

Synchronous Chorus and Human Origins

Björn Merker

Abstract

Evenly paced time marking in measured music allows us to predict where the next beat is going to fall. This makes musical pulse a cardinal device for coordinating the behavior of several individuals in a joint, coherent, synchronized performance. Such behavioral synchrony to a regular beat on the part of many individuals is rare among higher animals and raises the question of its origination in anthropogenesis. The fit between one of the evolutionary models proposed to explain synchronous chorusing in insects and basic aspects of our earliest hominid ancestors' social structure suggests that synchronous chorusing may have played a fundamental and hitherto unsuspected role in the process of hominid divergence from our common ancestor with the chimpanzee. The possible elaboration of such an adaptation through female choice (acting both between and within groups of cooperatively chorusing males) and vocal learning (in both its receptive and productive modalities) is discussed with reference to hominoid behavior, the fossil record of hominid brain expansion, and its bearing on the relationship between the origins of language and of music.

A Musical Lacuna

Sometimes an unexploited dimension of potential variation in an art form or other behavioral domain can tell us of underlying constraints whose influence is so pervasive as to escape easy notice. A case in point from the world of music would seem to be the fact that among the many kinds of structural variations we meet with, we hardly ever encounter music employing discrete, that is, stepwise (from one beat to the next), and frequent tempo changes as a structural device for generating variety. Instead, tempo changes are almost invariably gradual, taking the form of *accelerando* or *ritardando*, or else they conform to the arithmetic of whole integer ratios; that is, they introduce changes such as doubling or halving the tempo, or tripling a halved tempo.

The constraint underlying this structural lacuna is of course the prepotency of a regular beat or pulse as an organizing principle in measured music. The structural device of an evenly paced time giver appears to have such a hold over our sensibilities that music tends to come in two fundamental kinds. Either it is measured, that is, avails itself of a regularly paced timegiver, or it gives up reliance on time marking altogether, and is unmeasured (Arom 1991, and this volume). The half-way place between these two musical worlds that would be created by the device of discrete tempo changes, which necessarily violate the even spacing of the basic timegiver of the musical beat, is accordingly uninhabited, another way of stating our initial observation.

Within measured music the musical pulse is not an invariably fixed structural feature, but allows of different treatments of which there appear to be two principal varieties. In one, the even pace of the musical time marker is autonomous in the sense that deviations from it tend to be inadvertent or adventitious. In the other, the even spacing of the timegiver is not thus an ideal in its own right but is subject to manipulation as a means of expression through episodic stretching and compression (rubato and agogic accents). Since even in the case of such pulse subordination the stylistic effect is dependent on the presence of the regular pulse as a baseline from which deviations are made, it can be regarded as a special case of the more general pervasiveness of musical pulse in measured music. It is not possible within the confines of this chapter to discuss the voluminous literature on musical pulse and meter. Entry to this literature can be gained through Nielsen (1984), Kramer (1988), and Wallin (1991).

The musical pulse embedded in all measured music is what allows us to tap or clap to a piece of music. Fraisse (1982:154) pointed out a peculiarity in this behavior, namely, that whereas in most behaviors a response follows a stimulus, here the response is made to coincide with the stimulus (which can be as simple as the click of a metronome). The phenomenon is one of *entrainment*, and in this context the functional utility of an evenly paced time giver is immediately apparent: it allows us to predict where the next beat is going to fall and thus synchronize our behavior with that of the pulse. Since many individuals, no less than single ones, can synchronize their behavior to a common time giver, musical pulse is a cardinal device for coordinating the behavior of those individuals in a joint, coherent, synchronized performance, be they musicians among themselves or with dancers or soldiers (see McNeill 1995).

