Craniofacial Feminization, Social Tolerance, and the Origins of Behavioral Modernity

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The past 200,000 years of human cultural evolution have witnessed the persistent establishment of behaviors involving innovation, planning depth, and abstract and symbolic thought, or what has been called "behavioral modernity." Demographic models based on increased human population density from the late Pleistocene onward have been increasingly invoked to understand the emergence of behavioral modernity. However, high levels of social tolerance, as seen among living humans, are a necessary prerequisite to life at higher population densities and to the kinds of cooperative cultural behaviors essential to these demographic models. Here we provide data on craniofacial feminization (reduction in average brow ridge projection and shortening of the upper facial skeleton) in *Homo sapiens* from the Middle Pleistocene to recent times. We argue that temporal changes in human craniofacial morphology reflect reductions in average androgen reactivity (lower levels of adult circulating testosterone or reduced androgen receptor densities), which in turn reflect the evolution of enhanced social tolerance since the Middle Pleistocene.

Introduction

Humans are notable for their high degree of social tolerance and their remarkable capacity for prosocial helping and co-operation (Boyd and Richerson 1982; Burkart, Hrdy, and van Schaik 2009; Fuentes 2004; Hare 2011; Silk and House 2011; Tomasello 2009; Yamamoto and Tanaka 2009). Social tolerance and cooperation, in turn, appear to be necessary to another notable aspect of human behavior—our extraordinary capacity for cumulative technological evolution (CTE), or "cultural ratcheting" (Tennie, Call, and Tomasello 2009).

Based on the archeological record of the Middle Stone Age/

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Middle Paleolithic, CTE appears to have accelerated during the interval between about 80 and 30 Ka BP. Beginning sporadically in the later part of the Middle Stone Age (MSA) and continuing with increasing regularity into the Later Stone Age (LSA) and Upper Paleolithic (UP), this interval witnessed the rapid florescence of new technologies, including leptolithic and microlithic tools, greater artifact diversity, bone and antler working, heat treatment and pressure flaking of flint, long-range projectile weapons, grindstones, fishing and birding gear, trapping technology, sophisticated pyrotechnology, and possibly watercraft (Ambrose 1998; Backwell, d'Errico, and Wadley 2008; Brooks et al. 1995, 2005; Brown et al. 2009; Davidson and Noble 1992; d'Errico and Henshilwood 2007; Henshilwood and Sealy 1997; Henshilwood et al. 2001; Holliday 1998; Lombard and Phillipson 2010; McBrearty and Brooks 2000; Mellars 1989a, 1989b; Mourre, Villa, and Henshilwood 2010; Shea 2006; Straus 1991, 1993; Valde-Nowak, Nadachowski, and Wolsan 1987; Villa et al. 2009; Yellen et al. 1995). This period of rapid technological innovation is contemporaneous with the earliest evidence of symbolic behavior and abstract thought, in the form of pigment processing, personal adornment, incised notational pieces, musical instruments, and mobilary and parietal art (Bouzouggar et al. 2007; Broglio et al. 2009; Conard 2003, 2009; Conard, Malina, and Münzel 2009; d'Errico et al. 2005, 2009; Henshilwood et al. 2002, 2004; Henshilwood, d'Errico, and Watts 2009; Higham et al. 2012; Marean et al. 2007; McBrearty and Brooks 2000), as well as evidence for expanded diet breadth and innovations in subsistence strategies, expanded social net-

works, and long-distance exchange (Bar-Yosef 2002; Henshilwood and Marean 2003; McBrearty and Brooks 2000). Together these behaviors signal the emergence of what has been called "behavioral modernity" or "fully symbolic *sapiens* behavior" (Henshilwood and Marean 2003; Nowell 2010).

We hypothesize that this behavioral event was facilitated by a change in average human temperament toward less aggressive, more socially tolerant individuals. We argue that this shift is evident in the fossil record of later Pleistocene humans.

The Problem of Behavioral Modernity

New fossil discoveries and redating of key specimens, combined with analyses of variation in mtDNA in living humans, strongly suggest that the earliest members of our species appeared in Africa between 200–150 Ka BP (Cann, Stoneking, and Wilson 1987; Forster 2004; Ingman et al. 2000; McDougall, Brown, and Fleagle 2005; White et al. 2003), some time during the earlier part of the MSA. The timing of the emergence of symbolically mediated modern behavior (hereafter, "behavioral modernity"), however, is less certain. Evidence of symbolic behavior occurs sporadically in the MSA after about 100–80 Ka BP (Bouzouggar et al. 2007; d'Errico, Henshilwood, and Nilssen 2001; Henshilwood et al. 2004; Henshilwood, d'Errico, and Watts 2009; Texier et al. 2010; Vanhaeren et al. 2006) and may even date back to the initial MSA at 280 Ka BP (Deino and McBrearty 2002). Similar, sporadically occurring symbolic artifacts are found in contemporaneous Mousterian assemblages in Europe, presumably produced by Neanderthals, beginning as early as 90 Ka BP (Morin and Laroulandie 2012; Peresani et al. 2011; Soressi and d'Errico 2007; Zilhão et al. 2010). Despite these early beginnings, the persistent expression of symbolic behavior, as well as the marked acceleration of CTE described above, does not appear to be firmly established until the development of the LSA (in Africa) and UP (in Eurasia) sometime around 50 Ka BP (Bar-Yosef 2002; Klein 2000, 2008; Mellars 2006b; Nowell 2010). This 100–150,000 year gap between the emergence of modern human morphology and the consistent expression of symbolic behavior is often referred to as the "problem of behavioral modernity" and has generated heated debate about the cognitive and cultural capacities of the earliest modern humans.

One model holds that behavioral modernity resulted from some change in cognitive abilities (Nowell 2010), likely reflecting a relatively rapid appearance and fixation of new alleles governing neural development at around 50 Ka BP (Mellars 2006b) that enhanced human cognitive capabilities relative to earlier MSA modern humans and the contemporary Mousterian Neanderthals. Several different cognitive skills have been proposed as being key to the emergence of modern behavior, including enhanced working memory (Ambrose 2010; Wynn and Coolidge 2004, 2010), domain-general intelligence (Klein 1995), linguistic and symbolic capacities (Klein 2000, 2003; Mellars 1989b, 2007), abstract thinking (Lewis-Williams 2002), and increased flexibility in understanding the minds of others as intentional (Dunbar 2003; Tomasello et al. 2005). As noted above, however, there is growing evidence that both Neanderthals and modern humans prior to 50 Ka BP had the cognitive capacity to engage in symbolic behavior (d'Errico and Stringer 2011; McBrearty and Brooks 2000), which implies that the critical difference between modern humans before and after 50 Ka BP may not have been in cognitive capacity but rather in the prevalence and persistence of symbolic behavior.

An alternative model holds that the capacity for modern behavior emerged at the same time as, or before, anatomical modernity and that cultural, historical, ecological, or demographic factors were in play that prevented its consistent expression until the end of the MSA (Chase 2006; d'Errico and Stringer 2011; Jacobs and Roberts 2009; Nowell 2010). Demographic expansion and population density are increasingly being seen as critical components in the expression of behavioral modernity (Jacobs and Roberts 2009; Richerson, Boyd, and Bettinger 2009). Cultural ratcheting requires both cultural innovation and transmission, and variation in these processes is conditioned by the rate of interaction between social learners (Henrich 2004; Shennan 2001), which in turn depends on population size and structure. Both computer modeling (Powell, Shennan, and Thomas 2009; Shennan 2001) and analyses of cultural complexity in Tasmania and Oceania (Henrich 2004; Kline and Boyd 2010) reveal that populations with either large overall size or high connectedness between subpopulations are more successful in generating, retaining, and diffusing cultural innovations. Thus the sporadic occurrences of symbolic behavior and technological innovation in the earlier part of the MSA may represent geographically restricted, transient peaks in population density (in which CTE began to take off) followed by demographic crashes (possibly caused by downturns in climate; Jacobs and Roberts 2009; Mellars 2006a; Powell, Shennan, and Thomas 2009; Richerson, Boyd, and Bettinger 2009). Similar transient increases in Neanderthal population densities may account for the irregular manifestation of symbolic expression in the European Mousterian (compare the temporal pattern of Mousterian innovation in Langley, Clarkson, and Ulm 2008 with Mousterian site abundance evidence of Neanderthal population density in Stringer et al. 2003 and Lahr and Foley 2003). Later population expansion in Africa beginning in the late MSA (80–70 Ka BP) and continuing into the LSA/UP, as reflected in both genetic (Excoffier and Schneider 1999; Forster 2004; Harpending et al. 1993; Watson et al. 1997) and archeological evidence (Mellars and French 2011; Steele and Klein 2005; Stiner et al. 1999), produced population densities sufficient for a high rate of CTE, and thus demographic factors, rather than cognitive capabilities, might account for the persistent expression of behavioral modernity in the LSA and UP (Powell, Shennan, and Thomas 2009; Shennan 2001).

Temperament and Craniofacial Morphology

Demographic models for the origins of behavioral modernity do not require the evolution of cognitive capacities beyond those already possessed by the earliest modern humans and possibly (judging from the Mousterian evidence) by other archaic humans (Nowell 2010). Still, there is a biological constraint inherent in demographic models, in that sociality evolves at the cost of increased resource competition among conspecifics (Janson and Goldsmith 1995; Kappeler and van Schaik 2002), such that the intensification of the competition caused by increases in population density necessitates a complimentary increase in social tolerance. Therefore, we suggest that demographic models can only explain the persistent expression of behavioral modernity in concert with the evolution of a more cooperative temperament. Under this model, high social tolerance was positively selected because of the payoffs inherent in cultural transmission and cooperation, two human traits that underlie behavioral modernity (Hill, Barton, and Hurtado 2009). Evidence from other species suggests that this noncognitive shift could have happened relatively quickly, causing profound and equally rapid changes in behavior (Hare and Tomasello 2005; Hare, Wobber, and Wrangham 2012; Réale et al. 2007). While there is nothing inherent in the demographic models that requires that increased social tolerance emerged uniquely in *Homo sapiens* (i.e., these models work equally well if greater social tolerance had evolved earlier, so long as it was in place at the time that MSA population density began to increase), we suggest that increasing human population density, initially in the later MSA and continuing until recent times, provided the selective environment favoring enhanced social tolerance.

Social tolerance is necessary for effective cultural transmission of technological innovations and other behaviors. The probability that a learner will acquire a novel technique depends in part on the physical proximity between models and learners, as well as the number of accessible models (Coussi-Korbel and Fragaszy 1995; van Schaik, Deaner, and Merrill 1999; van Schaik and Pradhan 2003), both of which are enhanced with greater social tolerance. Increased tolerance would also greatly improve the fidelity of cultural transmission through the evolution of teaching and conformity (Tennie, Call, and Tomasello 2009; Thornton and Raihani 2008). Individuals of high tolerance can learn in a more relaxed atmosphere that allows close examination of the model by the observer (van Schaik, Deaner, and Merrill 1999; van Schaik and Pradhan 2003). The importance of tolerance is evident in observational and experimental studies on various primates (Horner 2010; van Schaik and Pradhan 2003), including one study (Horner et al. 2006) that found that chimpanzees failed to acquire a novel behavior if they were intolerant of the model, while the same subjects were able to learn when paired with a tolerant model, indicating that individuals who are cognitively capable of learning can be constrained by intolerant temperament (see also de Waal and Davies 2003; Drea and Wallen 1999; Hare et al. 2007; Melis, Hare, and Tomasello 2006).

