"Language impairment gene" does not necessarily equate to "language gene"

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Abstract: The finding of the same language deficit in half the members of the KE family is taken as suggesting that a specific allele (FOXP2) is normally involved in the development of language. Recent studies, however, question the exclusivity of FOXP2, and it is argued that the finding of a gene that disrupts language should not be taken as strong evidence for the existence of genes that underlie it.

Locke & Bogin's (L&B's) argument that life history theory provides a fruitful way of re-examining the relationship between evolution and language development is, for the most part, a compelling if somewhat speculative argument. Both the unique life history pattern and the uniqueness of language in our species require explanation. I agree that such patterns should be examined in the light of selective advantages. L&B provide evidence of selective advantages for a wide range of aspects of language development. Where I would urge caution, however, lies in the use of studies of language deficits in the "KE" family to imply that these provide evidence of the existence of genes directly related to the neurological substrate supporting language production and grammar.

In the early 1990s the KE family caused a stir among linguists when it was discovered that more than half of the 31 members of three generations of the family had impaired language abilities (sometimes referred to as specific language impairment, or SLI). It was found that individuals with SLI have a number of problems, including a deficit in the ability to use inflection (e.g., producing the past tense of a verb) and problems of articulation, comprehension, and orofacial dyspraxia (i.e., putting together orofacial movements; Bishop 2002; Gopnik 1990; 1997; Pinker & Jackendoff 2005).

The finding of the same language problem in such a high proportion of family members has been taken by a number of researchers as suggestive of a specific underlying genetic problem. If a specific allele leads to such problems then it has been argued that an alternative allele might normally be involved in the development of appropriate neural hardware to support language (Gopnik 1990; Jackendoff 1994; Pinker 1999). L&B are clearly sympathetic to such an argument.

In support of L&B's stance there is now strong evidence of a defective dominant allele of a single gene that is found on the long arm of chromosome 7 in the impaired members of the family – FOXP2 (Lai et al. 2000; 2001). Moreover, as L&B point out, scanning techniques have demonstrated associated neurological anomalies of structure and function in sufferers, such as a bilateral deficit in activation of Broca's area (Liégeois et al. 2003) and abnormal activation of the caudate nucleus (Vargha-Khadem et al. 1998). Although L&B do not explicitly label FOXP2 as a "grammar gene," their use of the KE family to back up their argument that "selection acted on [language] performance" (sect. 11 of the target article) implies that this is an allele directly related to language and hence has arisen via selection pressures for that purpose.

It is entirely possible that the KE family's SLI does provide evidence of an allele related to the development of language, but currently there are at least two problems with the argument as presented by L&B. First, the evidence is presented as if there is general consensus that an exclusive language-related problem is found in the KE family and that this provides support for the existence of a specific defective gene related to language production. In fact, Gopnik (1997) herself has documented how controversial this conclusion is, with some experts suggesting that the language impairments uncovered might be part of a more general cognitive deficit, which might include non-linguistic problems (Leonard 1994; Vargha-Khadem et al. 1995). It is certainly possible that the problem is a part of a more general cognitive deficit since afflicted members of the family have IQ scores 18 to 19 points lower than those of unimpaired members (including nonverbal aspects of IQ; Vargha-Khadem et al. 1995; 1998).

Second, even if an allele has been discovered that disrupts language production via the development of neurological abnormalities, this is not strong evidence that an alternate allele exists that is directly involved in the development of neural circuitry underlying language and speech (Karanth 2005). As Lai and colleagues caution with regard to the FOXP2 allele, the biological deficit may well be in the form of a trigger that disrupts a key stage of embryogenesis rather than the replacement of an allele coding for normal language development (Lai et al. 2001; Karanth 2005). Removing an air-filter from an internal combustion engine will stop a car from running but that does not mean that the air-filter is responsible for running the car (Workman & Reader 2004). Finally, Newbury et al. (2002), through association and mutation screening analysis, have thrown doubt on the argument that variants in FOXP2 underlie such forms of language impairment.

None of these misgivings constitutes a deathblow to L&B's argument; they may well be correct that language development and production are directly related to specific alleles. But, currently, the evidence from families that show language deficits such as the KE is equivocal and needs to be examined with a degree of caution. L&B have done a service to our understanding of the relationship between evolution and language by weaving together a number of sources of evidence using the framework of life history theory. They should be careful not to leave any loose threads.

Authors' Response

Life history and language: Selection in development

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Abstract: Language, like other human traits, could only have evolved during one or more stages of development. We enlist the theoretical framework of human life history to account for certain aspects of linguistic evolution, with special reference to initial phases in the process. It is hypothesized that selection operated at several developmental stages, the earlier ones producing new behaviors that were reinforced by additional, and possibly more powerful, forms of selection during later stages, especially adolescence and early adulthood. Peer commentaries have provided opportunities to explain human life history more comprehensively, and to add details to our account of spoken language. We made no attempt to explain syntax in the target article, but we propose here that selection for "vocal plumage" may have increased our species' capacity for utterance complexity, a development that would have benefited all levels of language.

It is a rare pleasure to have comments on our target article from so many thoughtful colleagues, representing such a wide range of academic disciplines and cultures. We will begin our response by addressing comments that relate

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particularly to our treatment of life history, and then turn our attention to replies that pertain more specifically to language.

R1. Life history

Any theory of human biology and culture needs to explain how *Homo sapiens* successfully combines delayed reproduction, helpless newborns, a short duration of breastfeeding, a vastly extended period of offspring dependency, an adolescent growth spurt in both sexes, and female menopause a decade or more before death. No other primate species shares all of these traits. Theory also is needed to explain the extraordinary size of the human brain, in relation to overall body size, and the extraordinary cognitive-behavioral abilities of the brain, including symbolic language, theory of mind, kinship, marriage, religion, and even nihilistic philosophy. In our target article, we apply life history theory in an attempt to better understand human nature regarding growth, development, and language.

One commentator, **Weisfeld**, denies that human beings have a unique or unusual life history; in fact he does not use the phrase "life history" at all in his commentary. If Weisfeld's critique is correct, then the whole of our argument falls. But, his citations regarding human life history and nonhuman primate growth are both selective and somewhat old. The most recent citation is from 1993, well before some of the most salient work on primate life history was published. We cite that more recent research in our target article, and we provide additional references in this response (see below). Moreover, Weisfeld's interpretations are idiosyncratic, do not reflect the broad consensus of primate life history researchers, or are incorrect. The studies he cites (also cited by **Ragir & Brooks**) alleging that all primates have a skeletal, or even a body weight, growth spurt at the time of puberty originated in the 1950s (Gavan 1953). Gavan's original paper concludes that chimpanzees (a sample of 9 males and 7 females) do not have a pubertal growth spurt. Watts and Gavan (1982) reanalyzed the 1953 chimpanzee data, along with new data for the rhesus monkey, and reported that a "very small" positive deviation in bone growth could be detected at the time of puberty. "Very small" means less than a 3.0-mm deviation, which occurs during one year, and the detection scheme required polynomial regression fitted to the bone growth data.