Synchronous Chorusing in Nature

Behavioral synchrony involving many individuals is not common in nature but is not altogether absent. Some species of fireflies synchronize their bioluminescent flashing in the tropical night (Buck 1988), a number of other insects synchronize their chirps in multimalle chorusing (Otte 1977; Greenfield and Shaw 1983), synchronous calling is found among chorusing frogs (Wells 1977; Klump and Gerhardt 1992), and clusters of male fiddler crabs wave their claws in synchrony to attract females for mating (Backwell, Jennions, and Passmore 1998). Behavioral synchrony in these cases differs from behavioral coordination between individuals in, for example, the duets of gibbons and some birds by featuring

rhythmic repetition of signals in conformity with a regular beat or pulse (Greenfield 1994). Such synchrony generally occurs in the context of multimale displays of sexual advertisement to attract females. Male cooperation in such displays raises the question of why a male should cooperate in attracting a female to a group with whom he might have to share her. Detailed studies of synchronous display have generated both formal treatments of mechanisms of entrainment (Sismondo 1990) and a number of models for the evolution of multimale synchrony (reviewed in Greenfield 1994).

For a number of chorusing species the assumption that synchrony represents male cooperation was overturned by good evidence that it is an epiphenomenal (nonadaptive) outcome of timing strategies employed in male competition to signal first (Greenfield and Roizen 1993; Backwell, Jennions, and Passmore 1998). Treatments of synchrony as an adaptation include its interpretation as an antipredator strategy to dilute predator attention to a male when his signaling attracts not only females but predators (Walker 1969; Otte 1977; Tuttle and Ryan 1982), and as a means of increasing peak signal output from a group of males competing with other groups of males to attract mobile females (Wells 1977; Buck and Buck 1978; Morris, Kerr, and Fullard 1978). This latter model is of particular interest in the present context, because its assumptions regarding the circumstances and function of male synchronous chorusing apply, in a most direct and robust manner, to the emergence of hominids from our common ancestor with the chimpanzees.

Synchronous Chorusing and Hominid Origins

The group sociality of our closest living relative among the apes, the chimpanzee, differs most markedly from that of, say, group-living common monkeys by featuring female exogamy. Females, rather than males, move from their natal group (Pusey 1979) to settle and to rear their young in a group where they may or may not have any kin and whose males jointly defend a group territory against similarly constituted groups of neighboring males (Wrangham 1975; Ghiglieri 1984, 1985; Pusey, Williams and Goodall 1997; see also Foley 1996). This pattern was suggested as a possible context for the evolution of male-male cooperation (Ghiglieri 1984; Rodman 1984). Under hunting and gathering (Ember 1978) and many other circumstances, humans share with chimpanzees the unusual social trait of female exogamy, and thus it presumably also characterized our earliest hominid ancestors. In the absence of strong reasons for assuming otherwise, we may picture the social behavior of our earliest hominid ancestors as based on groups of associated

males with a reproductive interest in attracting migrating females away from other similar groups of males.

But this pattern conforms strikingly to one model for the evolution of synchronous male chorusing, the one, namely, according to which synchrony serves amplitude summation of signals within groups of cooperating males competing with other groups to attract females. It only remains to suggest that those early hominids who eventually gave rise to *Homo* engaged in such synchronous vocal signaling for mate attraction. Such behavior is most easily derived from the noisy bouts of cooperative calling (cooperative in the sense of benefiting absent individuals of both sexes within the territorial group) in which groups of chimpanzee males engage on discovering large fruiting trees (Wrangham 1975,1979; Ghiglieri 1984). Synchronous calling in such circumstances would maximize the summed amplitude of the multivoice display to extend its geographic reach beyond territorial boundaries.¹ It would represent an honest distance signal of group resources and male cooperativity, a signal that ought to be of interest to migrating females deciding which territorial group to join. That is, since group members falsely attracted to a calling bout are likely to retaliate, the number of calling bouts in a given territory over time reflects a combination of its actual abundance of fruiting trees and the cooperation of males inhabiting that territory.

Assuming synchronous calling bouts, the quality of the synchrony itself provides a further measure of male cooperation as well as vocal skill. These factors ensure that the distance signal is informative, which in turn introduces female choice on the part of migrating females as a sexual selection pressure on the calling behavior of territorial groups. For males in neighboring territories the same signal conveys a double message: it advertises desirable resources that might stimulate them to intrude on the territory and broadcasts a deterrent to encroachment through the evidence of cooperation it provides. Under such circumstances the territorial group whose calling synchrony extends the reach of its signal by decibel summation is likely to attract a greater number of migrating females than it would in the absence of the cooperative synchrony, thus increasing the potential mating opportunities of individual males in the group.