Importantly, shifts in social tolerance can relatively quickly and profoundly change behaviors because they allow individuals to utilize preexisting cognitive abilities in a new set of contexts (Hare and Tomasello 2005), as demonstrated by artificial selection experiments in Siberian silver foxes. Over a period of 50 years, a captive population of foxes was experimentally selected for both an interest in and lack of fear of humans (i.e., tameness; Trut 2001; Trut, Pliusnina, and Oskina 2004). The tame strain of foxes displayed behavioral attributes normally associated with domestic dogs: less aggression toward humans, a greater propensity as adults to play with humans, increased sensitivity to human communicative gestures, and the use of juvenile vocalizations by adults—a suite of behaviors recognized as part of "domestication syndrome" (Hare et al. 2005; Hare, Wobber, and Wrangham 2012; Trut, Pliusnina, and Oskina 2004). These behavioral traits were never the target of selective breeding, yet selection for a single temperamental trait (tameness) was sufficient to generate associated behavioral changes in a very short time. A similar study in mice documented rapid and widespread changes in social behavior caused by selective breeding against aggression, resulting in the juvenilization of both aggressive and prosocial behaviors (Gariépy, Bauer, and Cairns 2001). Selection on temperament can also operate quickly in vertebrates (e.g., Dingemanse et al. 2004; Réale and Festa-Bianchet 2003), with human and nonhuman ape temperament being a viable target given the considerable individual variation that exists (Herrmann et al. 2011; Kagan and Snidman 2004). Increases in social tolerance can occur simply with selection favoring individuals with temperamental profiles that result in less reactivity during times of social stress or competition (Hare, Wobber, and Wrangham 2012; Melis, Hare, and Tomasello 2006; Whiten, Horner, and de Waal 2005).

Not only would similar selection for within-group social tolerance in early modern humans facilitate the consistent expression of behavioral modernity but we would also expect it to have left fossil evidence. The neurotransmitters and hormones that mediate aggressiveness, social dominance, and other social behaviors tend to have morphogenic and osteogenic properties, especially in craniofacial growth and development (see below). Accordingly, we would expect a major physiologically mediated shift in social tolerance to result in correlated, pleiotropic changes in skeletal morphology.

Serotonin levels, and possibly corticosteroid levels and reactivity, may represent one physiological axis along which individuals may vary in temperament and upon which selection may operate. In nonhuman primates, low serotonin levels are associated with severe aggression (Higley et al. 1996; Raleigh and McGuire 1994), most likely because of the role of serotonin in inhibiting impulsive behavior and unrestrained aggression (Higley et al. 1996; Summers and Winberg 2006). A similar relationship appears to hold in humans but has not been firmly established (Booij et al. 2010; Tuinier, Verhoeven,

and van Praag 1996). Corticosteroids lower serotonin levels (Pretorius 2004), and some (such as corticosterone) may directly stimulate the region of the anterior hypothalamus implicated in the initiation of aggression (Summers and Winberg 2006). The silver foxes bred selectively for tameness showed both higher basal serotonin levels and lower corticosteroid levels and reactivity (Kulikova, Zhanaeva, and Popova 1989; Popova 2004; Popova et al. 1980, 1997; Trut, Pliusnina, and Oskina 2004; Trut et al. 2006). While the role of serotonin and corticosteroids in craniofacial development is not clear, there is evidence that they have important cranial morphogenic and osteogenic effects (Byrd and Sheskin 2001; Pirinen 1995; Shuey, Sadler, and Lauder 1992; Warden et al. 2005).

Levels of prenatal and circulating androgens appear to provide a second physiological axis along which reductions in aggressiveness may derive. High circulatory levels of the androgen testosterone are associated with aggression and dominance behavior, including antisocial behavior and rebellion against authority (Archer 1991; Higley et al. 1996; Mazur and Booth 1998). Testosterone has also been observed to constrain some forms of social cognition and sociality, both through prenatal developmental effects on brain organization and activationally through inhibition of social empathy in adults (Baron-Cohen, Knickmeyer, and Belmonte 2005; Pennebaker et al. 2004; van Honk et al. 2011). Androgens appear to be implicated in temperament differences between chimpanzees and bonobos and may account in part for differences in cooperative problem-solving ability between these species (Hare et al. 2007; Wobber et al. 2010). Bonobo males do not show pubertal spikes in testosterone levels (Wobber et al. 2013) and are thought to have lower prenatal and circulating testosterone levels than their chimpanzee counterparts (Mcintyre et al. 2009; Sannen et al. 2003). Also, unlike chimpanzees, bonobos do not exhibit elevated levels of testosterone in anticipation of competing for food (Wobber et al. 2010). This may be part of the mechanism that allows bonobos to share potentially monopolizable food after jointly solving instrumental cooperation problems—problems that chimpanzees understand but appear to lack the social tolerance to solve (Hare et al. 2007). Chimpanzees and bonobos may also differ in the density of androgen receptors in target cells (Wobber et al. 2013). There is considerable interindividual variability in receptor density within humans, chimpanzees, and bonobos (Giovannucci et al. 1997; Hong et al. 2006; Sirugo et al. 1997), which may make receptor density, rather than testosterone levels per se, the target of selection when there is a reproductive advantage to greater social tolerance (unfortunately, there is currently a lack of data on interspecific differences in receptor densities). Given also that testosterone levels in ape and human males change throughout the day (following circadian rhythms and in response to reproductively meaningful stimuli, including male-male agonism; Archer 2006; Muller and Wrangham 2004; Wobber et al. 2010) and over the life course (e.g., Wobber et al. 2013), it is perhaps more appropriate to think of this physiological axis as one of androgen reactivity (involving rapidity and strength of activation, and sensitivity and extent of reception), rather than one of simple androgen levels.

In addition to moderating social tolerance, androgens play osteogenic roles and are important in the development of sexual dimorphism in craniofacial features (Barrett and Harris 1993; Enlow and Hans 1996; Penton-Voak and Chen 2004; Schaefer et al. 2005; Thornhill and Gangestad 1993; Thornhill and Møller 1997; Verdonck et al. 1999). Thus selection against the antisocial behavioral traits associated with high androgen reactivity would be expected to cause a reduction in average androgen levels or receptor density and result in craniofacial feminization in a population over time.

Support for a link between reduced aggression and craniofacial feminization again comes from the breeding experiment conducted with the silver foxes. In addition to the behavioral and physiological changes that were evident after 20–40 generations of selection for tameness, the morphology of foxes changed relative to the wild type. These changes included decreased sexual dimorphism in canine size, coat depigmentation and piebald coloration, reduced cranial capacity, and feminized craniofacial skeletons, with later generations of male foxes possessing skulls significantly shorter and wider (and thus more like female foxes) than the wild type (Popova 2004; Popova et al. 1980, 1997; Trut 2001; Trut, Pliusnina, and Oskina 2004; Trut et al. 2006). Craniofacial changes involving reduced sexual dimorphism and overall feminization have also been observed in other domesticated species: dogs show decreased canine dimorphism relative to wolves and increased relative facial width compared to similar-sized wild species (Wayne 1986). Comparison of wolves to domesticated dogs (including 5,000-year-old prehistoric dogs) emphasizes the role of reduced facial length in driving these relative facial width differences, especially when scaling against associated postcranial body size measures (Franciscus, Maddux, and Wikstrom Schmidt 2013). Dogs also have reduced cranial capacity relative to ancestral wolves (Hare, Wobber, and Wrangham 2012). Additionally, domesticated guinea pigs show reduced cranial capacity compared to wild-type cavies (Kruska 1988), and domestic pig breeds display juvenile skull proportions (Wayne 1986). Finally, the more socially tolerant bonobo exhibits reduced craniofacial sexual dimorphism relative to common chimpanzees (Cramer 1977; Fenart and Deblock 1972, 1973, 1974; Shea 1989), as well as a degree of paedomorphosis in cranial ontogeny (Lieberman et al. 2007; Williams, Godfrey, and Sutherland 2002; but see Durrleman et al. 2012; Mitteroecker, Gunz, and Bookstein 2005). Craniofacial changes within anatomically modern *H. sapiens* over the past 200,000 years (fig. 1), including reductions in the size of supraorbital ridges and other cranial vault superstructures, cranial vault thickness, cranial capacity, and canine sexual dimorphism (Brace and Ryan 1980; Hawks 2013; Lahr 1996; Lahr and Wright 1996; Leach 2003; Lieberman 1996, 2011) may indicate a morphological by-product of a reduction in average aggressiveness akin to that observed in bonobos, silver foxes, and domesticated animals.
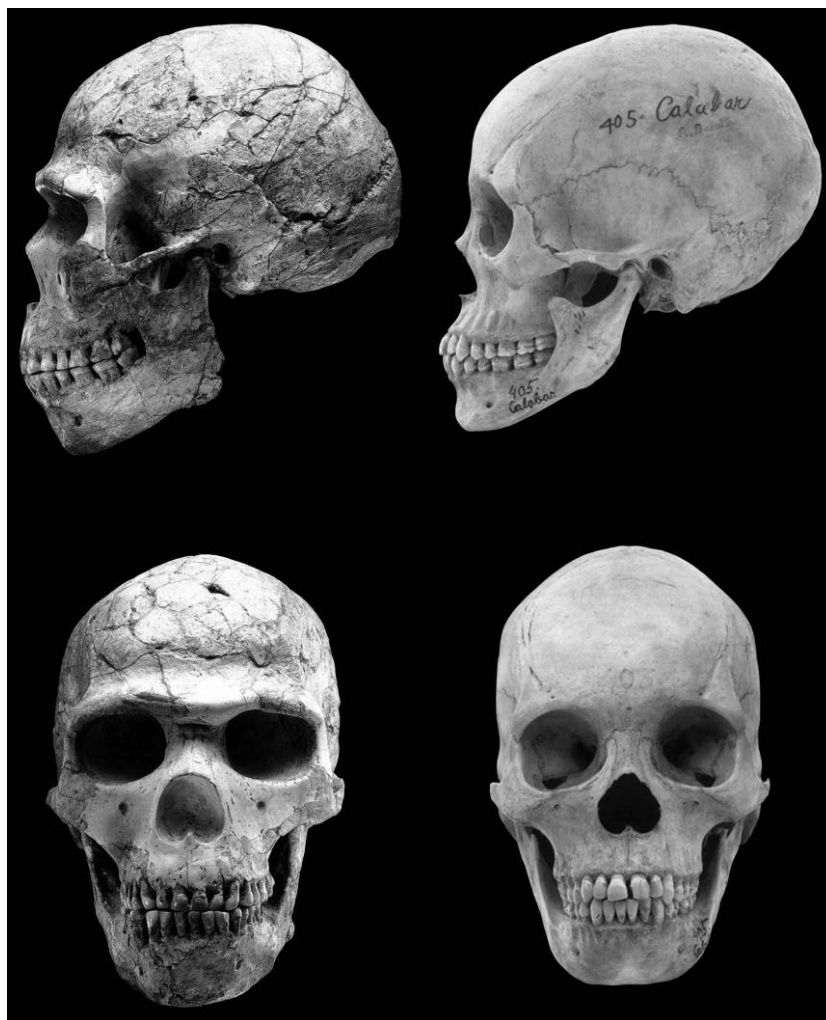
Figure 1. Craniofacial feminization in *Homo sapiens*. The 110–90 Ka year old male specimen Skhul 5 (*left*) in lateral (*top*) and frontal (*bottom*) views, compared to that of a recent African male (*right*), showing the large brow ridges and long and narrow, masculinized face characteristic of MSA/MP-associated modern humans. Both specimens have been scaled to the same nasion-bregma height and aligned on those landmarks. Photographs © David Brill, used with permission.