We have criticized the methods and statistics needed to show these "spurts" (Bogin 1999a; 1999b). The human adolescent growth spurt is measured in centimeters – with a mean peak velocity of about 7.5 cm per year for girls and 9.0 cm per year for boys. The human spurt takes about eight years to complete. Leigh (1996; 2001) shows that, among 61 primate species, weight growth spurts vary greatly in magnitude and even in their existence – only one species of New World monkey may have a weight spurt; gibbons do not, and only males of the common chimpanzee do. Leigh could not confirm that any nonhuman primate species has a skeletal growth spurt. Hamada and Udono (2002) published the first statistically sound and methodologically rigorous longitudinal study of chimpanzee skeletal growth. They found that chimpanzees reared within semi-natural social conditions at a zoological park in Japan show no increase in long bone growth velocity at the time of puberty (Fig. R1).

In contrast, chimpanzees used in medical research, who were taken out of their social groups prior to puberty, stopped or greatly slowed growth during the time of experimentation. When returned to their social group after experimentation these chimpanzees experienced rapid growth, imitating a growth spurt. But this is not at all similar to the human adolescent growth spurt. Rather, Hamada and Udono (2002) explain that it is a type of "catch-up" growth following the stress of social separation and medical experimentation. Human beings show this

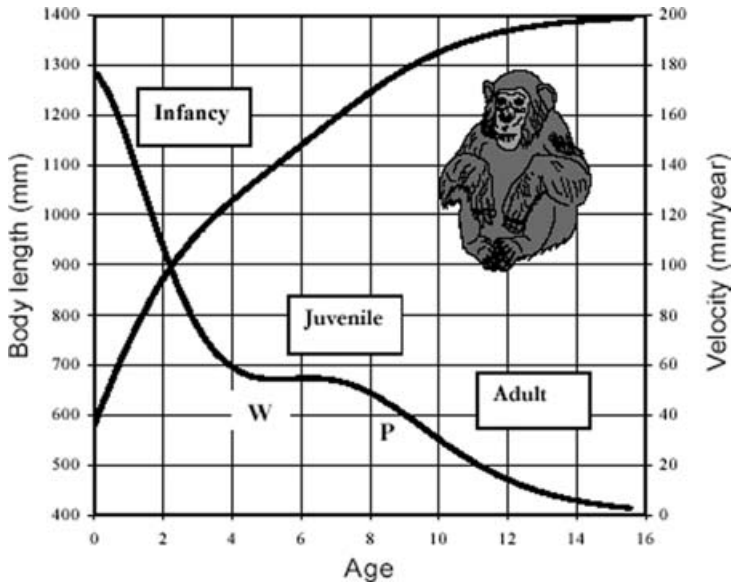


Figure R1. Model of distance (left) and velocity (right) curves for chimpanzee growth in body length by years of age. Data for the figure come from the longitudinal study of captive chimpanzee growth conducted by Hamada and Udono (2002). The infancy, juvenile, and mature adult life stages are labeled. In the wild, weaning (W) usually takes place between 48–60 months of age (Pusey 1983). In captivity, female puberty (P), assessed by age at first maximal perineal swelling, takes place at a mean age of 7.95 years (Littleton 2005).

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type of "catch-up" growth following chronic illness, nutritional deprivation, or severe emotional distress (Bogin 1999b; Prader et al. 1963).

Finally, **Weisfeld** writes that we should not abandon the convention of using the term "adolescence" to apply to simians. He states, "What would we otherwise call the period of puberty in simians?" How about "puberty"? Indeed, primate puberty is a neuroendocrine event of relative short duration, taking place in the brain (Plant & Barker-Gibb 2004). Human adolescence follows this event, lasts for eight years, and involves ritual behaviors that instruct the youth in economic, sexual, and political behavior, and eventually transform the youth into a socially acceptable adult ready for marriage and parenthood. No other species comes close to this biological, behavioral, and cultural stage of life history.

Eckhardt's comments remind us that the hominin lineage split off from other primates at least 6 million years ago. There is no evidence that chimpanzees, as we know them today, even existed at that time (McBrearty & Jablonski 2005). That chimpanzees knuckle-walk and humans have childhood and adolescence merely reflects their independent evolution and adaptation to different ecologies. Despite this separation in time, **King** makes a very good point about continuities between primate species in many aspects of communication and social interaction. The discontinuity, we believe, is the human capacity for emotional engagement between multiple caretakers and dependent young that is clearly different.

A few of the commentaries on our article seem to have a different notion of life history and life history theory than we do (e.g., **Bickerton; Dickins; Ragir & Brooks**). Others, including **Gogate**, **Kappeler**, and **Oller & Griebel**, have expressed legitimate differences of opinion with our model of human life history. Let us address their comments with a clear definition of our terms. Life history may be defined as the strategy an organism uses to allocate its energy toward growth, maintenance, reproduction, raising offspring to independence, and avoiding death. For a mammal, it is the strategy of when to be born, when to be weaned, how many and what type of pre-reproductive stages of development to pass through, when to reproduce, and when to die (Bogin & Smith 1996). Life history, in this definition, encompasses the major growth, development, and reproductive events that occur between the conception and death of an organism.

Living things on earth have greatly different life history strategies and life history stages – consider those insects with more than a dozen stages from conception to reproductive adult. The differences in life history characteristics can have profound effects in several biological domains, including growth dynamics, ecology, demography, behavior, and evolution of populations. Life history theory, which is the scientific study of life-cycle strategies and their evolution, provides a way to unify systematic research in the many separate domains, each studied by different groups of specialists. One of the best introductions to current life history theory is provided by Stearns (1992).

Part of the focus of our article links the way in which people grow and develop with human reproductive success, which is greater than that of any other mammal. The social mammals, such as wolves, lions, and elephants, rear about 12–18% of their live-born offspring to adulthood. Our closest living relative, the chimpanzee, rears about 36% of its live-born offspring to maturity. But human hunter-gatherers and horticulturists, living in traditional societies without the benefits of modern medical care, rear about 60% of their infants to adulthood. Industrial societies of North America and Western Europe successfully rear at least 95% of live-born infants to maturity (Bogin 2001). Some of the reasons for this amazing human reproductive success are short birth intervals due to early weaning, the evolution of the childhood stage of development, and human capital-building during the juvenile stage and the uniquely human adolescent stage of development (Kaplan et al. 2000). Despite the delay in first reproduction produced by the insertion of adolescence, primiparous human mothers are physically, socially, and emotionally better prepared than other primate females. This may be seen in the mortality rates for infants, which are lower for humans than any other mammalian species (Bogin 1999b).

Perhaps the most important attribute leading to reproductive success is human cooperative breeding. By this we mean the cooperative childcare and feeding by non-maternal kin and non-kin that is essential to ensure the survival of a weaned child. Cooperative breeding has evolved independently in several species of mammals, birds, and insects. In those species, and in many but not all human groups, the helpers are close genetic relatives of the mother (Clutton-Brock 2002). By assisting the mother to care for her offspring, the helpers increase their own inclusive fitness, meaning that they increase the chances that their genetic kin will survive to reproductive age (Hawkes et al. 1998; Paine & Hawkes 2006). Unlike other species, human societies define kinship relations on the basis of social as well as genetic ties. In traditional human societies, kinship is the central organizing principle for economic production, social organization, and ideology. Human cooperative breeding, therefore, enhances the social, economic, political, religious, and cultural "fitness" of the group as much or more than it contributes to genetic fitness.

