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Review Article

Parent-offspring conflict and the evolution of infant-directed song



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ABSTRACT

We present a theory of the origin and evolution of infant-directed song, a form of music found in many cultures. After examining the ancestral ecology of parent-infant relations, we propose that infant-directed song arose in an evolutionary arms race between parents and infants, stemming from the dynamics of parent-offspring conflict. We describe testable predictions that follow from this theory, consider some existing evidence for them, and entertain the possibility that infant-directed song could form the basis for the development of other, more complex forms of music.

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1. Introduction

The human music faculty has no established evolutionary basis (Fitch, 2005, 2006a; Honing, Cate, Peretz, & Trehub, 2015; McDermott & Hauser, 2005; Patel, 2008; Wallin, Merker, & Brown, 2000). This is odd, considering evolutionists' tendency to focus their attention on human behaviors that are complex, pervasive, and difficult to explain — all characteristics of music — and their success in explaining them. For example, theories of sexual selection (Darwin, 1871; Fisher, 1915, 1930), parental investment (Trivers, 1972), inclusive fitness (Hamilton, 1964), reciprocal altruism (Trivers, 1971), and parent-offspring conflict (Haig, 1993; Trivers, 1974) have helped to explain and predict swaths of extravagant, costly, and otherwise confusing phenomena in human behavior.

In each of these disparate areas the same analytic strategy has been productive: diagnosis of an adaptive problem present in ancestral environments, prediction of the design features of a potential adaptation which could solve that adaptive problem, and experimentation to examine the goodness-of-fit between those predicted features and real-world behavior. Research taking this approach has revealed, for example, that human incest aversion results from an adaptation for avoiding the genetic hazards of mating with close kin, not from social learning (Lieberman, Tooby, & Cosmides, 2007). Categorizing others on the basis of race is a byproduct of an adaptation for coalition categorization, not an adaptation for race detection per se (Kurzban, Tooby, & Cosmides, 2001). Sex differences in mate preferences result from sexually differentiated adaptations for minimizing cuckoldry (in men) and divestiture (in women), not from cultural happenstance (Buss & Schmitt, 1993).

Music is in principle no different than these non-musical behaviors in that it must be explicable either as the product of one or more adaptations or as a byproduct of one or more adaptations. A legitimate evolutionary theory of music can thus specify why a cognitive system with the properties of the human music faculty could emerge as a result of fitness-relevant goals that were reliably present in human ancestral history, and do so independently of anything already known about human music. Such an analysis requires the specification of a well-defined adaptive problem or problems and a correspondingly well-defined hypothesis for why some aspect of musical behavior is a candidate adaptation to solve that problem (or, rather, is a byproduct of some other adaptation). Together, these would yield predictions about the features music should and should not have.

Here, we attempt such an analysis, aiming to explain the emergence of a single, specific, well-defined form of music that is found in many cultures: infant-directed song. We examine the ancestral ecology of parent-infant relations and hypothesize that infant-directed song arose in an evolutionary arms race between parents and infants, stemming from the dynamics of parent-offspring conflict. We describe a series of falsifiable hypotheses that follow from this theory, consider existing evidence for and against each, and conclude by speculating on potential links between infant-directed song and music, writ large.

2. Why infant-directed song?

Music's immense feature space presents a significant roadblock to standard criteria for evolutionary analyses, as it includes a tremendous variety of content and behaviors. Many sounds that humans create constitute music and many behaviors in which humans engage include music. Consider the sounds of music: solo, duet, and group singing; chamber, symphony, and commercial studio orchestras; whistling, humming, and body percussion; recitative and underscoring; synth pop, folk singings and drum circles. Consider music's ubiquitous and diverse presence in human societies: we listen, sing, and play instruments alone for our own enjoyment, solo or in groups for audiences formal and informal; we use music in rituals and ceremonies political, religious, or otherwise; in education, for explicit instruction, or as a mnemonic

device in non-musical subjects; in film and television, where music often plays as much a role as the actors on screen; and in countless incidental contexts from radio segments to mobile phone ringtones to advertising slogans. Where should an evolutionary analysis begin?

2.1. The behavior to explain is song, not instrumental music

Typically, theories of music's evolution either do not distinguish between instrumental and vocal music or focus specifically on instrumental music. For instance, Dunbar, Kaskatis, MacDonald, and Barra (2012) interchangeably use instrumental and vocal music as examples of synchronized cooperative behavior (p. 698). Miller (2000) cites demographic trends in instrumental music performances as an example of a potential sexual dimorphism in music performance (pp. 354–355). Hagen and Bryant (2003) cite evidence for extensive drumming rehearsals as an example of coordinated musical activity (p. 31). This emphasis on instrumental music may be misplaced: just as evolutionarily-minded language scholars are concerned with speech and not with typewriters, we are unlikely to make progress in the study of music evolution by focusing on behaviors that rely on recent human inventions. Instead, we should focus on song.

While songs leave no fossils, Darwin (1871) and Helmholtz (1885) pointed out that it is a safe assumption that vocal song was the original form of human music. Several considerations support their assumption. First, the human auditory and vocal production systems are far older than the earliest known musical instruments (e.g., Fitch, 2006b; Martínez et al., 2004; Quam et al., 2013), as is the expansion of the thoracic vertebral canal, providing enhancements to respiratory control essential for speech (MacLarnon & Hewitt, 1999) and particularly important for singing (Fitch, 2006b); this makes it possible that song predates instrumental music. Second, the design features of the human vocal production apparatus are similar to many wind instruments, including ancient ones: a closed pipe (see Schwartz, Howe, & Purves, 2003). This suggests that these instruments mimic the voice (and not the reverse), consistent with the fact that reconstructions of the oldest known flutes yield a set of mutually consonant tones, remarkably similar to simple vocal melodies (supplementary audio in Conard, Malina, & Münzel, 2009; see also Section 4.5).

