions

Music as a cognitive domain has much to offer the field of cognitive science. It has a rich and complex organizational structure. This structure is parsed by an intricate set of cognitive mechanisms in specific regions of the brain. This brain develops as a function of an extremely rich cultural environment and a genome that is the result of millions of years of diverse selection pressures. Although music’s evolutionary past is an important part of the puzzle that it provides to cognitive science, inferring this past is far from trivial.

We believe that the two issues developed here—(a) determining the nature of the innate constraints underlying musical development, and (b) determining the degree of domain specificity and domain generality of those constraints—are essential first steps in addressing that evolutionary history. Without sufficiently addressing the issue of innate constraint, one might erroneously credit a cultural phenomenon to natural selection. Without sufficiently addressing the issue of domain specificity, one might erroneously credit a selection pressure to one domain when it belongs to another.

The evidence examined here suggests that some aspects of music may indeed be the result of innate constraints that are specified genetically, although future research using computational approaches, cognitive development, cross-cultural research, and cognitive neuroscience certainly must test and refine these candidate areas further. These possible constraints include the importance of simple pitch ratios, pitch processing relative to scales and contours, tonal hierarchies, and basic principles of grouping and meter. These aspects of music may be shaped by representational, architectural, and chronotopic constraints that are a product of natural selection.

However, these same candidate innate constraints show parallels in other domains. In some cases the parallels can be found across many perceptual and cognitive abilities, and in others they may be relatively restricted to a more limited set of domains, being neither truly domain-general nor domain-specific. In all of these cases, we can never know what domain or combination of domains provided the relevant selection pressures that left us with the legacy of innate constraints that we have today. Music may have played a role in their evolution by natural selection. However, it is also possible that musical behavior emerged in an already well-adapted ancestral form of Homo sapiens, as a product of processing capacities put in place exclusively by other means, and developed from there in the realm of culture without further altering the human genome. Future research in cognitive science, cognitive neuroscience, and genetics across cognitive domains must address issues of domain specificity to help evaluate such adaptationist arguments.

In our view, given the current state of knowledge about music cognition, there is no compelling reason to argue categorically that music is a cognitive domain that has been shaped directly by natural selection. Such a conclusion is still consistent with the belief that music is a universal and cherished part of being human, as many of humanity’s most important achievements share similar evolutionary pasts. It is also consistent with the idea that music is a product of human biology, as all cultural knowledge is represented and processed in a network of brains. Instead, music may be an example of a domain that emerged from selection pressures in other domains and that relies on cultural transmission to carry the greater portion of its evolved complexities.

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