Variation in craniofacial masculinity in modern human populations is at least partly conditioned by variation in androgen reactivity. However, the effect of testosterone on skeletal development depends upon the age at which exposure occurs and may produce differing growth patterns in the face at different developmental stages (Schaefer et al. 2005). Because prenatal exposure to testosterone affects digit development, the postnatal ratio of the lengths of the second to fourth digits (2D:4D) can be used as an inverse measure of fetal testosterone levels (Lutchmaya et al. 2004; Zheng and Cohn 2011), which in turn helps in identifying the craniofacial morphological consequences of prenatal versus adolescent exposure to testosterone. This approach reveals that some aspects of facial masculinity are organized before puberty, suggesting they develop in response to testosterone exposure in utero (Meindl et al. 2012): individuals with lower 2D:4D ratios tend to have smaller and shorter foreheads, thicker and lower brows, wider and shorter noses, broader faces (across the zygomatic arches), and more prominent chins than individuals with higher ratios (Meindl et al. 2012; Schaefer et al. 2005). Elevated levels of circulating testosterone beginning at puberty in males, on the other hand, tend to predominately affect facial elongation and brow ridge development. Individuals with higher adult levels of salivary testosterone tend to have superoinferiorly longer faces and more pronounced brows, with brows that are also mediolaterally expanded (with right and left sides tending toward fusing at midline)—a facial morphology that is absent in the masculinized faces of males with low 2D:4D ratios who do not have elevated levels of circulating testosterone (Schaefer et al. 2005). In males with delayed puberty, treatment with exogenous testosterone has been found to increase upper and total facial height and man-

Table 1. Facial morphology and endocranial volume in early modern human fossils

Specimen	Sex	Age[a]	Brow projection[b]	Face shape[c]	ECV[d]
MSA/MP (pre–80 Ka BP):					
Eliye Springs	F	> 200	. . .	. . .	1,212
Ngaloba LH18	M	≥ 200–108	157.5	. . .	1,284
Omo Kibish 1	M	198–104	153.2	. . .	1,430
Jebel Irhoud 1	?	190–90	166.7	207.9	1,363
Jebel Irhoud 2	?	190–90	. . .	. . .	1,450
Herto 16/1	M	160–154	162.5	179.7	1,450
Singa	?	> 133	. . .	. . .	1,550
Border Cave 1	M?	115–90	105.2	. . .	
Skhul 4	M	110–90	185.5	202.5	1,554
Skhul 5	M	110–90	164.9	190.3	1,519
Skhul 9	M	110–90	. . .	189.2	1,589
Qafzeh 6	M	100–90	162.2	203.1	1,552
Qafzeh 9	F	100–90	83.2	177.8	1,531
Mean			149.0	192.9	1,457.0
SD			32.8	11.9	118.1
n			9	7	12
LSA/UP (post–80 Ka BP):					
Liujiang 1	M	≥ 68[e]	83.6	. . .	1,480
Nazlet Khater 1	M	37.6[f]	. . .	. . .	1,420
Oase 2	M	35	. . .	188.6	1,600
Kostenki 2	M	33–30[f]	. . .	220.0	1,605
Kostenki 1	M	32.6[f]	. . .	226.6	. . .
Mladec 5	M	31[f]	162.8	. . .	1,500
Mladec 6	M	31[f]	99.5	. . .	. . .
Zhoukoudian 101	M	29–24[f]	104.9	184.1	1,500
Grotte des Enfants 4	M	≤ 28	. . .	225.1	1,745
Grotte des Enfants 6	M	≤ 28	55.8	201.0	1,580
Cro Magnon 1	M	27.7[f]	95.2	207.7	1,595
Predmosti 3	M	27–26[f]	133.1	186.8	1,594
Predmosti 9	M	27–26[f]	. . .	201.5	1,555
Pavlov 1	M	27–25[f]	. . .	. . .	1,522
Brno 2	M	23.7[f]	82.6	. . .	1,500
Arene Candide IP	M	23.4[f]	. . .	206.2	1,490
Sunghir 1	M	22.9[f]	. . .	182.1	1,464
Barma Grande 2	M	≤ 19.3[f]	. . .	198.5	1,880
Ohalo II H2	M	19[f]	100.8	215.5	. . .
Minatogawa 1	M	17.9	90.6	241.3	1,390
Minatogawa 4	M	17.9	96.6	. . .	. . .
Chancelade 1	M	17–14[f]	56.7	182.4	1,615
San Teodoro 2	M	14–10	. . .	204.5	1,569
San Teodoro 3	M	14–10	. . .	193.2	1,560
Oberkassel 1	M	12	137.1	217.0	1,500
Afalou 30	M	12–11	. . .	184.7	. . .
Afalou 31	M	12–11	. . .	205.4	. . .
Afalou 46	M	12–11	. . .	198.6	. . .
Jebel Sahaba 117–10	M	12–11	. . .	194.4	. . .
Jebel Sahaba 117–19	M	12–11	. . .	217.6	. . .
Jebel Sahaba 117–21	M	12–11	. . .	204.5	. . .
Jebel Sahaba 117–29	M	12–11	. . .	188.5	. . .
Taforalt 12c4	M	12–11	. . .	233.8	. . .
Montgaudier	M	11.9[f]	. . .	181.8	. . .
Arene Candide 1	M	11.3[f]	. . .	. . .	1,414
Arene Candide 2	M	11.3[f]	. . .	218.6	1,424
Arene Candide 4	M	11.3[f]	. . .	211.8	1,520
Arene Candide 5	M	11.3[f]	. . .	219.4	1,661
Maritza 2	M	10.5	. . .	226.6	. . .
Veyrier 1	M	. . .	. . .	. . .	1,430
San Teodoro 5	M	≤ 10	. . .	. . .	1,484
Mean			99.9	204.3	1,533.6
SD			30.2	16.3	103.9
n			13	34	31

Table 1 (*Continued*)

Specimen	Sex	Age[a]	Brow projection[b]	Face shape[c]	ECV[d]
Recent human foragers/horti-culturalists/pastoralists:					
Mean			87.0	204.3	1,451.7
SD			22.7	15.1	103.2
n			422	422	422
Recent human agriculturalists:					
Mean			83.5	197.3	1,464.6
SD			21.9	12.2	85.9
n			945	945	945

[a] Ka BP.
[b] $1,000 \times (SOS + GLS)/XFB$. See text for details.
[c] $100 \times ZYB/NPH$. See text for details.
[d] Endocranial volume (cm^3).
[e] Date is likely to be too old: see text for discussion.
[f] Denotes dates in uncalibrated radiocarbon years.

dibular ramus and total length but did not affect lower facial height, mandibular body length, or cranial base length (Verdonck et al. 1999). Selection for reduced levels of circulating testosterone in human evolution is suggested by studies of ontogenetic scaling in modern human facial development, which "suggest that, independent of any selection pressure on overall body size, it is upper facial height (and not facial breadth) that is the potential target of selection, as male upper faces are shorter than expected for their size" (Weston, Friday, and Liò 2007:e710).

Masculinized facial features appear to confer an honest biological signal of male social behavior, because the facial structure of high-androgen males appears more dominating to conspecifics (Fink, Neave, and Seydel 2007; Mazur, Mazur, and Keating 1984; Penton-Voak and Chen 2004; Puts 2010; Swaddle and Reierson 2002). There is solid experimental support for the idea that sexually dimorphic features of the human face serve as honest signals of temperament, although this appears to apply equally to aspects of facial shape that signal high prenatal testosterone (Carré and McCormick 2008, 2009, 2012; Geniole et al. 2012; Sell et al. 2009) as well as adult circulating testosterone (Fink, Neave, and Seydel 2007; Mazur, Mazur, and Keating 1984; Penton-Voak and Chen 2004; Puts 2010; Swaddle and Reierson 2002). Brow ridge morphology also appears to be important in how people perceive the aggressiveness and trustworthiness of others (Carré et al. 2010; Todorov, Baron, and Oosterhof 2008; Xu et al. 2012).

While an argument could be made that brow ridges perform a mechanical role in resisting stresses produced during mastication, and thus that their variation relates to masticatory mechanics rather than temperamental variation, experimental evidence suggests otherwise. Although the supraorbital torus is strained during mastication, the magnitude of strain is negligible compared to strain on the lower face, mandible, and zygomatic arches (Lieberman 2011), such that a modest supraorbital torus appears to be more than sufficient

to counter these forces (Hylander, Picq, and Johnson 1991a, 1991b, 1992). Because brow ridge projection is not driven solely by the requirements of craniofacial loading from mastication forces (Hylander, Picq, and Johnson 1991b), prehistoric reduction in supraorbital projection and a shortening of the upper face—that is, craniofacial feminization—should serve as a fossil indicator of contemporaneous changes in androgen reactivity and thus changes in social tolerance. Brow ridge reduction distinguishes archaic from early modern humans and might be considered a derived feature of *H. sapiens* (Stringer, Hublin, and Vandermeersch 1984). However, archaic/modern human differences in the projection and morphology of the supraorbital ridges appear to reflect architectural responses to differences in the spatial relationships between the face and neurocranium (Lieberman 1995, 1996), and thus interspecific variation likely has a different cause than variation seen within modern humans (the same holds for interspecific comparisons between other hominin species, or between primate species, in which differences in facial morphology between groups may be attributable to any number of factors, including masticatory biomechanics, olfactory demands, relative brain size, canine size and mating system, and the spatial relationships between the face and neurocranium. To be clear, we are only addressing the temporal trend seen within *H. sapiens*). A mid-Pleistocene to recent reduction in brow ridge projection within our species is clear from casual observation of early modern human fossils (Shea 2011; see fig. 1). Might this reduction reflect a broader pattern of craniofacial feminization in our species and attendant increases in social tolerance?

We sought to quantify relative changes in craniofacial morphology among anatomically modern human crania from the Middle Pleistocene to historic times to test the hypothesis that a major change in temperament occurred around the time of the persistent establishment of behavioral modernity. Additionally, given that further selection for enhanced social tolerance may have occurred with the great increases in pop-

ulation density that followed upon the establishment of se-dentized, agricultural economies in the Neolithic, we tested for differences in average measures of craniofacial masculinity between modern humans from foraging and pastoral econ-omies (living at lower population density) and those from agricultural systems. Specifically, we sought to answer these questions:

1) Do recent humans exhibit feminized crania (i.e., with re-duced brow ridges and shorter faces) and smaller brains relative to the earliest fossil representatives of our species?

2) Are there significant differences in measures of craniofacial masculinity between fossil crania pre- and post-dating the apparent increase in CTE at 80 Ka BP?

3) Among recent humans, do groups living at relatively lower population densities (foragers and pastoralists) differ in average craniofacial masculinity from groups living at higher densities (agriculturalists)?