While vocal music is subject to strict constraints of human anatomy, instrument use and design is not, and thus is highly variable across cultures (e.g., Lomax, 1968), includes features relevant to music perception that are known inventions (e.g., equal temperament; Patel, 2008), and, in our view, can only complicate the systematic study of music's evolution.

2.2. Infant-directed song is a good candidate for evolutionary functional analysis

In modern environments, parents sing frequently to their infants and children (Custodero & Johnson-Green, 2003; Mehr, 2014), as do parents in small-scale societies. This practice is described in the ethnographies of many world cultures. For instance, in the Probability Sample File (Naroll, 1967) of the Human Relations Area Files (Murdock et al., 2008), text pertaining to singing appears in conjunction with ethnography concerning "Infancy and childhood" in 54 of 60 societies.¹ Further, infant-directed song is present in both the Hadza of Tanzania and the !Kung San of Southern Africa's Kalahari desert, the two most distantly related human groups currently known (Knight et al., 2003). Konner (1974) reports that San mothers sing to their infants in an effort to quiet them:

¹ Interested readers can replicate this finding by conducting an eHRAF search for PSF cultures containing OCM Code 850 and the keywords SONG SONGS SING SINGS SINGER SINGERS SINGING SANG SUNG LULLABY LULLABIES.

“If the infant is with a caretaker other than the mother, the caretaker will make a brief attempt at quieting and then carry the infant to the mother. Unless the infant is completely satiated the mother almost always responds by trying to nurse him ... If nursing is ineffective or partially effective, *rocking and singing are the next responses*, often with the infant pressed, front-to-front, against her chest and shoulder.”

(p. 293, emphasis added)

Marlowe (2010) reports a similar behavior in Hadza fathers:

“All caretakers appear to be equally sensitive to fussing and crying, but the mother is far more effective at soothing the child. However, it is usually the father who holds a crying infant in the middle of the night and *sings to get the infant to go back to sleep.*”

(pp. 206–207, emphasis added)

Adult listeners distinguish infant-directed songs from other singing, even when examples are taken from unfamiliar cultures (Trehub, Unyk, & Trainor, 1993a). Moreover, adults attend to the features of infant-directed song in sufficient detail to reliably distinguish between its true form (recordings of a parent singing directly to an infant) and a simulated form (recordings of the same parent singing alone but imagining that their infant is present). Independent listeners rate such simulated forms as less emotionally engaging than true infant-directed song (Trehub, Hill, & Kamenetsky, 1997).

In contrast to many modern forms of music that require technology and/or modern cultural contexts, infant-directed song could plausibly have existed throughout our ancestral history as both the requisite physical features (vocal tract, hearing apparatus, auditory cortex) and behavioral context (parent-infant interaction) were reliably present in the human ancestral ecology — ancestral hominid infants are likely both to have been fussy and to have had parents with a nonzero fitness interest in calming them (e.g., Trivers, 1974).

Finally, the musical features of infant-directed song are mostly inclusive of the musical features of song in general, with only a few exceptions (e.g., polyphony, metrical complexity); thus, a theoretical account of infant-directed song is likely to be informative for understanding song in general, if not music writ large. Across cultures, songs tend to have melodies and rhythms set to a steady beat (e.g., Lomax, 1968; Savage, Brown, Sakai, & Currie, 2015; cf. Clayton, 1996), though cross-cultural variation in these features has not yet been fully characterized. Thus, if a plausible theory for the emergence of infant-directed song can be described, it may inform study of the evolution of other forms of human music, which could have arisen as subsequent adaptations or byproducts and via cultural evolution.

2.3. Music perception skills and interest in music appear very early in human ontogeny

Young infants demonstrate impressive musical abilities (reviews: Patel, 2008; Trehub, 2001, 2003), decoding auditory input into rhythms (e.g., Trehub & Thorpe, 1989), decoding melodies into relative pitch contours (e.g., Chang & Trehub, 1977), and showing signs of perceptual narrowing (e.g., Hannon & Trehub, 2005). Neonates are sensitive to rhythms, developing expectations for repeatedly occurring downbeats, demonstrated by event-related brain potentials during omitted downbeats (Winkler, Háden, Ladinig, Sziller, & Honing, 2009). Infants also remember the music they hear: one-month-olds recall a melody heard while in utero, with sufficient detail to discriminate it from a second melody (Granier-Deferre, Bassereau, Ribeiro, Jacquet, & DeCasper, 2011), and long-term memory for music has repeatedly been demonstrated later in infancy (e.g., Saffran, Loman, & Robertson, 2000; Trainor, Wu, & Tsang, 2004; Volkova, Trehub, & Schellenberg, 2006), including after substantial delays without intervening exposure (Mehr, Song, & Spelke, 2016). Infants are highly motivated to

listen to music, moving spontaneously to it (Zentner & Eerola, 2010), tolerating listening to it longer than adult-directed or infant-directed speech (Corbeil, Trehub, & Peretz, 2016), and glean information from the songs they hear about the social affiliation of those singers (Mehr et al., 2016).

2.4. Existing evolutionary ideas about infant-directed song beg the question

We are by no means the first to consider infants' music perception abilities, motivations to listen to music, and striking responses to music in the context of evolution. Several have posited an adaptive function for music in enhancing “cohesion” or “bonding” between mothers and infants (Dissanayake, 2000, 2008, 2009; Falk, 2009; Trehub, 2001, 2003). But this reasoning is circular: it takes as a given the fact that music performance and listening produces reliable effects on mothers and infants, and then argues that one or more parts of the music faculty evolved in order to produce these effects. But *why* should music produce these effects and not others? What specific musical features produce these effects, such that music (and not something else) evolved to produce them? While the various sources of evidence we cite in the above sections indeed call for explanation, their existence does not constitute evidence that they result from an adaptation. As an analogy, modern adults' impressive abilities to read and write do not imply that they result from an adaptation for literacy (see Pinker & Bloom, 1990).