Synchronous calling of the kind postulated here, that is, true cooperative synchronous calling rather than synchrony as a default condition of competitive signaling, requires a motivational mechanism for mutual entrainment. We assume that such a mechanism was selected for in the course of hominid divergence from our common ancestor with the chimpanzee, and was retained to the present day in the form of our propensity to join in and entrain to a repetitive beat. This propensity is apparently lacking in the common chimpanzee, which seems unable to

keep time even with training (Williams 1967), but may be present in bonobos. Such an ancestral adaptation for entrainment to a repetitive beat would supply, in other words, an ancient biological foundation for the musical pulse no human culture has failed to feature among its musical means of expression (Arom, this volume; Nettl, this volume). Indeed, if the present argument should turn out to have any merit, this adaptation for entrainment supplies an irreducible biological root of human music.

Genuine synchronous chorusing may exist, at least incipiently, among bonobos. A report by de Waal (1988: 202-203) on captive bonobos describes a call variant apparently lacking a homolog in the vocal repertoire of common chimpanzees, namely, a loud and explosive sound called staccato hooting. According to de Waal “during choruses, staccato hooting of different individuals is almost perfectly synchronized so that one individual acts as the ‘echo’ of another, or emits calls at the same moments as another. The calls are given in a steady rhythm of about two per second.” We note that both alternation and synchrony often occur in the same species of chorusing animals, and can result from a single timing mechanism (see Greenfield 1994:106). The issue of true synchrony is important in the present context because, of course, only simultaneous calling can serve amplitude summation. At least one field study of bonobo distance calls mentions only alternate and not simultaneous calling (Hohmann and Fruth 1994), but should simultaneous synchrony occur in wild bonobos and on further study be shown to conform to the regular beat of a pulse, humans would not be alone among higher animals in possessing pulse-born behavioral synchrony.

In contrast to the insect examples referred to above, the human capacity for entrainment is not tied to a fixed or narrow range of tempos, but extends more than an octave in either direction from approximately 100 beats per minute, a representative central tempo in an equally wide range of individual spontaneous tapping frequencies (see Fraisse 1982 for details). This, besides reinforcing the suggestion that adaptation must have motivational underpinnings, raises the issue of neural mechanisms capable of timing repetitive behaviors involved in synchronous chorusing over a wide range of tempos. It is to be noted that according to the above example the evolution of synchronous hominid chorusing took place *pari passu* with evolutionary changes in the control of locomotion linked to the fully upright mode of bipedalism (Leakey and Walker 1997). Motor and sensorimotor mechanisms for walking and running supply a convenient source of continuously graded (in tempo) and repetitive time-keeping signals on the simple assumption that our hominid ancestors paced and coordinated their calling bouts with the help of associated bodily movements derived from the repertoire of walking and running, but performed largely in place (with upright posture); that is, as

a form of dancing display (for the correlation between walking rhythm and spontaneous tempo (see Fraisse 1982:154; see also Melvill-Jones and Watt 1971). This would be a natural extension, in the context of group synchrony, of locomotor and other physical displays associated with hominoid distance calls (Mori 1983; Geissmann, this volume). Needless to say, synchronous chorusing and dancing to a repetitive beat qualifies as music in the human sense, according to a wide range of construals of that elusive term.

Specifically, it fits the origin of our term “music” in the Greek *mousike*, which included melody, dance, and poetry, whose common denominator is pulse-based rhythmicity. It is also in good agreement with the term *ngoma* of the Bantu language group, a term that subsumes drumming, singing, dancing and festivity under a single unitary concept. Similarly, the Blackfoot principal gloss for music, *saapup*, combines singing, dancing, and ceremony in a single concept (Nettl, this volume).