Method

To address these questions, we examined measures of brow ridge projection, facial shape, and endocranial volume in three temporal samples of modern human crania (table 1). These samples included a pre–80 Ka BP MSA/MP-associated group ($n = 13$, ranging in age from ca. 200–90 Ka BP), a post–80 Ka BP LSA/UP associated group ($n = 41$, ranging in age from ca. 38–10 Ka BP), and a global sample of recent (Holocene) humans ($n = 1,367$). The dating of many of the fossil spec-imens is problematic, but available radiometric dates on either the fossils themselves or on associated materials or strata, or their geological or archeological context, are generally suffi-cient to sort the fossil specimens into an MSA/MP pre–80 Ka BP group versus a LSA/UP post–80 Ka BP group (table 1). Some of the crania that we place in the pre-80 Ka *H. sapiens* groups (Eliye Springs, Ngaloba 18, Jebel Irhoud 1 and 2, and Singa) might be considered by some to represent a distinct species (*H. helmei*) antecedent to *H. sapiens* (see McBrearty and Brooks 2000) or an "African Transitional Group" (Cartmill and Smith 2009) morphologically inter-mediate between *H. heidelbergensis/rhodesiensis* and *H. sap-iens*. We follow Lieberman (2011) in considering these "*H. helmei*/transitional" specimens as early representatives of *H. sapiens*, because they possess derived cranial base angles (CBA) within the range of extant human populations. These specimens share with later modern humans a derived rela-tionship between the neurocranium and splanchnocranium, as well as a greater degree of neurocranial sphericity than earlier fossils, such that any differences that may exist between the pre–80 Ka BP and post–80 Ka BP groups is not likely to be a function of differences in CBA, facial hafting, or cranial vault sphericity.

By and large, the fossil specimens cluster into two temporal groups. One specimen, however, has especially problematic associated dates. The age of the partial skeleton from Liujiang in China, which derives from a cave breccia with a U-series date of 68–139 Ka BP (Shen et al. 2002), would place it in our pre-80 Ka sample. However, the relationship of the spec-imen to the breccia is not clear (Brown 1999; Wu and Poirier 1995), and given that the morphology of the specimen is most consistent with that of other later Pleistocene east Asian spec-imens (Brown 1999), we have included it in the post–80 Ka BP sample. Questions have also arisen about the sex of this specimen, but following Woo (1959), Wu (1997), and Ro-senberg (2002), we consider the fossil to represent a male.

Since brow ridge projection and lower facial shape are known to be sexually dimorphic (Meindl et al. 2012; Schaefer et al. 2005), and since testosterone-mediated changes in social tolerance and attendant reductions in craniofacial masculinity should be more pronounced in males, we limited our analysis to male crania for the post–80 Ka BP and recent samples. However, sample size limitations in the pre–80 Ka BP sample necessitated the inclusion of six female or possible female spec-imens in that group. Since we are testing for directional increase in craniofacial feminization over time, the inclusion of female specimens in the pre–80 Ka BP sample can be considered con-servative.

Craniometric data for most fossil specimens were taken on the original fossils and were supplemented with data from casts (collections of Duke University, New York University, and the American Museum of Natural History) and published sources. Endocranial volume (ECV) data for most specimens were taken from Beals, Smith, and Dodd (1984) and from the supplemental data provided by Ruff, Trinkaus, and Hol-liday (1997). Where these two sources disagreed, the average of the two values was used. The ECV value for Eliye Springs was taken from Bräuer et al. (2004), that of Omo 1 from Cartmill and Smith (2009), and that of Herto (BOU-VP-16/1) from White et al. (2003). While we know of no physio-logical basis for linking ECV with either prenatal or circulating testosterone levels, we have included this variable because of the empirical association between reduced ECV and domes-tication (i.e., tameness) in various mammalian species (Hare, Wobber, and Wrangham 2012; Kruska 1988).

Recent human data were obtained from the craniometric data set of William W. Howells (Howells 1973, 1989; available online at web.utk.edu/āuerbach/HOWL.htm). Because the data collected by Howells do not include ECV, this variable was estimated from cranial dimensions for the recent human specimens using the male-specific formula of Lee and Pearson (1901): $ECV = 359.34 + 0.000365(L \times B \times H)$, where L is is glabello-occipital length (GOL in the Howell's data set) and B is maximum cranial breadth (XCB in the Howell's data set). The variable H refers to auricular height, which was not taken by Howells. Thus we estimated H from Howell's basion-bregma height (BBH) following Kennedy and Levisky (1985) as $H = 51.0273 + 0.4998 \times BBH$. While the additional step of estimating H from BBH adds an unknown amount of error variance to the estimates, the use of cranial vault dimensions to estimate ECV produces results that are close to those de-

rived from conventional mustard seed methods (average difference = -40.8 ± 15.8 cm³; Dekaban and Lieberman 1964).

Finally, to examine patterns of variation in facial masculinity and ECV within the recent human sample, we subdivided the Howells data into two groups, one representing foragers (plus one pastoral group), drawn from groups that lived at population densities between 0.014–0.86 persons km^{-2} (based on data in Kelly 1995 from the included groups or neighboring groups in similar ecological circumstances). The second group represents agriculturalists, who are assumed to have lived at population densities ranging from 1.0–233.0 person km^{-2} (Turner, Hanham, and Portararo 1977). These groups are listed in table 2.

To evaluate temporal changes in brow ridge morphology, we used a composite variable that includes measures of both supraorbital and glabellar projection, as defined in figure 2, which was standardized by frontal breadth to produce an index of brow ridge projection. To quantify lower facial shape, we used an index of bizygomatic breadth (ZYB) to nasion-prosthion height (NPH; see fig. 2).

Imperfect preservation of fossil crania necessitated estimation of ZYB as the maximum distance between the intact part of the zygomatic arches for Jebel Irhoud 1 and Qafzeh 9. Since fossil samples are small and we cannot assume that variances are equal across samples, we used a nonparametric Wilcoxon test to examine differences in mean values between samples, with post hoc Tukey-Kramer HSD tests (all tests performed in JMP 9.0) following a significant test statistic.

Results and Discussion

Although fossil samples sizes are small, a temporal trend for brow ridge reduction is apparent from the late Middle Pleistocene (pre–80 Ka BP) to Late Pleistocene (post–80 Ka BP) samples and continuing to the recent human samples (table 1). The mean brow projection index for the MSA/MP sample falls more than 1.5 standard deviations above that of the LSA/UP group and between 2.7–3.0 standard deviations above the recent human sample means (table 1). The Wilcoxon test detected a significant difference between sample means ($X^2 = 26.8706$, df = 3, $P < .0001$), and post hoc testing revealed the following: (1) the MSA/MP sample had a significantly higher value than all other groups, (2) the LSA/UP and recent forager samples were not significantly different from one another, and (3) the LSA/UP and recent forager sample means were significantly larger than that of the recent agriculturalists. If the pre–80 Ka BP sample is restricted to only those specimens considered to represent males, the sample mean increases somewhat while the variance decreases (155.8 ± 24.6, n = 7). If the "*H. helmei*/transitional" fossils (see Method section) are excluded, the sample mean drops (145.2 ± 36.8, n = 7) but without altering the outcome of the statistical tests.

The data also document a reduction in facial length in the post–80 Ka BP samples, consistent with the hypothesis of higher levels of circulating testosterone during the MSA and

Table 2. Recent human samples

Sample	n
Foragers:	
Bushmen (San) (southern Africa)	41
Andaman Islanders (Indonesia)	35
Lake Alexandrina tribes (Australia)	52
Tasmanians (Tasmania)	45
Buriats (northern Asia)	55
Ainu (northeast Asia)	48
Arikara (North America)	42
Santa Cruz (North America)	51
Inugsuk Eskimo (Greenland)	53
Total *n*	422
Agriculturalists:	
Zulu (southern Africa)	55
Teita (east Africa)	33
Dogon (west Africa)	47
Egyptians (north Africa)	58
Norse (northern Europe)	54
Zalavar (central Europe)	53
Berg (central Europe)	56
Hainan (east Asia)	45
Anyang (east Asia)	42
Atayal (east Asia)	29
Hokkaido (east Asia)	55
North Kyushu (east Asia)	50
Philippine Islanders (Indonesia)	50
Northern Maori (New Zealand)	10
Southern Maori (New Zealand)	10
Guam (Micronesia)	30
Tolai (Melanesia)	56
Mokapu (Polynesia)	51
Easter Islanders (Polynesia)	49
Moriori (Polynesia)	57
Yauyos (South America)	55
Total *n*	945

Note. Group names as provided by Howells (1973, 1989).

MP. The MSA/MP sample has a mean face shape index below that of the LSA/UP and recent human samples, reflecting an average facial shape that is long relative to width. However, although the Wilcoxon test detected a significant between-group difference in mean face shape indices ($X^2 = 66.3884$, df = 3, $P < .0001$), post hoc testing did not find a significant difference between the MSA/MP sample and any other group. Consideration of the mean values of ZYB and NPH (table 3) shows that while the MSA/MP sample has the absolutely largest mean ZYB of any sample, their mean facial width is not significantly different than that of the LSA/UP sample (in turn, the LSA/UP sample is not significantly different than the forager sample, yet both the LSA/UP and forager samples have significantly larger mean ZYB than the agriculturalists). While facial width does not differ significantly between the MSA/MP and LSA/UP samples, facial length does. The MSA/MP sample has a mean NPH that is significantly larger than all the other groups (table 3). As with the index of brow ridge projection, the LSA/UP sample again did not differ significantly from the recent forager sample in face shape. However, the recent agriculturalists have a significantly smaller mean
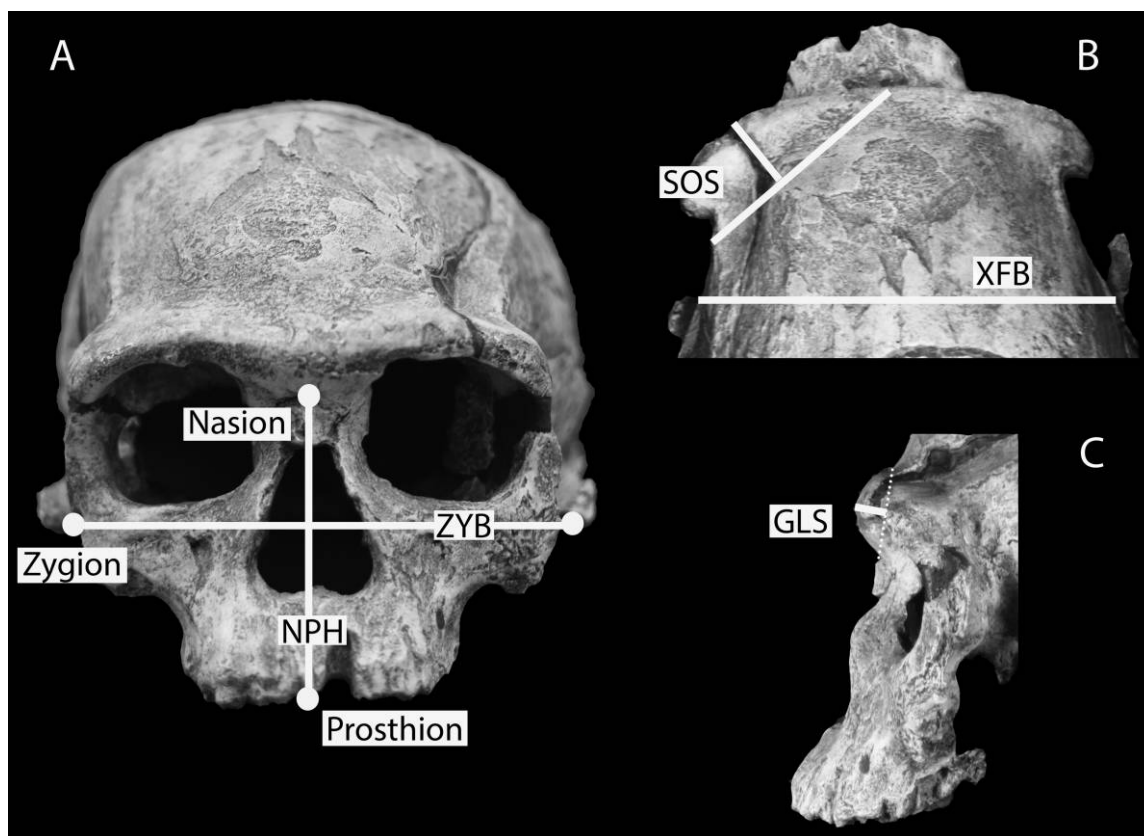
Figure 2. Facial measurements taken from and illustrated on a cast of the 190–90 Ka-year-old, MSA/MP associated specimen Jebel Irhoud 1. *A*, Upper facial shape was quantified by scaling bizygomatic breadth (ZYB: maximum breadth across the zygomatic arches, wherever found) by face height (NPH: upper facial height from nasion to prosthion). *B*, Supraorbital projection (SOS: maximum projection of the left supraorbital arch, taken as a subtense to a line between the midline in the region of glabella or above and the frontal bone just anterior to the temporal line in its forward part) was used as one measure of brow ridge size. *C*, Glabellar projection (GLS: maximum projection of the midline profile, taken as a subtense to a line between nasion and supraglabellare [or the point at which the convex profile of the frontal bone changes to join the prominence of the glabellar region]). Brow ridge projection was quantified by summing SOS and GLS and scaling the result by bifrontal breadth (XFB: maximum width across the coronal suture).