Incidentally, this same circularity undermines the most commonly cited claim concerning music's evolution, that music evolved to “bond the group together” or enhance cohesion between individuals (Barrow, 2005; Benzon, 2001; Brown, 2000a, 2000b; Conard et al., 2009; Cross & Morley, 2009; Dissanayake, 2000, 2008, 2009; Dunbar, 1996, 2012; Freeman, 2000; Fritz et al., 2013; Geissmann, 2000; Huron, 2001; Jourdain, 1997; Kirschner & Tomasello, 2009, 2010; Koelsch & Siebel, 2005; Kogan, 1994; Loersch & Arbuckle, 2013; McNeill, 1995; Merker, Madison, & Eckerdal, 2009; Morley, 2012; Pearce, Launay, & Dunbar, 2015; Reddish, Fischer, & Bulbulia, 2013; Richman, 1993; Roederer, 1984; Schulkin, 2013; Schulkin & Raglan, 2014; Trainor, 2015; Weinstein, Launay, Pearce, Dunbar, & Stewart, 2016; Wiltermuth & Heath, 2009). Pinker's (2007) critique applies to both “group cohesion” and “mother-infant bonding” accounts:

“Why do people crave sweets? Bad answers: because sweets give people pleasure, makes them feel satisfied; because eating sweets communally (at birthday parties, dates, and so on) brings people together. Better answer: because sugars contain accessible energy (a fact of chemistry), because the fruits of certain plants are rich in sugar (a fact of botany), because primates evolved in ecosystems with fruit-rich plants (a fact of paleoecology). Ergo, a drive to find and consume sweets would have provided an ancestral organism with energy, which is a prerequisite to reproduction. ... What about the arts? We can immediately see that any supposed function that appeals only to the effects we observe post hoc in people won't cut it. Perhaps singing lullabies soothes babies; perhaps dancing relieves tension; perhaps shared stories bond the community. The question is, why would anyone have predicted, a priori, that people would be constituted in such a way that these things would happen?”

(pp. 170–171)

Whether applied to groups or to mother-infant dyads, accounts invoking cohesion and/or bonding as an adaptive target provide neither a specific account of the ultimate functional mechanism by which music should increase cohesion, nor an account of how that cohesion would produce fitness advantages. And if cohesion is indeed fitness enhancing, why should individuals wait for music-making to produce that cohesion? Why not just be cohesive without music? Put another way, if music is not a necessary precondition for cohesion, why would natural selection design organisms that expend more effort than necessary to

produce a cohesive group via music, when they could otherwise do it in a fashion that is less costly?

In sum, while we agree that infancy is a promising time to investigate the evolution of music (e.g., [Dissanayake, 2000](#); [Fitch, 2005](#); [McDermott, 2009](#); [Patel, 2008](#); [Trehub, 2003](#)), existing ideas about infant-directed song do not provide an ultimate-level explanation of its emergence. The primary goal of the theory to which we now turn is to provide such an explanation.

3. A theory for the evolution of infant-directed song

3.1. Ancestral ecology of parenting

Infant mortality was a substantial risk throughout hominid history. Estimated rates of mortality by age 15 range from 40% to 60% ([Hrdy, 2009](#)), including deaths from infanticide (e.g., [Paul, Preuschoft, & Van Schaik, 2000](#)), starvation (e.g., [Kaplan, Hill, & Hurtado, 1990](#)), and/or disease (e.g., [Gottlieb, 2004](#)). This grim state of affairs implies that ancestral human parents were likely to outlive a substantial proportion of their offspring. As parents are infants' main source of sustenance and protection, parental behaviors are thus expected to have been subject to strong selection pressures, especially in terms of solving infants' crucial adaptive problems of maintaining adequate nutrition and safety.

In his 1974 theory of parent-offspring conflict, Robert Trivers described the contrasting fitness interests of parent and infant in terms of parental investment, predicting that the infant should attempt to elicit more investment than the parent should optimally provide to her (and therefore not to an existing or future sibling), because a gene present in the infant has only a 50% likelihood of occurring in either mother or sibling by recent common descent. As such, holding the degree of benefit constant, a unit of investment translates into greater reproductive fitness for the gene in the infant if invested in the infant, rather than in a parent or sibling. The original evidence for parent-offspring conflict was mostly limited to non-human species (e.g., weaning conflict in baboons; [DeVore, 1963](#)), but human evidence for it takes many forms. For instance, when parents are under resource deprivation, they are more likely to reduce investment in higher risk infants ([Beaulieu & Bugental, 2008](#)), or resort to infanticide ([Daly & Wilson, 1984](#)). This is not in the infant's interests, but makes sense for parents facing a tradeoff between the relative returns on investment in high- vs. low-risk infants. The regulation of parental investment, and in its absence, neglect, abuse, and infanticide by parental resource level has been observed in both industrialized and traditionally living populations ([Beaulieu & Bugental, 2008](#); [Daly & Wilson, 1988](#); [deVries, 1984, 1987](#); [Mann, 1992](#)).

3.2. Parental attention solves the safety problem, but attention is invisible

While parent-offspring conflict research often concerns material investment to solve the infant's nutrition problem (i.e., conflict over the age of weaning), conflict over investment is expected regardless of the specific content of that investment; that is, investment is defined generically, as a fitness benefit to the infant at a cost to the parent's ability to invest in other offspring ([Trivers, 1972](#)). Investment can thus include not only material provisions but also the immaterial, such as "attention paid to infant". We expect this form of parental investment, which we call *attentional investment*, to play an important role in infancy. Whereas nursing helps to solve the infant's nutrition problem, a parent's watchful eye helps to solve the infant's safety problem: infants have neither the motor abilities nor the requisite knowledge to keep themselves safe from predators and other environmental hazards, but an attentive parent can mitigate these risks. The degree of attentional investment should be subject to parent-offspring conflict because parental attention benefits a specific infant while imposing a cost on the parent (e.g., the parent could otherwise be foraging) and to the infant's siblings, present or future (e.g., the parent could otherwise be paying attention to them). Conflict is expected within the margin between the infant's preferences

and parent's preferences, but not outside that margin. Just as it is not in the infant's fitness interests to completely deplete a parent's material resources — this would reduce direct future investment from the parent and reduce production of and investment in siblings — it is not in the infant's fitness interests to consume all of her parent's attention.