We agree with **Gogate's** reference to Dynamic Systems Theory (DST), according to which causality should not be viewed as a linear sequence since the emergence of new systems is usually the result of interactions of many factors at multiple levels. Gogate makes two other points about DST, life history, and language – namely, that change is not predetermined, and that change is driven by instabilities within the system. We think that these aspects of DST and evolution help explain discontinuities in the biology and behavior of closely related species such as chimpanzees and people.

The concept and stark reality of biological costs and trade-offs are also part of life history theory. **Knight & Power** state that we do not consider biological costs in our article, but we do use the word "cost" or "costly" four times in both a biological and a social sense (also see sect. R9 of this Response). For some reason, we failed to use the term "trade-off" and that is a serious omission in any article on life history evolution. A trade-off may be thought of as the competition between two biological or behavioral traits. Stearns says that "trade-offs occur when two traits compete for materials and energy within a single organism" or, "when selection for one trait decreases the value of a second trait" (1992, p. 223). An example of the

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first type of trade-off is competition between organs or tissues of the body during growth. For example, should energy and materials be devoted to growing a large set of muscles or a larger brain? An example of the second type of trade-off is the choice of producing one large offspring (k-selection) or many, smaller offspring (r-selection; cf. Wilson 1980). All living things face these trade-off decisions. Some occur on a day-to-day basis, others occur over longer periods of time. Those that have reproductive consequences and occur over generations are subject to natural selection, and the effected traits may evolve over time.

Had we discussed trade-offs, we might have forestalled the comment of **Johansson, Zlatev, & Gärdenfors** (**Johansson et al.**) that our model does not "explain the *absence* of language in, for example, chimpanzees" (emphasis in original; also see sect. R9). Chimpanzees have taken one path in life history trade-offs, and it includes a long period of nursing of infants to ensure survival versus more rapid reproduction, in the hope that some offspring survive (also see the final paragraph of sect. 2.7 in the target article). Human ancestors evolved cooperative breeding to have both more offspring and more survival, but with a trade-off cost in terms of social interaction. That cost entails getting individuals with selfish interests to cooperate. Our model proposes that human ancestors intensified the use of honest signaling, the use of communicative displays such as smiles, and eventually language as a means to reduce social conflict and foster cooperation.

Bjorklund & Grotuss pick up the theme of evolutionary trade-offs in their commentary. They refer to developmental plasticity, another important concept and mechanism that we do not mention in our target article but have discussed at some length elsewhere (Bogin 1999b; Locke 1997). Bjorklund & Grotuss's proposition that language is a product of childhood plasticity in "sociocognitive abilities" is entirely consistent with the message of our article. We thank them for providing another important way to look at the question of the evolution of language.

The commentaries of **Brighton, Mata, & Wilke** (**Brighton et al.**) and of **Powers** point to another omission in our article, namely, the importance of mathematical modeling. Much of life history theory is predicated on mathematical models (e.g., Bogin 1988; Charnov 1993; Gage 1998; Gurven & Walker 2006; Kaplan et al. 2000; Stearns 1992;). Modeling adds clarity of conceptualization, delineates the variables and parameters to be considered, and offers one type of scientific testability. Modeling is akin to inductive reasoning, whereas the approach we take in our article combines deductive and inductive reasoning. We neither disagree with our critics nor do we grant their approach primacy.

Kaplan et al. (2000) and Gurven and Walker (2006) are two excellent examples of modeling human life history, not mentioned by any of the commentators. Kaplan and colleagues show that human life history differs from the life history of the chimpanzee in several key dimensions. Based on empirical research with living human foraging societies, they show mathematically that adults must provision human offspring for about 15 years. Until that age the young cannot produce enough food to meet their own energetic demands. The need for such lengthy provisioning requires the type of close, cooperative, honest, and, at times, deceptive social contact that is both a human defining trait and facilitated by symbolic language and human cultural behavior (Gurven et al. 2000). We also note that the provisioning of young and their language development takes nearly all of human ontogeny prior to reproductive age. This is not likely to be a coincidence.

Gurven and Walker (2006) build on Bogin's life history model. They use computer simulations inductively to show that slow childhood and juvenile growth allows for the type of food provisioning that defines human cooperative breeding. Moreover, Gurven and Walker's modeling shows that slow "growth followed by a rapid adolescent growth spurt may have facilitated rising human fertility rates and greater investments in neural capital."

A fundamental distinction in approaches taken in life history research is clarified by the work of mathematical modelers such as Gould (1977) and McKinney (2000), cited in some commentaries, as well as Charnov (1993) and Gage (1998), who were not cited by any of our respondents. Gould and McKinney employ models based on heterochrony, which is an evolutionary process that alters the timing of existing life history stages. The heterochrony model for human evolution holds that the existing life stages of human primate ancestors were lengthened to derive the human condition (McKinney & McNamara 1991). This is, essentially, the basis for the continuity model for primate biology presented in the commentaries already discussed. Heterochrony does have its place in life history evolution, but we have found it lacking for human evolution. We have reviewed the literature both for and against heterochrony and offered new empirical evidence – using our inductive approach – against heterochrony (Bogin 1997; 1999a; 1999b). Instead, we found evidence supporting the insertion of the novel life history stages of childhood and adolescence into human development. The insertion of childhood shortened the infancy stage and the juvenile stage of other primate species. The insertion of adolescence did lengthen the time to adulthood, but not by lengthening any pre-existing life history stage. The inductive model theorists Charnov and Gage support our view. Charnov finds that the life histories of most species of fish, insects, and mammals studied can be modeled with his invariant life history symmetries. The glaring exception is the species of Order Primates, especially *Homo sapiens*. Gage used both mathematical modeling and empirical data to contrast chimpanzee and human life history with regard to demography. He finds that these two most genetically similar primates are quite divergent. Chimpanzees have a longer reproductive life span than humans, due to both the later onset of fertility and menopause of human women (chimpanzee do not have menopause; see Littleton 2005). Chimpanzees suffer greater infant mortality than humans. Indeed, chimpanzee mortality is greater at all ages prior to sexual maturation. Human demography is unstable, meaning there is more variability in both mortality and fertility among humans than among chimpanzees. Humans are an unusual primate species for having "baby booms." Gage suggests that these fertility booms may have played an important role in the evolution of human culture. Finally, the life history pattern of the human species depends on low pre-reproductive mortality. This novel

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demographic condition evolved after the pongid-hominin split, perhaps after the evolution of the genus *Homo*. Gage's inductive modeling supports the essential features of our deductive empirical associations. The evolution of human childhood greatly increased the fertility of women by decreasing both birth spacing and mortality. Cooperative breeding to support weaned but still-dependent children was the key to lowering mortality. Human culture, including language, evolved as part of the "package" that enhanced both cooperative breeding and individual reproductive success.

Powers advises us to consider models based on genetic programming, evolutionary robotics, and artificial life. We are forced to leave such work to others as this lies outside our expertise. Of course, we would be pleased to work with experts in those areas. Powers says that our Figure 3 in the target article is "disconfirmed," but does not offer any reference citation to support that rather strong statement. We do not know of any disconfirming evidence for Figure 3, which is based on stages or grades of hominin evolution and not specific species of hominins. Several of our hominin paleontology colleagues have reprinted this figure in their own work, including textbooks (e.g., MacDonald & Hershberger 2005; Relethford 2006; Stanford et al. 2006).