face shape index than the LSA/UP and recent forager samples and one that is not significantly different than that of the MSA/MP sample. The convergence of face shape indices between the agriculturalists and MSA/MP samples appears, however, to be primarily driven by a reduction in facial width in the agriculturalists (table 3). Thus the temporal trend in facial shape appears to have been one of relatively long faces before 80 Ka BP, followed by relatively shorter faces in the post–80 Ka BP sample, with maintenance of this face shape into the Holocene among foragers, followed by a moderate narrowing and lengthening of the face (and attendant reductions in facial shape index) among Holocene agricultural groups (fig. 3). Note also that removal of the "*H. helmei*/transitional" fossils reduces the face index slightly (190.4 ± 10.8, $n = 6$) but in no way alters the outcome of the statistical tests.

To better control for the effect of head size on facial dimensions, we scaled ZYB and NPH to ECV (table 3, fig. 4). Non-parametric testing revealed significant differences in group means in both relative ZYB ($X^2 = 65.6272$, df = 3, $P < .0001$) and relative NPH ($X^2 = 20.8013$, df = 3, $P = .0001$). Means of the scaled values (table 3) reveal that the MSA/MP sample has faces that are larger relative to the cranial vault than do any of the other samples. In terms of relative facial width, the MSA/MP sample does not differ from the forager sample, although both have significantly higher ratios than the LSA/UP and agriculturalist samples. The MSA/MP sample, however, has a mean relative facial length significantly higher than all other groups (table 3). Both fossil groups show a similar relationship between relative facial width and length, with MSA/MP fossils tending to have greater relative lengths (fig. 4).

Temporal change in mean ECV does not follow the expectations of the feminization model. Mean ECV is almost 6% larger in the LSA/UP than MSA/MP sample (table 1), although the difference is not statistically significant. Fur-

Table 3. Absolute and relative facial dimensions in fossil and recent human samples (mean, SD, *n*), and post hoc test results

Group	ZYB	NPH	ZYB/ECV	NPH/ECV
MSA/MP	145.6	75.4	.09687	.05017
	10.9	3.0	.01052	.00383
	7	7	7	7
LSA/UP	139.0	**67.9**	**.08883**	**.04421**
	8.6	5.5	.00634	.00388
	34	38	22	25
Foragers	**136.3**	67.1	.09410	**.04628**
	6.3	4.3	.00447	.00383
	422	422	422	422
Agriculturalists	**134.6**	68.4	**.09211**	**.04682**
	5.5	4.3	.00471	.00306
	945	945	945	945

Note. ZYB = bizygomatic breadth; NPH = nasion-prosthion height; ECV = endocranial volume. Boldface denotes means significantly different than MSA/MP sample (based on Tukey HSD tests at family-wide α = 0.05).

thermore, when the "*H. helmei*/transitional" fossils are excluded, the mean ECV of the MSA/MP (1517.9 ± 57.8, *n* = 7) increases to close to that of the LSA/UP sample (and the means remain insignificantly different). The Wilcoxon test did detect a significant difference in mean ECVs across samples (X^2 = 19.9827, df = 3, *P* = .0002), and post hoc testing revealed significantly larger ECV in the LSA/UP sample relative to the two recent human samples (foragers and agriculturalists).

Recent humans do appear to have feminized crania relative to late Middle and Late Pleistocene *H. sapiens*. Brow ridge projection reduced consistently across the temporal samples, such that the mean measures of brow ridge projection in foragers (87.0) and agriculturalists (83.5) fall close to the single observation available for an MSA/MP female (83.2 in Qafzeh 9). Temporal changes in facial shape are a bit more difficult to interpret, although overall it does appear that recent humans are feminized relative to our Pleistocene conspecifics. The foragers in Howells's data set have faces that are relatively wide compared to the MSA/MP sample and have attained that morphology predominantly via a reduction in facial length (relative to cranial size), as would be predicted by a reduction in average levels of circulating testosterone from the Middle Pleistocene to the Holocene. The agriculturalists in Howells's data set, however, present an interesting challenge to the social tolerance model, since they secondarily converged on a relatively narrow-faced morphology (relative to the LSA/UP and forager samples), yet they represent groups living at relatively high population density, which would be expected to have high levels of social tolerance. However, consideration of facial dimensions relative to cranial size (as measured by ECV) suggests that the narrow faces of the agriculturalists are primarily due to facial narrowing (combined with a modest increase in facial length) relative to the LSA/UP and forager groups. This may reflect a signal of reduced

prenatal testosterone levels imprinted over a preexisting reduction in circulating testosterone. Interestingly, when consideration of facial shape is limited to only those MSA/MP specimens that can confidently be considered male, their mean shape index falls to 183.4 ± 21.2 (*n* = 4). While the MSA/MP male-only mean is still not statistically different from that of the agriculturalist sample, it is the case that the agriculturalist mean is closer to those of the LSA/UP and forager samples than it is to that of the MSA/MP sample. These results show that the recent human groups living at higher population density, notwithstanding a degree of convergence on the facial shape of pre–80 Ka BP humans, are
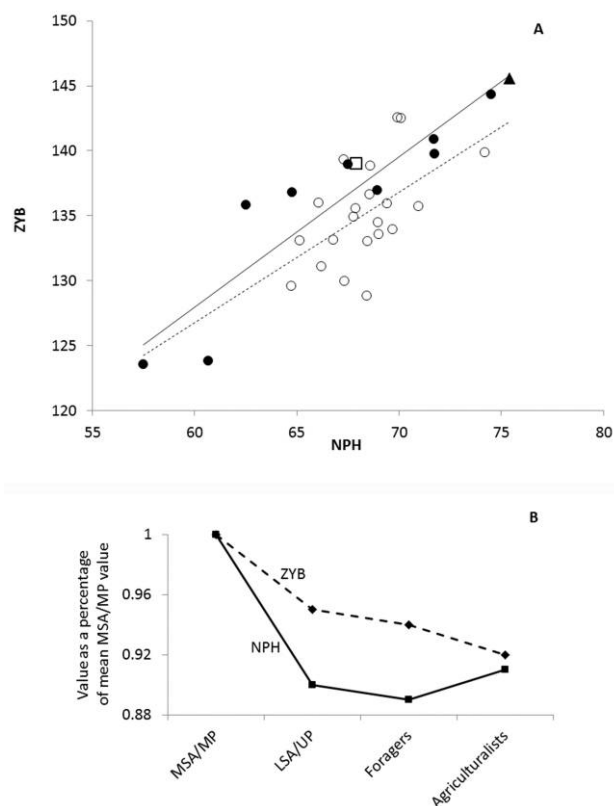

Figure 3. *A*, Mean bizygomatic breadth (ZYB, in mm) against nasion-prosthion height (NPH, in mm) in fossil and recent modern humans. Mean values for 21 samples of agriculturalists are represented by open circles, while solid circles represent mean values for nine forager groups. The MSA/MP fossils (solid triangle) have the absolutely longest and widest faces, while LSA/UP fossils (open square) and foragers have shorter and narrower faces. Agriculturalists are similar to foragers and LSA/UP samples in facial length but tend to have narrower faces. Ordinary least squares regression lines are provided for the recent human samples. Foragers (solid line), *y* = 1.1574x + 58.509, *r*² = 0.8263; agriculturalists (dashed line), *y* = 1.0067x + 66.343, *r*² = 0.3029. *B*, When mean facial length (NPH) and breadth (ZYB) are plotted as percentages of the mean values of the MSA/MP sample, temporal patterns of reduction in both dimensions are apparent, as is the greater magnitude of change in facial length.
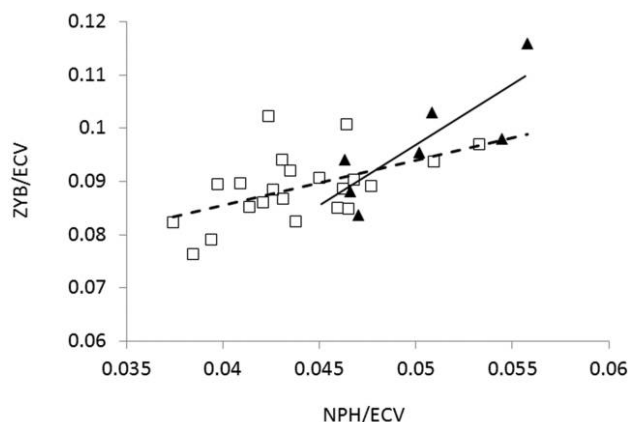
Figure 4. Relative facial breadth (ZYB/ECV) on relative facial height (NPH/ECV) in fossil modern humans. Slopes and intercepts of ordinary least squares regression lines do not differ significantly between the MSA/MP (solid triangles and solid line, $y = 2.2656x - 0.0168$, $r^2 = 0.6796$) and LSA/UP fossils (open squares and dashed line, $y = 0.8499x + 0.0515$, $r^2 = 0.2722$).

still characterized by relatively shorter faces than their MSA/MP ancestors. Finally, the data do suggest a reduction in ECV from the late Pleistocene to the Holocene and, as has been reported elsewhere (Beals, Smith, and Dodd 1984; Hawks 2013; Henneberg 1988; Ruff, Trinkaus, and Holliday 1997), this appears to be largely a Holocene phenomenon. However, differences in ECV estimation methods between the fossil and recent human samples warrant caution in uncritically accepting this result.