A problem for the infant emerges immediately, however: attention is invisible. How can an infant know that a parent is, in fact, attending to him? Infants routinely observe behaviors concomitant of parental attention. For example, the parent's gaze toward the infant is a cue of parental attention; at minimum, the infant is now in the parent's visual field. But the cue is imperfect, as the parent might be looking in her infant's direction while covertly attending to other things, leaving the infant's hazard management needs unmet. Selection on infants' appetite for attention should be relatively unsated by this sort of cue. Parents should thus have been under selection to *signal* their attention to their infants, to better sate their infants' appetites. And because parents' and infants' interests are not perfectly aligned, signals can be deceptive; infants should thus have been under selection to discriminate between signals, to attempt to detect faked signals, and to resist them ([Dawkins & Krebs, 1979](#)).

Like other animal signals, costs can keep them honest. These may include direct costs, in terms of energy or materials; opportunity costs, in terms of other activities forgone; and out-of-equilibrium costs, where it is costlier to fake the signal than to produce it honestly. These costs are easily manifested in vocalization: they might include intricacies requiring planning or memory (direct costs); they might require parents to control their breathing specifically for the act of vocalizing, requiring the parent to not be doing other effortful actions simultaneously (opportunity costs); they might include vocal patterns contingent on the infant's affective state and responses, requiring the parent to attend to that state (out-of-equilibrium costs); or they might include vocalizations whose rhythmic and melodic motifs develop over the course of a single performance, requiring the parent to not be distracted by other actions (all three). Vocalizations with some or all of these properties may satisfy infants' attentional demands more quickly, because their presence increases the perceived likelihood of the infant's safety problem being solved.

Given the substantial amount of time that parents must spend providing infants with attentional investment, we also expect selection pressures toward the development of defenses against infants' elicitation of such investment. By this logic, genes that increase the benefit-to-cost ratio of attentional investment, e.g., by supporting parental ability to provide higher-quality forms of attentional investment that satisfy infant demands more quickly, per unit cost, would be under positive selection. This prediction assumes that the increased costs of producing more intricate infant-directed vocalizations are dwarfed by the fitness benefits gained by calming infants more quickly and more reliably. Correspondingly, however, genes promoting infants' defenses against these more intricate vocalizations would also be under positive selection; infants can afford to demand more because parents have new residual budget, leading over time to an up-regulation of the threshold of attentional signal necessary to satisfy infants' elicitation.

3.3. Infant-directed song from arms-race coevolution between parents and infants

We therefore predict arms-race coevolution ([Dawkins & Krebs, 1979](#)), similar to mind-reader/manipulator relations implicated in intersexual selection across many species (e.g., [Fisher, 1930](#); [Krebs & Dawkins, 1984](#)). This proposed coevolution is the crux of our theory: it describes the evolutionary mechanism by which vocalizations could develop from the rather non-musical sounds of nonhuman primate parents, to the music-like cooing and sighing of human infant-directed vocalizations (whether or not those vocalizations include semantic or propositional content), and eventually to full-fledged infant-directed song.

Conflict cannot be the whole story, however: if this coevolution continued unabated, one would predict a bizarre world in which infants cry ferociously and constantly while parents spend all their time inventing ever-improved songs. Just as arms-race coevolution in sexual selection is limited in the extreme by fitness costs, both infant attention elicitation and parent production of infant-directed vocalizations must be limited by their potential risks to fitness. The infant who attempts to elicit *too much* attentional investment risks incurring fitness costs: a parent can cut her losses via infanticide, diverting the investment to other offspring. The parent who responds with *too much* attentional investment risks incurring fitness costs: parents who over-invest in singing for infants will be out-reproduced by those parents who invest less, because the extra, unnecessary effort could otherwise go to another offspring. Coevolution of infant preferences for costlier attentional investment and parental response to infant elicitation are thus constrained by the same fitness pressures that prompt them in the first place.

4. Goodness-of-fit of the proposed adaptation

Why should parents' ability and motivation to produce infant-directed song and infants' ability and motivation to elicit infant-directed song together form a good solution to the adaptive problems described above? In the next sections, we clarify what and whose behaviors our theory concerns, and consider comparative work on infant-directed vocalizations, the features of infant-directed song, why those features might have uniquely solved the adaptive problems described above, and relevant distinctions between music and language.

4.1. What should count as infant-directed song?

While infant-directed songs in modern environments may include play songs, lullabies, and other songs directed at infants, for the purposes of our theory, we are specifically concerned with those songs that provide signals of attentional investment in order to regulate behavior. While some songs may regulate infant behavior without satisfying an appetite for attention, the theory we present here does not address them. Thus, here infant-directed songs only include those that convey attention to satisfy a distressed infant's demands. There may well be other mechanisms by which infant-directed songs regulate infant behavior; for instance, infants' use of others' songs to identify caregivers or social partners (Mehr et al., 2016; Mehr & Spelke, 2017). The present theory is agnostic to this and other roles that music may play in infancy.

4.2. Who should count as an infant?

The present theory is most concerned with those children who depend on their parents' attentional investment to manage safety risks and are least able to control their own proximity to their parents with their own motor system. That is, our theory applies most to infants under a year of age, who do not yet walk; somewhat less to one- to two-year-olds, who walk efficiently; and much less to older children, who have a variety of strategies for maintaining proximity to parents and manipulating parental investment.