The net result of these conjectural developments would be the emergence among our hominid ancestors of a novel and unique social adaptation, namely, a behavioral forum featuring synchronous singing and dancing on the part of a higher animal. Just as chimpanzee pant-hooting displays at a newly discovered large fruiting tree attract mixed groups of males and females to the site of the commotion, we should picture these hypothetical hominid display bouts as key social gatherings with potential participation by all members of a given territorial group and attended by considerable excitement. Specifically, they would provide a convenient arena for the pursuit of individual mating tactics through efforts to attract the attention of members of the opposite sex in this setting of joint rhythmic singing and dancing. Sexual selection (see Kirkpatrick and Ryan 1991; also Miller, this volume; Todd, this volume) would, in other words, be capable of affecting the content of the display bout in a double, parallel fashion over evolutionary time: female choice would act between groups of chorusing males in connection with female migration as already described, and it would act between individual males within a group if, as assumed here, individual display behavior within the bout served as a means of mate attraction.² Should either or both of these pressures for elaboration of the content of the display bout have promoted the expansion of learning capacity in the relevant behavioral domains (vocal learning above all), far-reaching implications for our subsequent evolutionary trajectory follow.

Vocal Learning, Brain Expansion, and the Origin of Language

In mammals, expansion of cerebral capacity for a given functional purpose appears to proceed by global expansion of neocortical capacity

as a whole, along with a more modest expansion of cerebellar cortical volume (Finlay and Darlington 1995). This means that any selected-for capacity increase will tend to generate adventitious or free cortical expansion in other areas without selection for those ancillary increases. Any given selection pressure for a cerebral capacity increase might therefore initiate a cascade of brain expansion with functional consequences far beyond the confines of the initiating adaptation, provided the energetic costs both for nutrient supply (Martin 1981; Armstrong 1983; Aiello and Wheeler 1995) and heat removal (Falk 1990) of such a development can be sustained. Synchronous hominid chorusing is well suited to trigger such development on the simple assumption that the vocal behavior it featured involved vocal learning (Marler and Mundinger 1971; Nottebohm 1975, 1976; Janik and Slater 1997; for evidence compatible with vocal learning in chimpanzees, see Boesch 1991:83).

Vocal learning may occur in chimpanzees, to judge by a report of instances in which individual chimpanzees take over the distinctive panthoot pattern of a fellow group member after the latter's disappearance or death (Boesch 1991:83). We note also the tendency of chorusing common chimpanzees, whose chorusing apparently consists of alternating, and not synchronous, calling (see Mitani and Brandt 1994; Hohmann and Fruth 1994) to match their vocal output to that of their calling partner (Mitani and Brandt 1994). The latter authors discuss a number of possible explanations for the genesis of the observed between-partner similarity in call characteristics, some of which involve that matching between auditory-receptive and vocal-productive functions that figure in vocal learning.

To begin with, a selection pressure is required to account for the considerable advance in brain size over great ape levels of *Homo* at its first appearance in the fossil record about 2 million years ago. (Ruff, Trinkaus, and Holliday 1997; Falk, this volume). Vocal learning with its dual functional dependence on auditory-receptive and vocalproductive capacities (Marler 1990; Whaling, this volume) could supply the key to this increase by exerting a dual pressure for expansion of posterior as well as frontal cortical domains. Posteriorly its auditoryreceptive requirements would most plausibly act to extend further the asymmetric enlargement of the planum temporale region already in evidence in chimpanzees (Gannon et al.1998). Anteriorly, the functional requirements of vocal-productive capacity should promote elaboration, from a great ape starting point, of regions of the frontal lobe in which the endocast of KNM-ER 1470 (*Homo rudolfensis*) differs from the great apes (Tobias 1981; Falk 1983). Such changes are appropriate for growth of a cerebral substratum for increasingly elaborate vocal-musical behavior involving vocal learning, and offer no compelling reason to link

them with referential functions of language (see also Petersen et al. 1988:587).

A possible exception to this lack of referential function for the postulated complex ancestral vocalizations might be their use as individually specific vocal signatures. Since they are assumed to have involved vocal learning, they might be analogous to the signature whistles of bottle-nose dolphins (Caldwell, Caldwell, and Tyack 1990; see also Janik and Slater 1997:79-82) and function as the equivalent of personal names in social situations. If so, they might at some point have become the prototype for generalized naming by distinctive, presumably elaborate, vocal phrase patterns in the formation of a semantic lexicon (see Ujhelyi as well as Richman, this volume, for discussions bearing on this issue). Any such development would benefit from the availability of a highly differentiated repertoire of unsemanticized, syntactically structured phrases of the kind that make up the learned vocal repertoires of some birds and humpback whales, and would presumably have to await the development of such repertoires.