R2. Language

In the target article, we noted that theorizing in the area of linguistic evolution is incomplete in two major ways. The first is that most theories presuppose the existence of the word, relieving them of any perceived need to explain articulatory or symbolic capabilities. As words lie far beyond the reach of other primate groups, no theory of language can be complete without an account of speech. We proposed several evolutionary processes, and fitness benefits, that may have increased control over a range of speech sounds – something that language universally requires – and offered a brief remark about sound–meaning relations in the context of parental care.

The second characteristic that we noted also relates to an omission. Evolution is a two-stage process (West-Eberhard 2003). In the first stage, a plastic phenotype responds to environmental variation, producing novel forms that vary genetically. In the second stage, selection acts on the variants. From the late nineteenth century to the present it has been argued that the first stage, the origin of novel characters, can only occur in development. It is therefore strange, we asserted, that theories of linguistic evolution have been largely devoid of any developmental considerations. Few theorists say anything about the contributions of infancy, childhood, and juvenility, or even, specifically, adolescence. The relevant behaviors merely appear in adulthood.

One of the commentaries points out that we ourselves omitted something. **Bickerton** wonders why, in our attempt to explain certain aspects of the evolution of spoken language, we devoted so little attention to "the language faculty" that ultimately evolved – the capacity for a lexicon and especially the grammatical codes of modern languages – and so much attention to "the use to which it is put." No one, he suggests, would confuse objects such as cars and forks with the associated actions of driving and eating. Bickerton thus welcomes discussion around the possibility that language is an object. Its current use, he also claims, is primarily cognitive and private. These views of language surely present interesting implications, if not complications, for discussions of its evolution.

What is wrong with viewing language as an object? Surely it is not that language has *no* inventory of forms and rules, because it does. Indeed, if we are to achieve a comprehensive theory of linguistic evolution, we must explain how our species came to possess the capacity to learn and use linguistic codes. But in the context of evolutionary theory, language-as-code can have serious consequences if it distracts us from the *behavioral processes that led to language*. For the things that code excludes – the emotions, intentions, and interactions of living beings – are, or should be, the stuff of reproductive fitness accounts. Cues to personal identity, developmental stage, dominance, aggressiveness, health, and fecundity may be gleaned from the voices of humans and other primates (Cheney & Seyfarth 2005a; 2005b; Krauss et al. 2002), and a great deal of additional information, from honesty and character to personality and temperament, is to be found in speech. In many societies, speech also carries information about important cultural matters, such as social class, education, and region of birth.

If language can be so socially informative, and so animated, how did it come to be thought of as a static object? The culprit, to some extent, may be literacy. Since print is inanimate and stationary, one can examine and endlessly re-examine language that is expressed in this form. When words and sentences are written down, wrote Lakoff and Johnson (1980, p. 204), they "can be readily looked upon as objects." When literate individuals think about language, according to Linell (2005, p. 4), what they think about is "an inventory of forms, and rules for generating forms."

Is language-as-thought – either as a phenomenon or a proposal – also fostered by literacy? Goody and Watt (1968) suggested that "writing, by objectifying words, and by making them and their meaning available for much more prolonged and intensive scrutiny than is possible orally, *encourages private thought*" (p. 62, emphasis added). Comparative researchers have also expressed doubt about the naturalness or primacy of linguistic thought. Some point out that thought without language is already present in nonhuman primates (Seyfarth et al. 2005). Others fail to see how the linguistic thought hypothesis accounts for vocal learning or the meaning-to-sound mapping that occurs in language, or how one could appreciate the intellectual benefit of a private language "without a rich culturally-conveyed set of words, socially accreted over generations in the lexicon" (Fitch 2005, p. 211). But the problem with language-as-thought is not that it is incorrect; it is that this application, if it occurs with significant frequency, is likely to have originated fairly recently in evolutionary history.

Bickerton embraces Chomsky (1980) but neglects a more recent work, Chomsky (2002a), that seems to explain the latter's statements regarding language and thought. In this later work, Chomsky associates himself with a conclusion by Hauser (1996) to the effect that language fails to qualify as communication because it has different properties than the signaling systems of bees,

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wolves, birds, squirrels, frogs, apes, monkeys, and other nonlinguistic species that are addressed in *The Evolution of Communication*. What, then, *is* language? Chomsky responds that it is "a system for expressing thought" (Chomsky 2002a, p. 76). This, he says, makes language "quite different" from the signaling systems of animals. Fair enough, but the expression of thought is what people have in mind when they say that language is used to communicate. It is virtually the dictionary definition.

In the target article, we discussed Hauser et al.'s (2002) distinction between broad and narrow conceptions of the faculty of language. **Bickerton** suggests that we misinterpret this distinction "as licensing the subsuming of structural and pragmatic elements under a single umbrella" while evincing no awareness of the arguments that we actually made for the "single umbrella." In the target article, we sampled evidence from development, evolution, and genetics. The messages from these fields converge upon a single conclusion: the capacity for *speech* is intimately related to other levels of language. Developmentally, it is evident that infants who have difficulty with word learning are likely to have problems later on with grammar or pragmatics, even if their lexical difficulties abate. Evolutionarily, it is evident, on logical grounds, that grammar and other areas of language *must be* related. For if some observable behavior increased fitness at sexual maturity, then developmental precursors would have been incidentally reinforced – development being continuous – by virtue of facilitative relationships of the sort that have been documented in contemporary humans. In behavioral and molecular genetics, analyses of individuals with problems at multiple levels of language have revealed stronger or more consistent effects in the areas of phonetics and phonology, effects that imply a vocal influence in the development of all areas of language.

The commentary by **Bickerton** was not the only one to raise connections between language and thought. One other, that of **Van Herwegen & Karmiloff-Smith**, points out that we do not say whether it is language that makes humans intelligent. These commentators claim that the uniqueness of humans depends on the ability "to re-represent their representations into an explicit format, transportable from one domain of knowledge to another one." This may be true, but it has nothing to do with our stated objective, or with any claims that we have made.

Johansson et al. suggest that by failing to deal with "patterned content" (something that also concerned **Brighton et al.**, **Gogate**, and **Powers**) we do not actually explain language. What we did do was identify life history changes that would have provided critical opportunities for increased plasticity, flexibility, and innovation of relevant behaviors. We also presented arguments for the reproductive advantages of vocal, articulate, and referential behaviors during different stages of life history, from infancy to adolescence. We made no attempt to explain grammar, though a life history approach such as ours could well converge, at some point, with ongoing work on phonetic and phonological patterns (Locke 2000a; MacNeilage & Davis 2000; Ohala 2005; Studdert-Kennedy 1998; 2005). It could also produce an account of vocal complexity that interfaces with syntax (see sect. R5).