4.3. Relevant differences between humans and nonhuman primates

While nonhuman primate infants produce a wide variety of vocalizations, many to elicit care, their parents rarely vocalize in response (reviews: Maestripietri & Call, 1996; Falk, 2004). Goodall's (1986) inventory of chimpanzee calls includes none that are specifically infant-directed (p. 127). While Goodall reports chimpanzee mothers' clear reactions to their infants' vocalizations, those reactions are mostly physical or visual, and when vocal they are rare and limited to the "hoo", which is used in a variety of contexts outside of infant care (pp. 129–132). The only other notable examples of infant-directed vocalizations in Goodall (1986) are threatening barks or nondescript grunts to badly-

behaved infants (pp. 575–576). Plooj (1984) extensively describes infant chimpanzees' vocal repertoire, but barely mentions infant-directed vocalizations. Nicolson (1977) describes infant-directed gestures but makes little mention of vocalizations, and in an extensive study of mother-infant interactions, independent coders reliably identified parenting behaviors, but those behaviors did not include any reliably occurring vocalizations (Bard, 1994, 2000). A comparable lack of infant-directed vocalizations is evident from observations of bonobos (Bermejo & Omedes, 1999; Kano, 1992; Savage-Rumbaugh, 1984). Bonobo infants may vocalize to elicit care from their parents, and parents are responsive to these elicitation, but this care is given mostly in silence (Coe, 1990). Girney vocalizations in rhesus macaques have been observed in direction both to infants and to mother-infant dyads, but mothers do not typically use girneys with their own infants (Whitham, Gerald, & Maestripietri, 2007). The only nonhuman primate we know of whose vocal repertoire includes infant-directed vocalizations is the squirrel monkey: Biben, Symmes, and Bernhards (1989) provide evidence for an acoustically distinct class of "caregiving calls" which are modulated by the presence of different parenting behaviors.

This general lack of infant-directed vocalization in nonhuman primates is in stark contrast to human parents, who produce infant-directed vocalizations spontaneously and frequently across many, if not all cultures. Such infant-directed vocalizations consist of speech (Broesch & Bryant, 2015; Ferguson, 1964; Fernald, 1984; Fernald & Simon, 1984; Snow, 1972, 1977; Snow & Ferguson, 1977; Werker, Pegg, & McLeod, 1994) – a domain where clear form-function relationships have already been delineated (Bryant & Barrett, 2007; Falk, 2004; Fernald, 1992) – and song (Custodero & Johnson-Green, 2003; Trainor, Clark, Huntley, & Adams, 1997; Trehub et al., 1993a, 1997; Trehub, Unyk, & Trainor, 1993b), where they have not. This striking difference between humans' and nonhuman primates' vocal repertoires is not due to a lack of variance: the species mentioned above have wide repertoires of calls that are regularly used in social interactions, but their repertoires simply appear to not be specialized in any clear fashion for direct parent-infant communication. Presumably, early hominins were similar to modern nonhuman primates in this respect; considering these patterns of vocalizations in conjunction with nonhuman primates' rich auditory perception abilities (review: Rauschecker & Scott, 2009) supports the possibility that a somewhat primitive set of vocalizations could have been the seeds of infant-directed song.

Moreover, Falk (2004) points out a crucial difference between the parent-infant ecologies of humans and other primates: in most anthropoids, the infant is in constant physical contact with his mother, clinging directly to her chest or back and riding unaided (e.g., Ross, 2001). In contrast, human infants are unable to cling to their hairless parents (though they do display a vestigial grasping reflex; e.g., Halverson, 1937). Whenever this shift in ecology occurred, it would have created adaptive pressures in parents toward carrying, parking, or slinging, and in infants toward crying to bargain for proximity and investment. When infants are in constant physical contact with parents, as in chimpanzees, there would be far less opportunity for parent-offspring conflict over attentional investment: the infant chimpanzee riding his mother has no need for the signals attentional investment is predicted to contain (e.g., physical proximity). But once human infants could not easily ride along with parents, the adaptive value of attentional investment – and the frequency of behaviors that could elicit more of it – would rise. This prediction is borne out by one observational study of parent-infant interactions in chimpanzees and humans: while chimpanzee infants may cry for extended periods of time when alone, they calm immediately when a caregiver picks them up; in contrast, human infants may cry for long periods of time even when held by a parent (Bard, 2000).

4.4. What features should infant-directed songs have?

Because the proposed adaptation relies on parent-offspring conflict, we expect infant-directed song's design to conform to Krebs' and

Dawkins' (1984) predictions for ritualized signals, analogous to human advertising, with features that "lead to effective advertising including redundancy, rhythmic repetition, bright packaging and supernormal stimuli..." (p. 386). These conspicuous features follow closely with Wiley's (1983) criteria for reliable signal detection, reviewed in Fernald (1992). As human infants are physically separated from parents more often than the infants of many nonhuman primates, infant-directed song should thus function efficiently as a signal, even when used at a distance. Moreover, infant-directed song should have a high signal-to-noise ratio, such that it is immediately detectable in even noisy environments, and such that infants can immediately distinguish it from the surrounding auditory scene. These predictions go hand-in-hand with Wiley's criteria, and they dovetail with Morton's (1977) rules concerning form-function relationships in vocal behavior (see also Owren & Rendall, 2001). Fernald (1992) notes: "It is intriguing that the features that selection favors in enhancing signal detectability... are all robustly characteristic of infant-directed vocalizations in human speech and decidedly uncharacteristic of adult-directed speech" (p. 419). We note that they are even more characteristic of infant-directed song than infant-directed speech.