Although unrelated to referential language, the conjectural developments sketched above nevertheless bear strongly on the issue of language origins. The possibility that our remote ancestors might have engaged in complexly structured but unsemanticized vocal behavior prevents us from attributing brain expansion, even in the posterior temporal-parietal region and frontal areas related to Broca's area, to human language or protolanguage unless we know that the carriers of those brains were in fact linguistic creatures. All we know for certain about the time of appearance of referential language in the evolution of *Homo* is that it forms an integral part of the cultural history of all current populations of *Homo sapiens sapiens*. One possibility is therefore that the use of complex human vocal behavior for referential purposes is a bona fide cultural *invention* on the part of fully modern humans within, say, the past 50,000 years or less. If so, this function, in contrast to preexisting auditory-vocal capacities of an advanced kind on which such an invention might have been based, would lack both an evolutionary history and cerebral mechanisms of its own, in the sense that these mechanisms would have evolved specifically for human language. Rather, it would be analogous in this regard to reading and writing. The cerebral distribution of different types of word memories provides indirect (if tenuous) support for such a view (Martin et al. 1995).

Working backward from this null hypothesis, one may attempt to assign increasing antiquity to the origin of language. Specific regions of prefrontal and neocerebellar cortices associated with language functions (and some of them with music as well) on the basis of imaging studies

(Petersen et al. 1988; Sergent et al. 1992; Petersen and Fiez 1993; Martin et al. 1995; Khorram-Sefat, Dierks, and Hacker 1996; summarized by Falk, this volume; see also Hassler 1950; Leiner, Leiner, and Dow 1991; Thach 1996) are not present in middle Pleistocene fossil endocasts of archaic *Homo sapiens* from Greece and Africa (Seidler et al. 1997). They may accordingly have evolved under a linguistic selection pressure that brought us above threshold for referential speech, unless, of course, they happen to represent the final twist of a spiral of sexual selection for sophisticated syntactic structuring of impressive vocal displays of a musical kind, and only later were partially taken over by language, as it were.³

To proceed backward beyond this point in attempts to link stages of brain evolution (see Ruff, Trinkaus, and Holliday 1997) with human language requires far more precise knowledge of the nature of language and its cerebral dependencies than we currently possess, particularly since we know far too little of the neurological requirements and dependencies of vocal learning in mammals, and more generally, of a vast domain of human behavior characterized by rules without meaning (Staal 1989), including nonverbal song, music, mantras, and ritual. Capacities underlying such behaviors are prime candidates for supplying preadaptations for human language; that is, behavioral capacities and biases based on perceptual, motivational, cognitive, and motor mechanisms evolved for other purposes (such as display) but so constituted as to supply essential foundations for human language.

In the foregoing I emphasized vocal productivity based on vocal learning in this role, because in contrast to language, it has arisen again and again in the world of nature, in a variety of taxonomic groups including mammals (see Janik and Slater 1997, and discussion of vocal learning in chimpanzees), and in a diversity of forms with different mechanisms and modes of development. These are epitomized in genuine cultural song traditions of humpback whales with their complex shared repertoires, individual innovation, and cumulative seasonal turnover in the repertoire of a given group of singers (Payne, this volume). Unless and until we can eliminate adaptations of this kind from consideration as factors in the evolution of hominids and *Homo*, the fossil record of human brain development cannot usefully be related to human language. For that it is necessary to know whether or not we were in fact singing and dancing hominids before we became talking humans, and if so whether and how long we might have been singing and dancing humans before we started to employ our cerebral equipment for referential language. It is even conceivable that without such an essentially musical preadaptation, the long step to language might have remained forever beyond our reach.

Acknowledgments

I dedicate this chapter to Nils L. Wallin, without whose vision of a discipline joining biology to musicology it would never have been written. I am indebted to Maria Ujhelyi for calling my attention to the significance of female exogamy and to the possible existence of synchronous chorusing in bonobos, and to Nils Wallin, Simha Arom, and Steven Brown for stimulating discussions about the origins of music.