While the overall temporal trends from the Middle Pleistocene to Holocene might be complex, the changes across the 80 Ka BP boundary are clear (fig. 5). The MSA/MP sample, despite the incorporation of females, has significantly more projecting brow ridges and significantly longer, more masculine facial shape than the LSA/UP sample. ECV, however, does not differ significantly between the fossil samples, and the mean values suggest an increase, rather than a decrease, from the MSA/MP to LSA/UP. While reduction in ECV is an empirically observed consequence of domestication in many species (reviewed in Hare, Wobber, and Wrangham 2012; Leach 2003), there is no theoretical reason that it should be tied directly to androgen physiology. Thus the lack of a significant difference between the fossil groups does not necessarily argue against a major change in androgen reactivity between the MSA/MP and LSA/UP.

Patterns of variation in craniofacial feminization across recent human samples are less clear. The forager sample had significantly larger brow ridges than the agriculturalists. The ECV did not differ significantly between the two, and the agriculturalists had faces that, in terms of their relative length, were moderately more masculine than their forager counterparts. Again, however, the difference between the samples in

facial shape appears to be driven by a narrowing of the face in the agricultural groups.

The fossil evidence reflects a significant reduction in androgen-mediated craniofacial masculinity between the MSA/MP and LSA/UP, coincident with genetically and archeologically visible increases in human population size and density and with a markedly increased rate of cultural evolution. Craniofacial feminization appears to have continued into the Holocene, as did human population growth and cumulative cultural evolution. This suggests to us a change in average human temperament toward greater social tolerance and reduced aggression during the Late Pleistocene and continuing into the Holocene, in the context of greater population density and improved payoffs for cooperation. We can envision several selective scenarios that may have been in operation during the later part of the MSA and MP. Reduced aggressiveness and enhanced social tolerance may have had direct reproductive benefits in the later part of the MSA and MP. In the context of increased population density (Jacobs and Roberts 2009; Richerson, Boyd, and Bettinger 2009) and possibly expanded social networks (Bouzouggar et al. 2007; Marwick 2003; McBrearty and Brooks 2000; Stiner and Kuhn 2006), more tolerant males may simply have enjoyed a greater number of cooperative exchanges with others, which would have served to improve foraging return rates (through cooperative foraging and through shared innovations in subsistence technology) and reduce the risk of foraging shortfalls (through food sharing). Increased population density may have changed the ecological landscape from one characterized by exploitation of patchy resources to one of exploitation of resources controlled by other humans (Foley and Gamble 2009). In this context, cooperation and the formation of extensive social bonds would become a risk-avoidance strategy, promoting social tolerance toward unrelated and unfamiliar individuals, drastically extending the reach of social networks (Ambrose 2010; Hill et al. 2011; Seabright 2004). High-risk extractive foraging would have became viable, since greater sharing tendencies would have served as social insurance during temporary shortfalls (Greenberg et al. 2010; Gurven and Hill 2009; Hamann et al. 2011; Kaplan et al. 2000). These benefits would have been of growing importance as humans became obligate cultural animals and would have offset the cost of demographic expansion by creating a niche of technological dependence (Foley and Gamble 2009; Kaplan et al. 2000; Sterelny 2011). Higher rates of calorie capture, and reduced variance in capture rates, translate to improved somatic maintenance and greater ability to invest in reproduction (through both mating effort and offspring provisioning). Since facial masculinity appears to be an honest signal of behavioral tendencies, there may also have been some degree of sexual selection in operation as well. As population density and social complexity increased, females may have preferred males with more feminized faces that signal a greater propensity to invest in parenting effort (Kruger 2006).

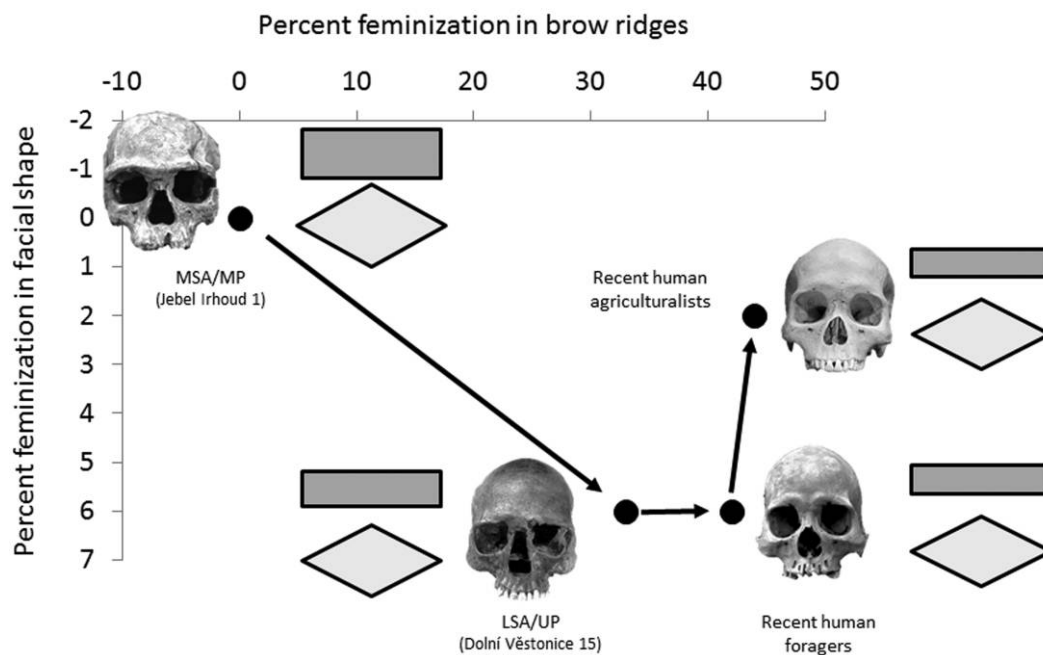Regardless of the selective mechanism at play, it is clear

Figure 5. Summary of craniofacial feminization trends in anatomically modern *Homo sapiens* over the past 200,000 years. Feminization increases to the right (brow ridges) and downward (face shape) as a percent reduction from the original MP/MSA condition. The degree of feminization is also represented graphically by the adjacent geometric shapes: the height of the rectangles reflects the proportional difference in absolute brow ridge projection (SOS + GLS) relative to the pooled recent human male sample; the height and width of the diamonds reflect the proportional difference in absolute facial height (NPH) and width (ZYB), respectively, relative to the pooled recent human sample. The arrows reflect presumed increases in population density. Although agriculturalists have masculinized facial shapes relative to LSA/UP and recent human foragers, it is clear that the greatest changes in both brow ridge projection and facial shape occurred between the MSA/MP and LSA/UP samples.

that living humans are remarkably socially tolerant relative to other primates, and this tolerance is without doubt a significant component of our derived ability to engage in cooperative behaviors. While the question of self-domestication in humans remains open, the fossil record of *H. sapiens* does reflect reductions in craniofacial masculinity since the Middle Pleistocene. Given the empirical relationships that exist between temperament, androgen reactivity, and craniofacial morphology in humans, and between temperament and craniofacial morphology in both domesticates and wild animals, it seems likely that important increases in human social tolerance developed during this interval. In light of the variation that exists between foragers (both LSA/UP and recent) and agriculturalists, we might predict that humans living at very high population densities, such as those from city-states or industrialized agricultural economies, would show even greater levels of craniofacial feminization than do the small-scale agricultural groups that dominate the comparative data used here. Likewise, we might expect hunter-gatherers who lived at high population density (such as certain northwest coast Native Americans) to exhibit a level of feminization similar to that seen among the agriculturalists. These and other avenues (such as ancient DNA studies) should help to

clarify the proposed relationship between androgen reactivity, temperament, and social tolerance in human evolution.

Acknowledgments

Comments

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Cieri and colleagues present a clear hypothesis about the re-

lationship between social structure and biological changes associated with "modernity" and offer quantifiable predictions and excellent documentation from a wide range of literature to support their model. On the whole I agree with their premise—namely, that increased population density is expected to be correlated with increased social cooperation in humans. The authors also make a good case for the relationship between hormonal changes that would affect these cooperative behaviors and also contribute to craniofacial feminization. While the authors never overtly define specific behaviors as "feminine," they implicitly do so by linking the evidence for craniofacial feminization with both reduced aggressiveness and reduced testosterone/testosterone receptors in humans.

In considering this model, I was struck by the possibility that perhaps both the biological and behavioral definitions of "feminization" used here are culturally embedded in Western notions of masculine/feminine and thus not necessarily good measures of social change. In light of this, I offer some data from my work on modern human frontal bone variation for consideration, some of which does not conform to their predictions. My goal here is to hopefully assist in further refining their predictions.

Both biologically and behaviorally there is a valid basis for making predictions following the assumption that females are more gracile than males. This is true of most dimorphic primates. Likewise, the majority of primates are polygynous with greater aggressiveness by males versus between females. But can this be translated to humans today or in the past? We do not know the pattern of sexual dimorphism in the Middle Pleistocene at all, and the earliest *H. sapiens* emerged at the end of this period. If we do not know the pattern, I would hesitate to use "gracile" to define "feminine" for all humans. My own research has shown that not all modern human groups are sexually dimorphic in the frontal bone or even characterized by males being more robust than females.

In a global study (in preparation) of modern human frontal bone morphology, I found that only one aspect is significantly different between males and females in any sample: Khoi/San South Africans are differentiated by the presence of prominent frontal bossing on females versus males. However, no group was sexually dimorphic in browridge morphology or prominence. Interestingly, this absence of dimorphism did not always follow a pattern that we would call "feminine" as would be predicted by Cieri et al.'s model. In both Native Australians and Tierra del Fuegians, both sexes had equally prominent browridges and sloping frontal squamae. Among Central Europeans and Khoi/San, on the other hand, both sexes shared extremely gracile browridges.

The authors here do restrict their sample largely to populations from Europe, West Asia, and Africa—regions where a sexually dimorphic pattern is more likely to occur. However, when the assumption of gracile = female/robust = male is applied to our whole species, with respect to the browridge, my data do not quantitatively support this. Maybe our results differ because I used different ways to measure browridge

prominence. However, because of these results I wonder if the correspondence between physical feminization and behavioral cooperation may not be as tightly linked as is proposed here.

The idea that female behavior is more cooperative and male behavior is more aggressive is well understood in most primates. But the role of mate selection exerts power. In foraging societies studied here, who has the power of mate selection? Do males do all the provisioning and thus become the object of selection? Females often provide equal provisions as males in foraging societies, whereas the division of labor and sexual dimorphism is increased in agricultural societies. In my sample there is less dimorphism in foraging societies but not less masculinization, as evidenced by the shared gracility of the Khoisan but the shared robusticity of the Tierra del Fuegians and Aborigines.

This does not negate the fact that recent humans are characterized by a reduction in browridge prominence—they certainly are relative to archaic *Homo* (Athreya 2009). But there as well, I did not find the same pattern of temporal gracilization that Cieri et al. did—geologically older modern humans were not more robust, and younger ones were not more gracile. I wonder what would happen if the authors were to study trajectories toward "modernity" in regions with less dimorphism or more robust modern populations—would they see gracilization there over time?