Further, if infant-directed song honestly signals parents' attention, its features should not only attract infants' attention, but they should facilitate infants' detection of the signal's honesty. One fashion in which this could play out is in the multimodal experience of infant-directed song's use in parenting (e.g., Dissanayake, 2008), which includes a wide variety of sounds in conjunction with motions, facial expressions, and touch. To illustrate this point, consider the many differences between the experience of listening to a high-quality recording of a solo voice, and the experience of listening to an attentive parent's infant-directed singing. The parent has ample opportunity to fine-tune their actions, in real time, tailoring them to the infant's responses, with respect both to the singing itself (e.g., tempo, accent, timbre, lyrics) and to physical actions (e.g., touching infant, rocking, dancing, facial expressions). The recording does not (for further discussion, see Mehr et al., 2016). A parent can only provide such a responsive, multimodal experience to an infant to whom he or she is directly attending.

4.5. Features of the natural world may provide a musical foundation for infant-directed song

What reason is there to expect that elaboration of vocalizations via arms-race coevolution would yield proto-melodies? Whereas the in-nateness of a preference for harmonic consonance (i.e., combinations of pitches that humans typically consider pleasant-sounding) has recently been called into question (McDermott, Schultz, Undurraga, & Godoy, 2016), some evidence suggests that such a preference could arise from the particular harmonic spectra of naturally occurring sounds (McDermott, Lehr, & Oxenham, 2010). Notably, such preferences are not found in cotton-top tamarins (McDermott & Hauser, 2004) or common marmosets (McDermott & Hauser, 2007). Evidence from the statistical structure of human speech (Ross, Choi, & Purves, 2007; Schwartz et al., 2003) suggests that the segmentation of pitches into chromatic scales may arise naturally from the simple fact that all humans experience human voices throughout their lives – both their own voices and those of the humans they listen to (see Gill & Purves, 2009). In the same vein, the spectra of major and minor melodies are differentiable from one another in a fashion similar to excited and subdued speech (Bowling, Gill, Choi, Prinz, & Purves, 2010). We note, however, that it is not known if the distinction between major and minor keys are structures found universally in vocal music; indeed, the origins and degree of universality of both melodic and harmonic consonance are controversial topics deserving of much more discussion. At present, we note only the following: if one or more of the above explanations for consonance proves to be correct, it would provide evidence in favor of a musical constraint on the elaboration of infant-directed vocalizations from other, non-infant-directed vocalizations over evolutionary time.

The division of the entire human vocal range into discrete pitches and the limiting of those pitches to particular consonant sets provide only one half of the necessary components for infant-directed song. What of rhythm? Here, we note that several nonhuman species spontaneously entrain to isochronous beats (Cook, Rouse, Wilson, & Reichmuth, 2013; Patel, Iversen, Bregman, & Schulz, 2009; Schachner, Brady, Pepperberg, & Hauser, 2009). While this evidence has previously been interpreted as a musical behavior, Patel (2014) notes both that the ability to synchronize is present in non-auditory domains in several species (Greenfield, 2005) and that synchrony emerges as a stable state in systems of simple biological oscillators (Patel, 2014, p. 1; see Mirolo & Strogatz, 1990). The predisposition to entrain to repetitive events (acoustic or otherwise) combined with early-appearing preferences for consonant tones may thus have provided a mechanism with which infant-directed song could be built up from prior infant-directed vocalization. While the adaptation we propose likely does not account for the full complexity of musical rhythm, the signal that infant-directed song sends is thus likely to be enhanced by a predisposition toward synchrony; such a predisposition could be enhanced by further adaptations, such as the use of music as an honest signal of a group's cooperative ability and coalition strength (Hagen & Bryant, 2003).

4.6. A note on language

The theory we have described is fully agnostic to the evolution of language, a human faculty with much more obvious adaptive value than that of music (see, e.g., Pinker & Bloom, 1990). We make no claims about the representational or propositional content of infant-directed vocalizations, only their signals of parental investment. The development of infant-directed song can proceed with or without words and we assume that its proposed adaptive value would be no different whether or not it originated at a time during which language was already present. In work that helped to motivate the present theory, Fernald (1992) described the communicative functions of infant-directed vocalizations as potential seeds of language (a view elaborated in part by Falk, 2004). We find it more likely that infant-directed vocalizations are the seeds of music.

5. Predictions concerning infant-directed song

We predict that infant-directed song should be produced universally by parents and should universally provoke positive responses in infants; infant-directed song should be an effective means by which to calm a distressed infant; infant-directed song should be a supernormal stimulus and that the features that make it so should be universal; and that people with genomic imprinting disorders should exhibit abnormal responses to music consistent with parent-of-origin effects specific to each disorder.

5.1. Universality of parent production of infant-directed song and infant response to it

Parental production of infant-directed song should be universal across human cultures, regardless of the presence of other forms of music. The design features of infant-directed song should also be consistent across cultures, including both its musical features and the behavioral contexts in which it is used by caregivers. This prediction has already been supported by two sources of evidence: first, that infant-directed songs from some cultures are differentiable from adult-directed songs from the same cultures by naïve listeners (Trehub et al., 1993a), and second, that a distinctive style of singing to infants exists in at least three cultures, detectable by both adults (Trehub et al., 1993b) and children (Trehub, Unyk, & Henderson, 1994).

The universality of infant-directed song, including the proclivity of parents to sing to infants, the style thereof, the particular musical features it has, and infants' responses to it, has not yet been systematically

described.² A comprehensive feature analysis of infant-directed song from a standardized cross-cultural sample could determine which of its acoustic features are universal; our theory predicts reliable differences between infant-directed song and other forms of music (e.g., regardless of cultural origin, lullabies could be slower than dance songs and include smaller melodic intervals). Corresponding experiments could test infants' responses to and adults' recognition of unfamiliar cultures' infant-directed song; we predict that it should soothe infants regardless of whether or not it is foreign (assuming universal acoustic features exist) and that adults from all cultures should recognize infant-directed song from all cultures at rates higher than chance (assuming its universal existence; initial evidence with a small set of cultures is in *Trehub et al., 1993a*).