Notes

1. An individual chimpanzee pant-hoot used in fruit tree signaling carries at most 2 kilometers, whereas a chimpanzee group territory spans some 10 to 30 square kilometers (Ghiglieri 1984). It is, in other words, approximately 4.5 kilometers across. The “square law” relating sound level to distance gives us the rough estimate that four well-synchronized callers would have to be heard from any point on their territorial boundary irrespective of the location of their calling within the territory, and sixteen males would have to synchronize their calling to be heard from any point within any immediately neighboring territory, irrespective of the location they happened to be calling from within their own territory. With a chimpanzee total group size of around fifty individuals, these rough estimates do not exceed the bounds of biological plausibility.

2. It should be noted in this connection that there is no good reason to confine the effects of sexual selection to the vocal content of display behavior. Rather, it would presumably affect any traits or behaviors involved in mate choice. If, for example, females preferred males who were unusually steady on their feet as evidenced by the greater elegance or complexity of their dancing movements, sexual selection could have been a factor accelerating the perfection of the upright posture and bipedal locomotion.

3. Assume that, in parallel with the evolution of syntactically elaborate but unsemanticized synchronous chorusing from the hominoid distance call and its associated locomotor displays, our ancestral proximity vocalizations were also developing (perhaps as a side effect of brain expansion driven by vocal learning, as already explained, or through their own utility, possibly accentuated by developments such as a trend toward vocal grooming [Dunbar 1993]) by a differentiation of their capacity to convey a wide range of information concerning matters of rank, sex, age, class, emotional state (satisfaction, fear, aggression, affiliation, etc.), food source quality, predator classes, and other environmental contingencies (see Hauser, this volume). This is the domain of vocal semantics, encoded in the patterns of pitch, articulation, and dynamics of the primate voice. Against such a background, the radical novelty of human language might have been born in the appropriation, *by* the semantic capacity for conveying meaning socially through the voice in proximal communication, *of* the syntactic capacity for sequential patterning of vocal output evolved for musical display purposes, perhaps at a late date in our history as a species (see also Ujhelyi, this volume).

References

- Aiello, L. C. and Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Current Anthropology* 36: 199-221.
- Armstrong, E. (1983). Relative brain size and metabolism in mammals. *Science* 220: 1302-1304.
- Arom, S. (1991). *African Polyphony and Polyrhythm*. Cambridge, UK: Cambridge University Press. I
- Backwell, P., Jennions, M., and Passmore, N. (1998). Synchronized courtship in fiddler crabs. *Nature* 391: 31-32.