It is possible that our conventional use of the browridge to sex skeletons does not have validity in a global context, but rather is a product of a sample bias (perhaps in forensics as well) based on populations that are more dimorphic. Notions of "feminization" would be hard to define if our study of human evolution was focused on Aboriginal Australians as the final morphological end product. In light of this, I propose that maybe both sexes underwent a paedomorphic transition independent of sex but due rather to changing spatial relationships. And if they did not undergo a feminization biologically, can we then assume that they underwent one behaviorally? Or, conversely, if there are groups in the world that are not dimorphic but both are robust—are they less cooperative? It would be intriguing to hear the authors' ideas on these questions, which follow on their provocative and interesting model.

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The authors of this contribution have done a great job bringing together data from fields as diverse as animal behavior, ontogenetic studies, human and mammalian endocrinology, neuroscience, archaeology, and human paleontology, and combined them into a single coherent, well thought-out, and ultimately highly stimulating narrative. While many pieces of

their grand argument can be found in various places in the scientific literature, here these data are woven together with new data and fresh ideas in a truly novel (and to my mind) very rigorous fashion. I find myself in particular agreement with the authors' assertion that since at least some nonmodern forms of the genus *Homo* engaged (at least sometimes) in what would be broadly recognized as "modern" symbolic behavior, it is unlikely that differences in cognitive capacity for symbolism underlie the recurring pattern of the appearance, disappearance, and reappearance of archaeological evidence for symbolic behavior in the MSA, Mousterian, or the so-called transitional European Paleolithic industries such as the Châtelperronian. I also find compelling their arguments for the critical role played by population density in generating environments that would favor selection for cooperation, enhanced social tolerance, symbolic behavior, and ultimately, cumulative technological evolution. The authors have given us much to contemplate in this paper.

That being said, like all seminal pieces of work, the current contribution raises almost as many questions as it answers, and I would like the authors to address in this venue a couple of questions that occurred to me as I read it. My questions revolve around the decrease in cranial robusticity documented in this study from the early (i.e., > 80 Ka) to late (i.e., < 80 Ka) *Homo sapiens* samples. As my colleagues and I note in an upcoming article in *Current Anthropology* (Holliday, Gautney, and Friedl, forthcoming), beginning in the Pleistocene and continuing into and within the Holocene, there appears to be a decrease in robusticity (or, following the wording of the current contribution, increased feminization) in multiple mammalian lineages, not just our own, including taxa as diverse as wild boar, gazelle, horses, American black bear, black wildebeest, *Bison*, bighorn sheep, Steller's sea cow, wild bezoar goat, and aurochs (see references in Holliday, Gautney, and Friedl, forthcoming). Surely not all of these shifts were accompanied by increased social tolerance in these taxa? After all, while most of the above taxa in fact are gregarious, some (e.g., American black bear; wild boar males) tend to be solitary, and so for these species, at least, there would seem to be less impetus for selection to enhance feminization in response to increased sociality.

Some caveats about these observed changes should be mentioned. First, it is possible that most, if not all, of these observed "trends" in mammalian robusticity reduction during the Pleistocene and into the Holocene are in reality just variations due to cladogenetic differentiation between collateral relatives–the very type of relationship the current authors are so careful to avoid. Second, even assuming that we are observing change within lineages, it is difficult to evaluate how much of the observed shift in these other taxa is merely a reduction in overall size versus a decrease in actual robusticity (i.e., increased feminization) per se. Even today it remains difficult to disentangle skeletal and cranial size from robusticity (see references in Holliday, Gautney, and Friedl, forthcoming). In addition, few mammalogists have collected the kind of data

the current authors have taken for investigating the overall feminization of the human cranium. This is an enormous lacuna in our knowledge that should be further investigated.

There is, however, one possibility discussed in Holliday, Gautney, and Friedl (forthcoming) that may have interesting implications for the current contribution. Specifically, Leonard et al. (2002) note that in humans, life in a cold climate is associated with overall higher circulating thyroid hormone levels, seemingly an evolutionary adaptation. Since hypothyroidism is associated with lower free testosterone levels in men (Meikle 2004), it is possible that exposure to cold climates could result in higher free testosterone levels. Following this, as was first hypothesized by Perez, Bernal, and Gonzalez (2007), cold climate could at least partially explain the more "robust" (or "masculinized") faces of some human groups. An obvious implication of this, then, is that the shift from the colder Pleistocene to the warmer Holocene may have been a "happy accident" that led to increased feminization of the cranium in *Homo sapiens* (note, too, that the earliest "feminized" *H. sapiens* crania are found in tropical Africa, or just outside of the continent in the southern Levant). Is it possible, then, that this hormonal relationship could explain (or at least play a role in) many of the apparent mammalian trends for decreased robusticity from the Pleistocene to the Holocene?

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While there are many interesting aspects of this paper to discuss, I will limit my comments to the relationship between increasing population size and the emergence of behavioral modernity that is its foundation. I am in agreement that population size and changing population dynamics are important factors in understanding patterning in the archaeological record. I have argued previously that changes in life history and metapopulation ecology can be used to understand both local and global patterning including, for example, the surprising diversity and evidence of innovation but lack of directional trends in the Acheulian (Hopkinson, Nowell, and White 2013; Nowell and White 2010) and the similarities and differences in the lives of Neanderthals and modern humans in the MP/MSA and early UP/LSA (Nowell 2013).

In their article, Cieri and colleagues argue that selection for greater social tolerance and lessened aggression is a necessary prerequisite for cultural ratcheting and the emergence of behavioral modernity, because social tolerance is linked with enhanced cooperation, more effective cultural transmission of technologies, and increased learning and teaching opportunities. I agree that demography on its own is not the answer to the emergence of modern behavior and that we must also look at social mechanisms, among other factors. For example, consider the case of the late Neanderthals, that

is, those younger than 50,000 BP; 50,000 BP is an important temporal boundary because this is when, according to Cieri et al., sufficient population size, increased social tolerance (as evidenced by craniofacial feminization), and the "prevalence and permanence" of symbolic behavior (a generally agreed upon hallmark of behavioral modernity) coalesce for modern humans.

Before 50,000 BP there are few symbolic artifacts associated with Neanderthals that most paleoanthropologists would accept as authentic—many are best explained by taphonomic causes (e.g., the putative Molodova IV engravings, the Neanderthal bone "flute," etc.) but late Neanderthals do appear to engage in the production of personal ornaments, with broadly accepted examples from sites such as Fumane, Quinçay, Cueva de los Aviones, Cueva Antón, Grotta del Cavallo, les Fieux, Klisoura 1, and Meged Rockshelter (e.g., Koumouzelis et al. 2001; Morin and Laroulandie 2012; Roussel and Soressi 2010; Zilhao et al. 2010). Even if some of these examples are not accepted by all paleoanthropologists, there is enough evidence to suggest that the pace and nature of symbolic behavior among Neanderthals changes both quantitatively and qualitatively after 50,000 BP (Nowell and Chang 2012). However, it is clear that at this time Neanderthal populations are not increasing but are in decline.

Most of the examples of personal ornaments with late Neanderthals are artifacts that come from sites in southern France, Spain, and possibly Italy in areas that are often interpreted as refugia for late Neanderthals (Nowell and Chang 2012). Southern Europe, in particular, seems to have been continuously occupied by Neanderthals (although not perhaps by continuous populations) ca. 100,000 − < 30,000 BP, whereas northern Europe exhibits apparent hiatuses in occupation associated with the coldest periods (H4, H5) that have been interpreted as either local extinctions or emigration (Roebroeks, Hublin, and MacDonald 2011; Stewart and Stringer 2012). Based on these paleoclimatic reconstructions, Roebroeks, Hublin, and MacDonald (2011) argue that northern populations of Neanderthals may have undergone local extinctions due to an inability to move south into refugia because these areas were already occupied by other Neanderthals. Paleoclimatic and genetic data support the hypothesis that Neanderthals may have retreated to refugia in the most isolated parts of western Europe during periods of extreme cold, experiencing bottlenecks or local extinctions followed by repopulation during warmer periods, perhaps by migrants from the eastern parts of the Neanderthal range (Dalén et al. 2012). If the data are correct, then it is possible that the investment in making items of personal adornment (and likely other nonvisible, nonarchaeologically preserved signs or symbols) functioned to distinguish Neanderthal groups from each other and prevent outsiders from encroaching on group territories (which may have been even more important if they served as refuge areas). Dalén et al. (2012) have argued that European Neanderthals may have already been on the verge of extinction before modern humans ar-

rived, and therefore Neanderthal-associated ornaments may represent reactions to crowding among Neanderthals themselves in refuge areas, or encroachment/social stress by other Neanderthal culture groups or modern humans, even before moderns arrive in western Europe around 40,000 BP (Nowell and Chang 2012).

While Cieri et al. emphasize that they are studying modern humans only, what this example shows is that two very closely related hominin populations came to a place culturally and socially where it made sense to produce symbolic artifacts on an accelerated scale but for different reasons: one in the context of a population in ascendancy and one of a population in decline. Both are examples of demographic packing, but the relative scales and the social and environmental contexts appear to be very different. Thus, I agree with Cieri et al. that demography alone may not be sufficient to explain the emergence of behavioral modernity. However, I would suggest that there are more variables at play than their model takes into account.

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We commend Cieri and colleagues for proposing an original and thought-provoking model that links evidence from breeding experiments, fossil morphology, and archaeological signatures of behavioral changes. Their aim seems to be to spark discussion; in this spirit, we have a few points for them and others to consider.

The authors' model, as we understand it, can be summarized by the following logical chain. Growth in human population size in Africa beginning 200,000 years ago led to higher population densities, which resulted in natural selection for increased social tolerance. Certain cranial features, such as browridge projection and upper facial height, would have become reduced as correlated responses to selection for social tolerance. Enhanced social tolerance, in turn, would have allowed for even higher population densities, which would have established the necessary demographic conditions for "behavioral modernity." Although we find this model intriguing, to be widely accepted it will need to overcome some challenges: ambiguous evidence, data deficiencies, and contradictory evidence.

In some cases, it is difficult to make connections between the components of the model because the evidence is ambiguous. For example, although the older mitochondrial DNA studies cited by the authors concluded that human population size in Africa grew rapidly during the past 200,000 years, more recent analyses of autosomal DNA paint a more complicated picture. According to Li and Durbin (2011), effective population size in Africa started to increase 700,000–500,000 years ago to a peak 200,000–100,000 years ago; this growth was

followed by a drop in effective population size, until it began to increase again 50,000–30,000 years ago. Effective population size roughly corresponds to the number of breeding individuals in an idealized population that would have as much genetic drift as in the actual population, so its relationship with census size may vary with time, but researchers have generally assumed that effective population size and census size correspond at least approximately (i.e., when effective size is large, census size is large, and when effective size is small, census size is small). Making this assumption, if the authors' model is correct, one might expect there would be pulses of behavioral modernity and social tolerance, and their archaeological and fossil manifestations, 150,000 years ago and 40,000 years ago. These dates are certainly subject to change given uncertainty in the appropriate mutation rate to use (Scally and Durbin 2012). Our point is simply that it is not clear whether the genetic evidence for changes in population size in Africa matches well with purported signatures of behavioral modernity or increased social tolerance.