5.2. Effectiveness of infant-directed song as an infant behavior manipulator

Infant-directed song should be an effective method of calming an attention-seeking infant: infant distress should be assuaged more quickly and more reliably by infant-directed song than by related vocalizations that lack its acoustic and behavioral features. Direct byproducts of infant-directed song (such as sound recordings of vocal music) should still produce positive infant responses, but should less efficiently modulate infant temperament to the extent that they lack these features.

Some evidence supports this prediction. While listening to looped recordings of infant-directed song, 7- to 10-month-old infants take roughly twice as long to exhibit signs of distress than while listening to adult-directed speech or infant-directed speech (*Corbeil et al., 2016*), despite the fact that infants will attend comparably long to the same stimuli in a preferential listening paradigm (*Corbeil, Trehub, & Peretz, 2013*). Further, infants recover from induced distress (in a still-face paradigm) more quickly when presented with maternal song than speech (unpublished work described in *Trehub, Ghazban, & Corbeil, 2015*). These promising results merit replication and extension, so as to determine the extent of music's effects on infant behavior.

In randomized trials, infants in neonatal intensive care units have improved feeding behaviors when given a pacifier that plays a recording of maternal singing (*Chorna, Slaughter, Wang, Stark, & Maitre, 2014*), and songs produced live by a non-parent induce several positive health-related outcomes in neonates (*Loewy, 2015; Loewy, Stewart, Dassler, Telsey, & Homel, 2013*). But it is not yet known whether these effects are attributable specifically to music, or whether they can be elicited by any positive auditory stimuli, because these studies lack comparison groups that receive non-musical vocalizations (i.e., comparing effects of infant-directed song to infant-directed speech). If and when such studies are conducted, we predict that infant-directed song will elicit the strongest effects, non-infant-directed music will be moderately effective, and non-musical vocalizations will be least effective.

5.3. Infant-directed song as supernormal stimulus

Implicit in our theory is a scaffolding of infant-directed song on other infant-directed vocalizations, which themselves are built from other, non-infant-directed vocalizations. We have described several potential criteria on which infant-directed song should differ from these putative precursors (see above); this prediction is testable via an acoustic analysis of infant-directed song, infant-directed vocalization, and primate vocalizations (as a stand-in for early hominin vocalizations, which of course are unavailable). We predict that such an analysis would show progressive increases in the salience of acoustic features predicted for ritualized signals (see *Section 4.4; Fernald, 1992; Krebs & Dawkins, 1984; Wiley, 1983*). For example, an acoustic analysis of primate vocalizations might show the shortest attack envelopes (i.e., corresponding to startling beginnings of tones), generic infant-directed vocalizations

should show longer ones, and infant-directed song should show the longest (i.e., smoothest contours). Comparable progressions might be tested for many other acoustic features (e.g., amplitude decay; F0 mean, variability, and range; vowel prolongation and stability). We predict that those acoustic features that appear most consistently in infant-directed song across cultures should be the same acoustic features that develop from primate vocalizations to generic infant-directed vocalizations to infant-directed song. Because the universal acoustic features of infant-directed song have yet to be documented, this prediction is necessarily vague with respect to which particular acoustic features these should be.

5.4. Genomic imprinting disorders as test cases

Genomic imprinting is a mechanism whereby a common set of genes can differentially express the fitness interests of their parent of origin (e.g., *Haig, 2002*). Because human maternity certainty is always greater than paternity certainty, paternally inherited genes in offspring (relative to maternally inherited genes in offspring) are under stronger selection to more selfishly weight the offspring's interests vis-à-vis her putative siblings. Several human disorders of genomic imprinting, Prader-Willi, Angelman, and Beckwith-Wiedemann syndromes, include dysregulation of investment-related traits that promote maternal or paternal fitness interests as part of their more diverse symptom profiles. For example, Prader-Willi syndrome often results from a loss of paternally inherited regions of chromosome 15q11-13 (through maternal uniparental disomy, mutation, translocation, or deletion). The absence of these paternally influenced genes results in a variety of symptoms that express maternal interest by reducing demands on investment, such as reduced intrauterine growth of the fetus, reduced sucking reflex and lethargy in the infant, and hyperphagia following typical weaning age (review: *Haig, 2010*).

Moreover, imprinted genes tend to be clustered such that imprinted regions coordinate multiple adaptive targets relevant to parental conflict of interest (*Bartolomei & Ferguson-Smith, 2011*). If parent-offspring conflict is the driving force behind the origins of infant-directed song, genes in this region may regulate design in offspring for eliciting it from parents. If so, pairs of genomic imprinting disorders may be associated with predictably divergent musical behaviors. For instance, if genes in the 15q11-13 region regulate design for song elicitation, people with Prader-Willi syndrome should show decreased appetite for infant-directed song, which would benefit maternal fitness by reducing demands on her, while individuals with Angelman syndrome should not, or would show the reverse (i.e., an increased appetite for infant-directed song, increasing demands on the mother).

Preliminary evidence supports these predictions. Prader-Willi syndrome is associated with low participation in musical activities (*Sellinger, Hodapp, & Dykens, 2006*) and reduced enjoyment of music listening (*Rosner, Hodapp, Fidler, Sagun, & Dykens, 2004*). In contrast, Angelman syndrome is associated with strong preferences for musical stimuli (*Cassidy & Schwartz, 1998; Didden et al., 2006*) and also with distinctive smiling and laughter in response to tones produced with a tuning fork (*Hall, 2002; Hall & Cadle, 2002*). However, no studies have directly tested differences in musical response across these and other populations with genomic imprinting disorders, whether these effects are specific to infant-directed song rather than music in general in these populations, or whether parents of children with genomic imprinting disorders sing atypically frequently (or infrequently).

6. Predictions concerning music, writ large

If our evolutionary account of infant-directed song is empirically validated, an important question will arise: Did the emergence of infant-directed song lead subsequently to the development of the rest of the human musical faculty, and to human music, writ large?