R3. Developmental contributions to the evolution of language

It was gratifying to receive comments on the role of development in evolution by several scholars who have inspired our own thoughts in this area. **Gardner** congratulates us for adopting a biological framework, and for achieving an account that is more credible and relevant than strictly linguistic formulations. **Bjorklund & Grotuss** commend us for focusing on the role of childhood in evolution. Our own valuation of the young emphasized their creativity, in the contexts of parental care and play. These commentators call attention to a possible extrafamilial contribution of the young: play groups in which words are combined in novel ways to form new words and rudimentary syntax. They also point to the unusual plasticity of the developing brain, suggesting that this might have endowed the young with a responsiveness to environmental change surpassing that of mature individuals. We see merit in both ideas, and also in their suggestion that language, and its antecedents, may have altered the contexts in which the young found themselves, exposing them to novel selection pressures.

One change of context may have involved increases in the size of working groups. In hominins, the ability to speak may have facilitated new levels of organization, enabling increases in group size. This would have increased cooperation in some areas, such as predator defense, while increasing within-group competition for physical resources (Locke 2005), though a reverse-order effect has been argued in which larger groups encouraged a transition from manual to vocal grooming and speech (Dunbar 1993). Larger groups would also have increased sociosexual competition, as we suggested earlier, which may have affected males and females, and their uses of vocal and verbal behavior, differently (see sect. R4).

When **Kuiper** refers to "analytic decomposition" of an enlarging "phrasal" vocabulary, he is proposing that such an act promoted the evolution of grammatical mechanisms. We agree, having argued in the past that in *development*, too, grammatical mechanisms are pressured into action by a burgeoning store of prosodic forms. In the second year of life, about half of infants' distinct utterances may be of this sort (Lieven et al. 1992; Locke 1997). Many persist in prosodic form, seemingly immune to segmental decomposition. We have proposed elsewhere that when this sort of material begins to overflow its memorial banks, typically in the third year, it triggers activation of a system that analyses entries into elements corresponding to linguistic units (Locke 1993; 1997). This leads to more efficient storage and permits grammatical computation. Hence, it may be said that words and phrasal words not only precede grammar, but provide its justification.

Johansson et al. say that we fail to show why chimpanzees did not evolve language, but that "buried" in our account "is the germ that may save" us. Fortunately, they were not forced to dig too deeply to find it. The germs – bipedalism, pelvic narrowing, and helplessness – were key components of our argument. We, like Johansson et al., proposed increases in proximity, attention, and care as key ingredients in the evolution of language as well as its development (Locke 1993).

King and **Cowley** wish we had placed more emphasis on interaction. We agree with Cowley that language, which is typically manifested as speech, is more often

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produced *with* others than *to* them, a pattern initially manifested in infancy. King sees antecedents in the actions of other primates, ones that result in "mutually constructive meaning-making." We would like to know more about the actions King has in mind. King welcomes our emphasis on parent-infant engagement, suggesting that message-making activity, and especially the emotional energy that drives it, represents a powerful force in the evolution of linguistic structure. We agree. Several years ago, we wrote that infants acquire language "merely by dancing with mature humans," the dance following on from "previous success in the area of emotional development and attachment" (Locke 2002, p. 633).

Spoken language owes its existence, and a great deal of its flexibility and utility, to a "comparably complex, flexible phonological system" (Fitch 2005, p. 200), something not present in the Last Common Ancestor shared with apes. One of the more important goals of evolutionary research is to achieve an account of how vocal tract activity was submitted to cortical control. **Oller & Griebel** take this on, asking how our hominin ancestors achieved the capacity to disconnect vocal or, more precisely, articulatory activity from its previous environmental and emotional moorings. In their own research, taking a recapitulatory stance, they ask how this now occurs in developing infants. Oller & Griebel offer an interesting theoretical and analytic framework, one that deserves to be adopted by other researchers. They fully understand the possibility that vocalization may be associated with requests for care, just as it affects parental decisions regarding the quality or quantity of care to provide. Nearly two thousand years ago, a medical doctor, Soranus of Ephesus (96–138 A.D., translated by Temkin in 1956), claimed that certain newborns were "not worth rearing." The newborns he had in mind, significantly, included those who cried atypically and failed to respond appropriately to external stimulation.

Oller & Griebel stress developments in the first six months of life. Cooing, perhaps the first nonstress vocalization, appears at about three months. This is an interesting age. It is also when crying declines, along with infanticide (Locke, in press c), and it is generally assumed that this age is when instrumental crying (and smiling) begin. When the infant is finally freed from internal discomforts that block optional and playful forms of vocal behavior, it may begin to "read" others to see how they are affected by his vocalizations. Doing so will make it easier to use syllables strategically to attract and engage others.

It is of course possible for articulatory control to emerge in association with endogenous variables, such as the development of arm and hand activities, as may have occurred in response to environmental changes that freed the limbs from their earlier role in ambulation (cf. Locke, in press a). But there may also have been pressures to signal that added to the benefits of articulated phonation by itself.

Sharing **Oller & Griebel's** concern with the emergence of vocal-motor control, **Lenti Boero & Bottoni** see value in comparative studies of vocal development, especially in songbirds and parrots, and of various communicative practices in nonhuman primates and vocal behavior in human infants. **Schleidt** also emphasizes comparative studies of development. For him, the chief contribution of different ontogenetic stages relates to social factors, primarily the formation of close ties to new types of companions. **Powers** chides us for not saying more about fetal learning. At one time, we could have been accused of saying *too much* about it (Locke 1993; 1994a; 1994b; 1994c; 1997; 1999; Locke & Snow 1997), but we repeat here: linguistically relevant stimulation appears to begin at some point in the final trimester of gestation, possibly with the onset of audition.

R4. Oral societies: Verbal performance

In the target article, we devoted some space to oral societies in which orators – and in segments of industrial societies, "street orators" – exercise a number of impressive vocal and verbal skills to attract audiences and persuade them to their point of view. No formal training is needed to do these things, as the work on "Brazilian bards" confirms (Roazzi et al. 1993; 1994). **Kuiper,** in commenting that literate societies "contain many subcultures which are oral societies," stresses that orality is a hardy disposition that endures in spite of literate pressures. Even in the highly literate corridors of academia, oral story-telling reigns supreme (Wickham 1998).

"Some people have a way with words," comedian Steve Martin once joked, "other people ... not have way." **Kuiper** points out that in many societies, those who "not have way" cannot handle phrasal vocabulary (colloquialisms and other forms of formulaic material) with some degree of skill and may become "social lepers." In various cultures, people who do not speak well are disrespected or even censured (Edwards & Sienkewicz 1990; Peek 1981). In the target article, we pointed out that African Americans who lack the knowledge and skill needed for verbal duels are derided as "lames" (Abrahams 1989; Labov 1972; 1973), and if they fail with women, their raps are ridiculed as "tissue paper" (Anderson 1990, p. 115).

Clearly, various sorts of verbal gamesmanship are beneficial in adolescence and early adulthood. This is also true in the preceding stages of juvenility and childhood, when riddling and formulaic jokes become popular in a variety of cultures around the world. McDowell (1979) encountered four different genres of verbal performance in "chicano" and "anglo" children and juveniles in Texas: stories, rhymes and songs, taunts, and riddles. The riddles were used in a competitive or agonistic arena. The taunts expressed aggression in verbal form, thereby preventing physically injurious activity. These genres also help increasingly autonomous individuals to make decisions about which others to include as friends and future collaborators, and to decide which groups to join. In adolescence, they may be used as a means of judging intelligence and suitability for long-term relationships (see sect. R5).