325 Synchronous Chorusing and Human Origins

- Boesch, C. (1991). Symbolic communication in wild chimpanzees? *Human Evolution* 6: 81-90.
- Buck, J. (1988). Synchronous rhythmic flashing in fireflies. II. *Quarterly Review Biology* 63: 265-289
- Buck, J. and Buck, E. (1978). Toward a functional interpretation of synchronous flashing in fireflies. *American Nature* 112: 471-492.
- Caldwell, M. C., Caldwell, D. K., and Tyack, P. L. (1990). Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In S. Leatherwood and R. R. Reeves (Eds.) *The Bottlenose Dolphin* (pp. 199-234). New York: Academic Press.
- Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences* 16: 681-735.
- Ember, C. R. (1978). Myths about hunter-gatherers. *Ethnology* 17: 439-448.
- Falk, D. (1983). Cerebral cortices of east African hominids. *Science* 221: 1072-1074.
- Falk, D. (1990). Brain evolution in *Homo*: The "radiator" theory. *Behavioral and Brain Sciences* 13: 333-381.
- Finlay, B. L. and Darlington, R. B. (1995). Linked regularities in the development and evolution of mammalian brains. *Science* 268: 1578-1584.
- Foley, R. A. (1996). An evolutionary and chronological framework for human social behavior. *Proceedings of the British Academy* 88: 95-117.
- Fraisse, P. (1982). Rhythm and tempo. In D. Deutsch (Ed.) *The Psychology of Music* (pp. 149-180). New York: Academic Press.
- Gannon, P. J., Holloway, R. L., Broadfield, D. C., and Braun, A. R. (1998). Asymmetry of chimpanzee planum temporale: Humanlike pattern of Wernicke's brain language area homolog. *Science* 279: 220-222.
- Ghiglieri, M. P. (1984). *The Chimpanzees of Kibale Forest*. New York: Columbia University Press.
- Ghiglieri, M. P. (1985). The social ecology of chimpanzees. *Scientific American* 252: 102-113.
- Greenfield, M. D. (1994). Cooperation and conflict in the evolution of signal interactions. *Annual Review of Ecological Systems* 25: 97-126.
- Greenfield, M. and Roizen, I. (1993). Katydid synchronous chorusing is an evolutionarily stable outcome of female choice. *Nature* 364: 618-620.
- Greenfield, M. D. and Shaw, K. C. (1983). Adaptive significance of chorusing with special reference to the Orthoptera. In D. T. Gwynne and G. K. Morris (Eds.) *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects*. Boulder, CO: Westview Press.
- Hassler, R. (1950). Über Kleinhirnprojektionen zum Mittelhirn und Thalamus beim Menschen. *Deutsche Zeitschrift für Nervenheilkunde* 163: 629-671.
- Hohmann, G. and Fruth, B. (1994). Structure and use of distance calls in wild bonobos (*Pan paniscus*). *International Journal of Primatology* 15: 767-782.
- Janik, V. M. and Slater, P. J. B. (1997). Vocal learning in mammals. *Advances in the Study of Behavior* 26: 59-99.
- Khorrām-Sefat, D., Dierks, T., and Hacker, H. (1996). Cerebellar activation during music listening. *NeuroImage* 3: S312.
- Kirkpatrick, M. and Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature* 350: 33-38.
- Klump, G. M. and Gerhardt, H. C. (1992). Mechanisms and function of call-timing in male-male interactions in frogs. In P. K. McGregor (Ed.) *Playback and Studies of Animal Communication* (pp. 153-174). New York: Plenum Press.
- Kramer, J. D. (1988). *The Time of Music*. New York: Macmillan/Schirmer.
- Leakey, M. and Walker, A. (1997). Early hominid fossils from Africa. *Scientific American* 276: 60-65.
- Leiner, H. C., Leiner, A. L., and Dow, R. S. (1991). The human cerebrocerebellar system: Its computing, cognitive and language skills. *Behavioral Brain Research* 44: 113-128.
- Marler, P. (1990). Song learning: the interface between behaviour and neuroethology. *Philosophical Transactions of the Royal Society of London B* 329: 109-114.