² This level of detail is generally not available from ethnographic text searches of the type described in *Section 2.2*.

There are two possibilities: first, that the only adaptation for human music is infant-directed song (leaving the rest as byproduct), and second, that infant directed song is one of potentially several sources of adaptive design in the human music faculty. Both accounts inherit a common base of non-musical design features that will additionally influence the resulting psychology of music and associated behaviors, such as general properties of the auditory system, vocal communication, social learning, cooperation, and so on. Thus, the task for applying our theory to music outside of the domain of infant-directed song is not to explain every feature of music and every musical phenomenon in the modern world. Many of these features and phenomena will be byproducts of either musical or non-musical adaptations, the idiosyncrasies of human cultural history, and the products of cultural evolutionary processes. Rather, the task is to find those musical features that are best explained by our theory, and to systematically determine whether those particular musical features could, in principle, underlie the rest of the musical faculty. Some attempts at this follow.

6.1. Comparisons between adult and infant responses to music

Adaptations present in infancy that are not detrimental to survival in childhood and adulthood will not necessarily be under negative selection in later development. Because responses to infant-directed song are not likely to become maladaptive after infancy, we see no reason that those responses should have a developmental expiration date. This raises the question of what adult responses to songs in general should look like. We predict that adult responses to music should correlate roughly with infant responses to music, especially in cases where the features of that music overlap strongly with those of infant-directed song. This idea, which is shared with a byproduct account, is supported by some preliminary evidence: neural signatures of pitch processing mechanisms are comparable between infants and nonmusician adults (Perani et al., 2010), and like adults, infants spontaneously engage in physical motion in response to music (Zentner & Erola, 2010), though with less rhythmic accuracy. The prediction could be better tested by systematically examining adult behavioral responses to a variety of musical forms, and comparing those responses to those of infants, with the same musical material; we predict that adults and infants should show generally comparable behavioral trajectories in these cases.

To differentiate this first prediction from those of a purely byproduct account, it could be extended to other psychological domains: for instance, adults should show more robust memory for infant-directed songs (and those songs that share its stylistic features) than adult-directed songs (and those songs that do not), remembering infant-directed songs in more detail after longer delays, and discriminating them more accurately and more rapidly against foils. Moreover, adults' response to music should be more variable than infants' response to infant-directed song: we predict that typically developing infants are uniformly predisposed to attend to and engage with infant-directed song, but no corresponding prediction holds for adults. Consistent with this prediction, Mas-Herrero, Zatorre, Rodriguez-Fornells, and Marco-Pallarés (2014) demonstrated specific musical anhedonia in a group of adults who had normal music perception abilities and normal responses to monetary reward; this demonstrates a great deal of variability in adult individual differences in musical response. We predict that infant responses to infant-directed song should show less variability. Large studies of infant responses to music would provide a useful comparison, as would longitudinal studies that include within-subject comparisons of response to infant-directed song in infancy to response to music in general, in adulthood (i.e., what were musical anhedonics like as infants?).

6.2. Bootstrapping from infant-directed song to other forms of music

If infant-directed song evolved by the mechanisms we describe herein, it may be possible to account for the musical features of other,

non-infant-directed music, as byproducts of infant-directed song. Tests of this prediction could compare both the musical features of and listeners' subjective ratings of infant-directed song to those of other musical genres. From these data, one could construct a multidimensional scaling of music, enabling tests of several questions. Is infant-directed song a prototypical form of music, a centroid in that feature space? Put another way: if infant-directed song has ten universal features, would altering a few of them produce a love song? Would adjusting a few others produce a dance song? Would infant-directed song be the only prototypical music form? Perhaps it is one of several prototypes whose musical features can be systematically varied to model much of human music across cultures; given that the present theory accounts well for melodic features, but less well for rhythmic features, perhaps a second, more rhythmically-centered prototype would be necessary to explain the rest of music's feature space. Hagen and Bryant's (2003) predictions for the musical features of group performances that constitute honest signals of cooperative ability and coalition strength could provide such a prototype.

These ideas are highly speculative and can only be tested when large and highly detailed cross-cultural databases of the features of human music are available. We note, however, that the central argument of the most parsimonious theory of musical grammar (Lerdahl & Jackendoff, 1983) operates by reducing highly complex pieces of music, via prolongational reduction, to their melodic underpinnings, yielding simple melodies of the sort parents routinely sing to infants.

6.3. Cultural evolution of music

If principles of adaptation and natural selection can eventually be used to explain the origins of other basic forms of music than infant-directed song (whether as byproducts of it or further adaptations), principles of cultural evolution can then be invoked to help explain the great diversity of music performance documented throughout human history (e.g., Lomax, 1968). We aim here to explain infant-directed song, and with it, potentially, a few fundamental features of the human music faculty in general, but even if we are successful, our approach will be at pains to explain many of the most interesting and most puzzling musical behaviors observable across human societies. For these — from throat singing to musical theatre — a cultural evolutionary approach will be productive.

7. Conclusion

“Pitched sounds became the basis for a great art form despite having no survival implications whatsoever ... to trace a continuous route from primordial calls to The Art of the Fugue will never be possible.” (Dutton, 2009, p. 218)

We do not share Dutton's pessimism. Here, we have assumed that music is no different than any other human behavior: when subjected to evolutionary functional analysis, we argue that music can be broken down into parts that are explicable through basic principles of adaptation and natural selection. In other domains, this process has yielded theories that make falsifiable predictions; in keeping, the theory we present herein can be shown to be incorrect. Indeed, at the time of this writing, we do not know whether infant-directed song was a target of natural selection, or whether our speculative extensions from infant-directed song to the rest of the music faculty will prove to have any merit. The engine of science is the empirical evaluation of theories; in our laboratories, we are beginning to test many of the predictions described above. We invite others to join in these investigations — whatever the results, we believe that a clearer understanding of music is within reach.

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