Several peers, including **Benga**, have commented on our treatment of verbal performance. **Knight & Power** indicate that we use the term "performative" differently from Austin (1975), who cast about for alternatives before he settled on this term, and who clearly felt a need to justify his final choice (Austin 1975, pp. 6–7). However, our use is completely consistent with the relevant literatures. "Performer" and "performance" frequently appear in the accounts of oral societies (e.g., Abrahams 1968; Bauman 1975; Gossen 1974; Ong 1982),

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as does "performative" (e.g., Edwards & Sienkewicz 1990; Finnegan 1969; Linell 1982). This is unsurprising since the phenomena in question involve verbal artistry and an audience. Still, to ensure that readers would not confuse our meaning with Austin's, we referred to pragmatics *and* performance five times. In section 2.8 of the target article, we pointed out that a number of verbal functions that belong to the performative function (e.g., joking, mollifying) fall outside the area of pragmatics as usually defined, and in section 10 (title "Pragmatics and performance"), we further discuss these categories.

Knight & Power imply that we erred in claiming that "performative applications of language, in the form of speech and voice, consistently favor males." Evidence from the (heavily Western) anthropological literature indicates that males are, in fact, more likely to engage in public displays of vocal and verbal prowess than females. There are cultures where both men and women speak in public, but we have yet to find a culture where the male dominance pattern is reversed, and would expect to find few in which females outperform males in agonistic displays.

Knight & Power suggest that any evolutionary accounts based on male dominance in the public display of vocal and verbal behavior are necessarily limited, since these would only take place in hierarchical or stratified societies. If this were true, it would be difficult to square with anthropological accounts. Consider, for example, the song duels of the Hindi-speaking Fiji Indians, an "unstratified" society in Bhatgaon. In these duels, sung by men in groups of three to six, the "singers usually attack, insult, and slander the religion, relatives, and persons of their opponents," attempting "to lower the prestige of their opponents and their opponents' religion" (Brenneis & Padarath 1975, p. 283). "Despite an apparent *lack of stratification*," the authors conclude, "the nature of one's standing relative to other men is a recurring concern for villagers" (p. 284, emphasis added).

In the target article, we claimed that "important aspects of language cannot appear until sexual maturity." **Knight & Power** chose to conflate this claim with an equally uncontroversial statement in section 10, that "the ability to infer intentions presupposes real-world knowledge," (sect. 10, para. 2) and then drew the conclusion that the knowledge we had in mind had something to do with sexual behavior. It does not. What we stated is that pragmatics is the last area of language to develop, and must be, because it depends on knowledge that could not be present until the individual had witnessed, and engaged in, behaviors that typically emerge in the run up to adulthood. The knowledge we had in mind concerned the social, economic, political, and physical world as it can only be known to those who interact with it outside of the familial context, with some degree of autonomy.

Knight & Power again merge separate statements from section 6. There, we pointed out that the verbal dueling of males may be supported by testosterone, which is related to dominance and aggression (Puts et al. 2005), and that it may be adaptive for them to use verbal sport and humor in place of physical combat. Knight & Power take this to mean that *in females*, lower levels of testosterone are somehow responsible for the documented gossip preference associated with that sex; they then interpret gossip, as a means of disseminating socially relevant information, to be syntactically more complex than the elaborate verbal performances of males.

There are at least two things to say here. The first is that in males, testosterone contributes to aggression, which is frequently exercised physically (Dabbs 2000). To avoid physically harming each other, some other behavior must be substituted. Marsh (1978) has described the "aggro" of young British men, a ceremonial display of physical posturing and verbal taunting that expresses aggravation in a fairly harmless manner. Aggro, he writes, "is an all-male affair ... females are irrelevant – they form no part of the ceremony and, more importantly, they are not legitimate objects of attack. There is no conflict here except with other males" (Marsh 1978, p. 28). It is widely recognized that male adolescents and young men need ways to avoid physically injuring each other. Although this can be accomplished with nonverbal as well as verbal displays (Kochman 1969; 1983; Marsh 1978), in practice, the two work together. Street gangs that are physically violent have a high rate of verbal duels (Short & Strodtbeck 1965).

Although aggrieved members of both sexes swear at, scold, scorn, and chastise others, the second thing to note is the strong tendency of females to engage in gossip – a private verbal behavior used primarily or exclusively with other females – to lower the status of perceived opponents, and to do so during the same life history stages, juvenility and adolescence, in which males engage in verbal duels – public verbal behavior used primarily or exclusively with other males – in an effort to compete for status and other resources. However, in our reference to gossip (sect. 6), we pointed out that the stronger female disposition to gossip "may have to do with the fact that gossip serves an *affiliative* function," and that females, in times of stress, "tend to *come together*," turning to each other "for *mutual aid*" (sect. 6, para. 2, emphasis added). It was in this context that we discussed sexually dimorphic applications of speech.

In searching for the biological bases of such differences there are plenty of places to look. Consider the birth process. In the other primates, there appears to be a tendency to give birth alone. Women, on the other hand, seek each other out at the time of childbirth (Trevathan 1999; Walrath 2003). Even in the case of apparent contradictions to this pattern, the woman typically does not leave the group for her first child, or go too far to summon help if needed (Biesele 1997).

If women gossip more than men, **Knight & Power** say, this should give them an advantage in the area of syntax, but this takes several things for granted. First, it assumes that gossip is syntactically complex. We accept that it may be. Second, it assumes that the more public displays of verbal prowess by male speakers are syntactically deficient. To our knowledge, no such evidence exists. Indeed, the reports indicate that the more powerful individuals in traditional societies are unusually expert in manipulating sentential material.

Studies of baboons indicate that here, too, females are less aggressive than their male counterparts. Seyfarth (1976) has reported that the ratio of approach-retreat interactions to bouts of overt aggression is less than 2:1 in males, but 20:1 in females. The affiliative function that is fulfilled by human gossip may also have antecedents in nonhuman primates. Elsewhere, we have reviewed

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research indicating that social grooming is carried out predominately by females (cf. Locke 2000b; in press b). When grooming, monkeys characteristically emit lipsmacks and girneys – low amplitude oral and vocal activity that, to some ears, bears faint resemblance to speech (Richman 1980; 1987) and also is displayed in the context of appeasement. In a study of captive Japanese macaques, 90% of all the girneys were produced by females (Blount 1985).

There is evidence in our own species that girls are less competitive and domineering than boys (Benenson et al. 2001; Miller et al. 1986; also see review in Campbell 1999). A factor in this pattern may be the size of social groups. Left to their own devices, females prefer dyadic interaction. Males, by contrast, prefer larger groups (Belle 1989). The significance of this is that larger groups foster competition. In Benenson et al. (2001), 6- and 7-year-old boys, but not girls, made a higher proportion of competitive moves in tetrads than in dyads.

Liénard asks if there is evidence that women are verbally dominated by men, and there is evidence – at least when it comes to interruption and volubility. Investigators typically find that females are more inclined to speak than males when interacting with a same-sex conversational partner of their own choosing, and in this context they also tend to be more talkative in juvenility, childhood, and infancy (see Locke & Hauser 1999 for references).