- Marler, P. and Mundinger, P. (1971). Vocal learning in birds. In H. Moltz (Ed.) *The Ontogeny of Vertebrate Behavior* (pp. 389-450). New York: Academic Press.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., and Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science* 270: 102-105.
- Martin, R. D. (1981). Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 283: 57-60.
- McNeill, W. H. (1995). *Keeping Together in Time: Dance and Drill in Human History*. Cambridge: Harvard University Press.
- Melvill-Jones, G. and Watt, D. G. D. (1971). Observations on the control of stepping and hopping movements in man. *Journal of Physiology* 219: 709-727.
- Mitani, J. C. and Brandt, K. L. (1994). Social factors influence the acoustic variability in the long-distance calls of male chimpanzees. *Ethology* 96: 233-252.
- Morris, G. K., Kerr, G. E., and Fullard, J. H. (1978). Phonotactic preferences of female meadow katydids (Orthoptera: Tettigoniidae: *Conocephalus nigropleurum*). *Canadian Journal of Zoology* 56: 1479-1487.
- Mori, A. (1983). Comparison of the communicative vocalizations and behaviors of group ranging in eastern gorillas, chimpanzees and pygmy chimpanzees. *Primates* 24: 486- 500.
- Nielsen, F. V. (1984). *Oplevelse af Musikalisk Spaending*. Copenhagen: Akademisk Forlag.
- Nottebohm, F. (1975). A zoologist's view of some language phenomena, with particular emphasis on vocal learning. In E. H. Lenneberg and E. Lenneberg (eds.) *Foundations of Language Development* (pp. 61-103). New York: Academic Press.
- Nottebohm, F. (1976). Discussion paper: Vocal tract and brain: A search for evolutionary bottlenecks. In S. R. Harnad, H. D. Steklis, and I. Lancaster (eds.) *Origins and evolution of language and speech*. *Annals of the New York Academy of Sciences* 280: 643-649.
- Otte, D. (1977). Communication in Orthoptera. In T. A. Sebeok (ed.) *How Animals Communicate* (pp. 334-361). Bloomington: Indiana University Press.
- Petersen, S. E. and Fiez, I. A. (1993). The processing of single words studied with positron emission tomography. *Annual Review of Neuroscience* 16: 509-530.
- Petersen, S. E., Fox, T. P., Posner, M. I., Mintum, M., and Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 331: 585-589.
- Pusey, A. (1979). Inter-community transfer of chimpanzees in Gombe National Park. In D. A. Hamburg and E. McCown (Eds.) *The Great Apes* (pp. 465-479). Menlo Park, CA: Benjamin/Cummings.
- Pusey, A., Williams, I., and Goodall, I. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277: 828-831.
- Rodman, P. S. (1984). Foraging and social systems of orangutangs and chimpanzees. In P. S. Rodman and I. G. H. Cant (eds.) *Adaptations for Foraging in Nonhuman Primates* (pp. 134-160). New York: Columbia University Press.
- Ruff, C. B., Trinkaus, E., and Holliday, T. W. (1997). Body mass and encephalization in Pleistocene *Homo*. *Nature* 387: 173-176.
- Seidler, H., Falk, D., Stringer, C., Wilfing, H., Muller, G. B., zur Nedden, D., Weber, G. W., Reicheis, W., and Arsuaga, J. L. (1997). A comparative study of stereolithographically modeled skulls of *Petralona* and Broken Hill: Implications for future studies of middle Pleistocene hominid evolution. *Journal of Human Evolution* 33: 691-703.
- Sergent, J., Zuck, E., Terriah, S., and MacDonald, B. (1992). Distributed neural network underlying musical sight-reading and keyboard performance. *Science* 157: 106-109.
- Sismondo, E. (1990). Synchronous, alternating, and phase-locked stridulation by a tropical katydid. *Science* 249: 55-58.
- Staal, F. (1989). *Rules Without Meaning. Ritual, Mantras and the Human Sciences*. New York: Lang.

327 Synchronous Chorusing and Human Origins

- Thach, W. T. (1996). On the specific role of the cerebellum in motor learning and cognition: Clues from PET activation and lesion studies in humans. *Behavioral and Brain Sciences* 19: 411-431.
- Tobias, P. V. (1981). The emergence of man in Africa and beyond. *Philosophical Transactions of the Royal Society of London B* 292: 43-56.
- Tuttle, M. D. and Ryan, M. I. (1982). The role of synchronized calling, ambient light, and ambient noise in anti-bat-predator behavior of a treefrog. *Behavioral Ecology and Sociobiology* 11: 125-131.
- de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. *Behavior* 106: 183-251.
- Walker, T. J. (1969). Acoustic synchrony: Two mechanisms in the snowy tree cricket. *Science* 166: 891-894.
- Wallin, N. L. (1991). *Biomusicology: Neurophysiological, Neuropsychological, and Evolutionary Perspectives on the Origins and Purposes of Music*. Stuyvesant: Pendragon.
- Wells, K. D. (1977). The social behavior of anuran amphibians. *Animal Behaviour* 25: 666-693.
- Williams, L. (1967). *The Dancing Chimpanzee: A Study of Primitive Music in Relation to the Vocalizing and Rhythmic Action of Apes*. New York: Norton.
- Wrangham, R. W. (1975). *The Behavioural Ecology of Chimpanzees in Gombe National Park, Tanzania*. Doctoral dissertation, University of Cambridge.
- Wrangham, R. W. (1979). On the evolution of ape social systems. *Social Sciences International* 18: 335-368.