We welcome **Wermke & Mende**'s emphasis on melody. They argue that melody may provide the immature infant brain with "a kind of filter to extract life-relevant information out of the complex parental speech stream" (last para.). They remind us that, to infants, the most salient of all acoustic components in speech is prosody, a feature that parents exaggerate when addressing their infant. It is also a feature that figures into the identification of prepackaged phrasal material, as **Kuiper** understands.

Johansson et al. ask why protohumans need to have spoken when they could have achieved similar benefits by singing. Our mission, of course, was broader than vocal control; we also took up reference, within the context of interactions between parents and their young, as did Fitch (2004; 2005). Still, there are at least three reasons to study speech in conjunction with song. First, there is, as we have pointed out, a logical connection between the use and control of the voice in singing and speech – an excellent reason for collaboration between speech researchers such as **Oller & Griebel** and those who study music and song (e.g., Merker 2000; Mithen 2005). Second, verbal duels and vocal contests appear to serve similar social functions in several different societies. Finally, competitive pressures in both modalities may have increased our species' capacity for vocal complexity. We discuss these functions and pressures in the section that follows.

R5. Verbal plumage: Folk IQ?

Functional connections between speech and song are implied by research revealing a male bias and an agonistic tone in vocal as well as verbal dueling. Herndon and McLeod (1980) observed that in Malta, the most frequently performed style of folk music, the song duel, or *spirtu pront*, "is an improvised poetic duel, sung by two men, which develops a subject by means of complex metaphorical insult." The *spirtu pront* is completely *improvised*, except for the melody. "Due to the complexity of this sung poetry," according to Herndon and McLeod, "those who attempt it *must be extremely intelligent*" (p. 147, emphasis added).

Several years ago, we suggested that modern men attract and impress listeners "with verbal *plumage* – fluent mastery of a broad range of words and phrases, many of them outside the more limited repertoire of their audience" (Locke 1998c, p. 92, emphasis in the original). In the target article (Note 6), we pointed to evidence in industrialized societies that the use of rare, long, abstract, diverse, or unusual words is correlated with formal measures of intelligence. Here we speculate that in evolution, verbal ornamentation was created *so that* performers' cognitive abilities could be displayed and, thus, evaluated by others. If so, verbal plumage is something on the order of a folk IQ test.

It is evident that precisely this purpose – intelligence assessment – is now served by the Maltese song duels mentioned above, and that riddles permit similar judgments in the wide range of cultures in which they are used. In 1783, Chrisfrid Ganander described an ancestral Finnish tradition in which riddles were used to test "the acuity, *intelligence* and skills" of suitors. When a young man sought romantic commitment, "three or more riddles were posed to him, to *test his mind* with them," wrote Ganander, "and if he could answer and interpret them, he received the girl, otherwise not, but was classified as stupid and good for nothing" (quoted by Maranda 1976, p. 127, emphasis added; also see Burns 1976).

Associations between verbal ability and intelligence have been described in members of African and African-American cultures. In a review, Peek (1981) points out that among the Igbo of southeastern Nigeria, oratorical ability "is directly equated with *intelligence* and success," and that the Barundi people of central Africa associate verbal ability with "successful *cleverness*" (Peek 1981, p. 22). In Sierra Leone, "it is noticeable how strongly the Limba connect *intelligence* and speaking" (Finnegan 1969, p. 75, emphasis added). In African American communities too, "rap" and "the dozens" permit evaluations of an individual's ability to compete and adapt. "Black culture," Kochman (1971) has noted, "promotes the development and demonstration of those skills which reflect on an individual's underlying *intelligence*, verbal ability, speed, strength, agility and endurance" (p. 19, emphasis added).

But the association between speech and intelligence is not limited to individuals of African descent. Among the Chamula Indians of southern Mexico, the ability to perform well in "truly frivolous talk," a verbal duel fought exclusively by young men, "serves as a fairly dependable index of a man's social maturity, linguistic competence, *intelligence*, and political potential" (Gossen 1974, p. 106, emphasis added).

Since each developmental stage contributes to language, we should not be surprised to encounter nascent forms of verbal performances and duels long before adolescence. In his fieldwork with the Chamula Indians, Gossen (1976b) heard attempts by 2- or 3-year-old boys to verbally duel with their older brothers, with increases in phonological proficiency at ages 5 and 6 years. In a rare report, verbal

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performances of 3- to 5-year-old African American boys were captured on audiotape and transcribed. In one case, a spontaneous rap, a boy expressed his feelings toward one of the female research assistants on whom he had developed a crush. In the other case, three boys engaged in "the dozens" (Wyatt 1995; 1999). These boys were playing, but a decade later they would be expected to enlist their verbal abilities as adaptive strategies, ones that would help them to attract females, avoid violence, and compete for status with same-sex peers.

To this point, we have exposed few connections between linguistic function and form, but if there was a reproductive advantage of vocal and verbal complexity, runaway selection – which, as Harvey and Arnold (1982) point out, would certainly have applied to vocalization – may have produced a huge increase in the complexity of speech and, therefore, the possibility of complexity *at other levels of language*, and possibly in other modalities. If speech were kept simple, observers would have to find other ways to make the necessary inferences.

If a performance is rhythmic or euphonious, and the material novel or complex, then it is possible that form and function interact. Are there relationships between the quality of the dance and the ornamentation of the dancer? There are multiple cues to attractiveness in other species, and these interact in extremely complex ways to produce their effect (Badyaev & Hill 2003; Candolin 2003; van Doorn & Weissing 2004). They even complement each other (Badyaev et al. 2002; Coleman et al. 2004; Johnson 1999). In our own species, too, speakers are evaluated along with their messages. It is possible that in display mode, the evaluations of others are based both on structural complexity and behavioral finesse.

R6. Genetic support of verbal performance

We have proposed that vocal and verbal skills enable adolescents and young adults to engage and compete with others, and to perform in public arenas – the relevant abilities increasing their fitness. Now it could be said that these verbal dimorphisms were merely brought to the surface and made observable by underlying sex differences in the tendency to compete and aggress (Fitch 2005, p. 212). But, for behavioral traits, as opposed to physical ones that are readily perceptible, such as size, the individual must be motivated to act in the first place, and the source of the motivation may be an internal change. In fact, if anything was selected directly, it was vocal and verbal ability. The indirect effects were the supporting physiological variables. Thus, males' greater disposition to compete – secondary to increases in testosterone – may have increased the functionality of their vocal and verbal ability while also making it public, raising the probability that these skills would be selected, and tightening the links between speech and testosterone. If so, one might expect a genetic legacy: genes that code specifically for verbal expressivity and dominance in modern humans. Recently we came across several reports indicating that monozygotic twins, but not dizygotic twins, are highly concordant on measures of social potency and expressive control, tests that tap the ability to act or perform in social situations, even where the twins have been reared apart (Gangestad & Simpson 1993; Lykken 1982). Significantly, individuals who were unusually social and expressive reported that they had engaged in sex with more partners, and with more partners on just one occasion, than their less social and expressive peers (Snyder 1987).

With such high concordance rates, one might expect to see differences in sociality and expressiveness appearing early in life history. It is interesting, in this connection, that investigators in other fields have documented the existence of unusually social and expressive individuals in infancy (cf. Nelson 1973; 1981), termed "dramatists" by Wolf and Gardner (1979) since they appear to learn at an early age that different individuals can exchange roles in identical social situations. Dramatists also like to tell dramatic stories and display elaborate forms of imitation. On the basis of content validity, Gangestad and Snyder (1986) speculated that such expressive differences in infancy and adulthood are manifestations of the same latent factor.

This section on the genetics of verbal performance is a convenient place to acknowledge the kind remarks of **Workman**, who does, however, misinterpret our discussion of FOXP2, thinking that we see in this gene a basis for linguistic grammar. In fact, we referred to the behavioral research leading to the identification of this gene because it related to the role in language that is played by "production factors." We pointed out that problems experienced by the KE family "included a severe *oral and verbal dyspraxia*, accompanied by deficits at other levels of language" (emphasis added), and quoted from several theorists who suggest that speech might have a certain primacy that has been neglected in the past. This supported our argument that verbal performance was selected.

R7. Performance as adaptation

What supported the use of vocal and speech-like activity before there was speech? **Knight & Power** doubt our account of reproductive advantages because, they say, linguistic signs represent no "cost" or investment. They fail to recognize several things. First, the resting metabolic rate (RMR) of the human brain exacts a continuously high energetic cost from infancy, as mentioned in the target article and in section R1. Were this not so, many complex human activities, including language, would be impossible. Second, articulated phonation carries a great deal of information *about the individual*, whether or not it is consciously transmitted. Apes rely on this information and so do we. Third, potentially informative components of the voice are supported by physiological activity that is energetically expensive (e.g., pulmonary pressure; cf. Fitch & Hauser 2002). Fourth, traits will be selected if females prefer them, and not everything females prefer is costly (Johnson 1999). Finally, the mere uttering of certain words (or other constructions), especially rare ones, may reflect a great deal of prior learning – learning that presupposes the efficient action of relevant mechanisms. Merely to use a behavior that was learned, or requires an unusual mode of articulation, can mean that the individual has an intact nervous system, has the ability to attend, perceive, store, retrieve, and reproduce complex patterns of behavior, and can do so meaningfully

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in an appropriate social context. The energetic requirements of the motoric act, and the veracity of any statements, are not the only relevant factors.

Dickins sees a need to identify proximate mechanisms for the actions that we propose, and **Powers** would like us to have made more explicit predictions. Perhaps we underplayed our effort to construct an adaptive account of vocalization in relation to social dominance and courtship. In section 8, we suggested that women who are attracted to men with a commanding way of speaking may get a mate for themselves, and a father for their children, who has high levels of testosterone and status, and unusual access to valued resources. Specifically, we evaluated research that reveals connections between properties of male voices, as measured acoustically and appraised perceptually, and both virility and social dominance. In light of other research, we would predict that women prefer the voices of men who are high in testosterone, especially when heard during ovulation (Fisher 2004; Puts 2005).

In the target article we reviewed research indicating that the speech of courting men contains unusually wide frequency and intensity swings, and that young women, when asked to evaluate utterances extracted from children's conversations, expressed a preference for selections that were classified as excitable, loud, and uncontrolled, among related variables. Taken together, these behaviors could suggest the operation of a sensory trap (after the pattern described in insects and other animals) in which sexually mature males mimic the vocal qualities that appear to excite females (Christy 1995; Enquist & Arak 1993; Macias Garcia & Ramirez 2005). Surely there is raw material here for testable hypotheses on the fitness benefits not just of speech, but of particular aspects of prosody, and investigations could easily be extended into lexical and other areas of spoken language. To implement such an agenda in the context of linguistic evolution, it will of course be necessary to investigate the perceptual preferences of sexually mature females and the use of male vocalization and speech in social competition and courtship, and this is exactly the kind of research that we propose. In line with a standard approach in biology, it would then be possible to look at which vocal variables were most strongly linked to perceptions and proximate variables that index fitness. By carrying out a research agenda of this sort, one does not show how language evolved, of course, but one may be able to argue for the plausibility of a particular proposal on the basis of empirical data.

Dickins is not sure that we adequately supported our claim that the components of language are related, but it can only be so if, as we argued in the target article and repeated earlier in this response (sect. R3), they were stitched together by sequential patterns of selection. Behaviors that were selected at sexual maturity, such as verbal persuasiveness, could not have appeared without some level of pragmatic development, and without linguistic skills that rest on previous accomplishments in the area of lexical, phonological, morphological, and syntactic development. We noted in this context, additionally, the well-attested observation that development is continuous, behaviors not usually emerging de novo in later ontogenetic stages without an appearance, in some form, in one or more of the preceding ones. We also cited evidence suggesting that individuals having problems in one area of language tend to have problems in other areas.

Johansson et al. say that we failed to show "that language was useful and adaptive specifically for proto-humans *and not* for proto-chimpanzees." **Ragir & Brooks** seem to think, in parallel, that if language benefits humans, it should have benefited the other primates equally. If it did, they say, the behavior would have followed. But these comments miss the point. The question is not who language could have assisted, but rather, in whom it could have evolved. In section R1, we point out that hominins took a different path, one that led to cooperative breeding and protolanguage, and therefore evolved a completely different life history.

Ragir & Brooks comment that performance is beneficial at every stage of language development, not just in adolescence. That we also believe this is why we devoted so much attention to proposals regarding infant behavior, including parental selection and trickle-up phonetics. In the target article, we argued that skillful vocal performances by adolescent and adult *male hominins* would have facilitated their quest for rank and reproduction. Ragir & Brooks express doubt about a portion of this argument since, they say, *female apes* fail to show a preference for alpha males. The relevance of this is unclear, since our claim is that there were changes in *hominins* that occurred *following* their divergence from shared lineage. As indicated in the target article, we trace these changes to pre-adult stages when control over new and more variegated vocal behaviors emerged under environmental pressures that remodeled *human* infancy and contributed to the evolution of childhood.

R8. Pluralism

We noted at the beginning of section R2 that in the first stage of evolution, environmental variation produces novel forms that vary genetically, and that in the second stage of evolution, selection acts on the variants. According to our account, infancy and childhood produced new abilities to effect and manipulate vocal forms, with selection occurring in those stages and perhaps more powerfully at sexual maturity. To us, the development and evolution of language – and ultimately its nature – are interrelated. Work in one area potentially affects progress in the other. Theorists must integrate findings in psychology, biology, animal behavior, anthropology, archaeology, genetics, and linguistics if these benefits are to be appreciated. In our own attempt to explain the evolution and modification of life history stages, we needed to integrate findings from archaeology with findings on the development of brains, teeth, endocrine systems, and other characteristics of modern humans. We think that such efforts will eventually produce a small step toward the unification of a broad base of language-relevant knowledge, emanating from a wide range of disciplines. Theorists also need to explain developments across the various stages of linguistic evolution, not merely those pertaining to language as it is, or as it appears, now. We have claimed that insertion of new ontogenetic stages into human life history, and the remodeling of others, produced new developmental processes that fashioned novel communicative behaviors and increased fitness. If so, reciprocal action by evolutionary and developmental mechanisms – working in an "evo-devo-evo" sequence – may have played a major role in the evolution of language.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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