In other cases, data deficiencies hinder the testing of aspects of the model. For example, according to the authors' interpretation of the archaeological record, an important shift in the amount of cumulative technological evolution occurred between 80,000 and 30,000 years ago, but their (and everyone else's) fossil sample includes very few specimens that are likely to come from this interval. In table 1, the Middle Stone Age/Middle Paleolithic crania are all > 90,000 years old, and most of the Later Stone Age/Upper Paleolithic crania are < 30,000 years old (even after adding a few thousand years to the uncalibrated radiocarbon dates). In fairness, this is a general problem for models attempting to explain the advent of behavioral modernity in Africa and the expansion of modern humans to other parts of the world. We lack fossils, and in many parts of Africa archaeological sites, from this critical interval.

Finally, some evidence appears to contradict the model. For example, the authors cite Steele and Klein's (2005) research on the relationship between the size of shellfish found in archaeological sites, collection intensity, and human population densities as evidence that human populations began to expand during the late Middle Stone Age and that the resulting increased population densities allowed for more cumulative technological evolution. However, at Blombos Cave, which has yielded arguably the best evidence for behavioral modernity in the Middle Stone Age—in the form of engraved ochre, perforated shells, bone points, and finely crafted stone tools—the size of the shellfish from the Middle Stone Age levels indicate consistently low human population densities (Klein and Steele 2013). Unlike estimates of effective population size from DNA sequences, which at best reflect large-scale fluctuations in human population size, shellfish size potentially provides information about local changes in population density, which would seem to be the relevant scale for making mechanistic links with cumulative technological evolution. In the case of Blombos Cave, apparently, the expected pairing of high population density and archaeological signatures of behavior modernity does not hold.

These concerns aside, Cieri and colleagues have produced a stimulating piece of work. We expect that their model will generate useful discussion, prompt further testing, and lead to new and productive avenues of research.

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Cieri and colleagues have focused a wide range of data and ideas on an appealing set of hypotheses: that is, that increasing population density at the end of the Pleistocene favored the characteristically high level of human social tolerance; that because this increased tolerance enabled individuals to cooperate more easily, it contributed to the cultural evolution of behavioral modernity; and that reductions in androgens or androgen receptors were particularly important mechanisms in the promotion of tolerance both theoretically and because they allow empirical tests. Their analyses testing whether craniofacial feminization has increased steadily from the Middle Pleistocene onward, and whether such feminization is greater in farmers than foragers, are therefore valuable. They show that some detectable effects are as predicted, namely, a reduction in masculine facial proportions up to the Upper Paleolithic, while others are either more complex than expected or directly challenging to the core hypotheses.

Here I focus on two problems concerned with the mechanisms underlying the postulated changes in behavior and anatomy.

1) Cieri et al. claim that an increase in population density should be expected to promote social tolerance but offer no supporting evidence. Their idea seems surprising when applied to humans since, even when population density is low, individuals gather in small face-to-face groups with a high local density of interaction. Two tests suggest themselves with other species. First, Thierry (2007) classified *Macaca* species into four grades of tolerance. According to Cieri et al.'s hypothesis, population density should rise from grade 1 to grade 4. However, no such trend appears for 12 species listed by Jones et al. (2009): mean population densities were 20.6 (grade 1), 34.1 (grade 2), 12.9 (grade 3), and 27.9 (grade 4; see table 4). Second, bonobos are more socially tolerant than chimpanzees, which would predict that bonobos live at higher-population densities than chimpanzees. I know of no evidence in favor of this idea (e.g., compare Balcomb et al. 2000 with Fruth et al. 2008). Further examination of the relationship between tolerance and density is needed, but these initial comparisons suggest that increasing population density is an unpromising explanation for rising social tolerance.

2) Cieri et al. discuss the factors that could have favored

Table 4. Population densities of *Macaca* species in relation to social tolerance

Common name	Species	Population density (#/sq km)	Tolerance grade
Rhesus	*M. mulatta*	11.1	1
Japanese	*M. fuscata*	30.2	1
Longtailed	*M. fascicularis*	50	2
Pigtailed	*M. nemestrina*	18.1	2
Toque	*M. sinica*	30	3
Liontailed	*M. silenus*	1	3
Bonnet	*M. radiata*	8.23	3
Barbary	*M. sylvanus*	12.5	3
Tonkean	*M. tonkeana*	10	4
Booted	*M. ochreata*	15	4
Crested black	*M. nigra*	66.7	4
Moor	*M. maura*	20	4

Note. Population densities are from Jones et al. (2009). Tolerance grade is from Thierry (2007).

a reduction in male aggressiveness but focus only on the benefits of tolerance rather than on the mechanisms by which aggressive behavior would be selected against. They propose that by allowing better cooperation, reduced aggression could have led to increased foraging success (through superior cooperation and improved access to contested patches) and possibly to positive mate choice by females. A complementary kind of proposal emerges from considering the costs of aggression. In recent nomadic foragers, aggressive men are liable to be socially ostracized, exiled, or executed (Boehm 2012). The mechanism for these sanctions is language, which allows conspiratorial planning. Thus, if communal decisions to sanction aggressors have been a consistent feature of linguistically competent *sapiens*, as seems plausible, the emergence of sophisticated language can explain the reduced fitness of aggressive males. Reduced aggression is then seen as an incidental consequence of a novel social dynamic (Boehm 2012). This view is consistent with the emergence of social tolerance in domesticated foxes and bonobos, where the ability to cooperate is an incidental side-effect of selection against aggression (Hare et al 2005, 2007).

In summary, Cieri et al.'s argument that social tolerance is an important human trait that demands evolutionary explanation is important because it unites many relevant observations, and the possibility that reduced aggression is anatomically detectable is exciting. However, it is worthwhile to consider a broader set of mechanisms for explaining why aggression was reduced and tolerance favored.

Reply

We are grateful to all of the commentators for their thoughtful, and thought-provoking, responses, which highlight some of the issues inherent in trying to infer the evolution of human

behavioral tendencies and temperament from skeletal morphology. While the commentators raise a number of good points that add to discourse about the evolution of modern human behavior, we see four main issues that emerge from the responses: (1) the use of browridge morphology as a reflection of facial masculinity may be problematic, given that many modern human populations do not show expected patterns of sexual dimorphism in this feature (Athreya); (2) a comparative perspective suggests that skeletal gracilization (of which craniofacial feminization may be a part) is a late Pleistocene and Holocene pan-mammalian trend (perhaps related to interglacial warming) that is not unique to humans and thus not requiring a human-specific explanation (Holliday); (3) a direct causal relationship between metapopulation size and CTE may require rethinking, both because Neanderthals appear to have experienced some degree of CTE at a time that their numbers may have been waning (Nowell) and because a late MSA/early LSA increase in modern human population size is poorly supported by genetic and archeological data (Steele and Weaver); (4) our model predicts a general relationship between population density and social tolerance in other social species, but this prediction is not borne out in other primates (Wrangham). We address each of these in turn.

Athreya's comments highlight a problem that is common to most, if not all, studies of craniofacial dimorphism in humans: in many skeletal samples, especially cranial samples lacking associated postcranial material, sex is ascribed to specimens on the basis of craniofacial morphology, of which browridge projection is a heavily weighed character. The circularity inherent in trying to assess dimorphism in these samples is well recognized (see, e.g., Lahr 1996) and prevents us from examining patterns of browridge dimorphism in our recent human data (since Howells used cranial morphology to sex specimens; accordingly, our recent human "male" samples might best be considered samples of the most craniofacially masculine individuals, which is still conservative with respect to our hypothesis). We are not in a position to comment on Athreya's unpublished data, but her finding that some populations do not adhere to expected patterns of browridge dimorphism is somewhat concerning (assuming, of course, that the skeletons were sexed using postcranial features). Studies involving documented individuals of known sex, or individuals sexed from associated postcranial material, conform to expected patterns of browridge dimorphism in multiple populations (Garvin and Ruff 2012; Perlaza 2014; Shearer et al. 2012), which makes Athreya's findings all the more surprising and which suggests that more research is needed in this area. We agree that one central question concerns the extent to which both sexes may have undergone feminization (or a paedomorphic transition, to use Athreya's term) and what this means in terms of evolving human temperament. We note that, among the Siberian foxes, cranial morphology of males in the tame strain approaches that of females, while in the strain selected for aggressiveness, female morphology

tends toward that of males, such that both strains show similar overall levels of dimorphism (LN Trut and AV Kharlamova, personal communication to Robert G. Franciscus; it is not widely known that the farm fox experiment also involved the development of an aggressive strain of foxes). This suggests that levels of dimorphism within populations are not the appropriate measure of temperament but rather that one must examine evolutionary change in craniofacial morphology within sexes.

We find provocative Holliday, Gautney, and Friedl's (forthcoming) observation that several mammalian taxa underwent skeletal gracilization across the terminal Pleistocene and Holocene, a trend which we have noted in some taxa as well (Churchill, Brink, and Gruss 2000; Lewis et al. 2010). For most taxa, however, the empirical temporal trend is based almost exclusively on postcranial measures of size coupled with subjective impressions of robusticity, and at present it is unclear what role allometric relationships between body size and robusticity may play or the extent to which craniofacial feminization may have characterized nonhuman taxa. Late Pleistocene size reduction in hominins is unlikely to explain craniofacial feminization. When femoral head diameter is used as a measure of body size, lineages of both hominins (archaic vs. early modern vs. recent modern humans) and canids (wolves vs. prehistoric dogs vs. modern dogs) show much greater reduction in facial length than facial breadth relative to body size (Franciscus, Maddux, and Wikstrom Schmidt 2013), consistent with the model presented here. Furthermore, the most striking changes in human body size occurred in the last 30 Ka (Ruff, Trinkaus, and Holliday 1997), well after the greatest changes in craniofacial masculinity in modern humans. We also find intriguing the suggestion that colder Pleistocene climates may have selected for adaptive hyperthyroidism in humans, which in turn may have increased levels of circulating testosterone and thus produced greater facial masculinity. However, when we separate the recent human data into high (Norse, Ainu, Eskimo, and Buriat: $n = 210$) versus low (all others: $n = 1,157$) latitude subsamples, mean values of brow projection are actually significantly lower in the colder-climate crania (77.8 vs. 88.7), while the face shape index does not differ significantly between samples (197.5 vs. 199.8), which does not lend support to this hypothesis.

We agree with Nowell that the apparent cultural ratcheting seen in the terminal Mousterian, and attributed to Neanderthals, deserves special consideration. She suggests that innovations in Mousterian material culture and in symbolic expression were occurring at a time in Marine Isotope Stage (MIS) 3 that Neanderthal populations were in decline but that the more southerly parts of Europe (exactly where these innovations appear in the archeological record) may still have seen locally high population densities sufficient to stimulate CTE. Archeological site density suggests that Neanderthal metapopulation sizes were waxing and waning across MIS 3 (see Churchill 2014), and given the error inherent in the radiocarbon chronology, an alternative hypothesis is that brief

periods of CTE in the Mousterian correspond with ephemeral upturns in population density, similar to what was happening in the African MSA prior to 50 Ka BP. Regardless, Nowell is correct that the Neanderthal/Mousterian record serves as a parallel case of CTE, and it would be worthwhile to ask if later (post-50 Ka BP) Neanderthal crania are feminized relative to their earlier conspecifics.

Steele and Weaver correctly note that an increase in human population density in the later part of the African MSA is central to our model of the evolution of human social tolerance. They are also correct that the evidence for late MSA population growth is mixed. We note, however, that effective population size (n_e: as reported in recent mtDNA studies) is not an appropriate measure of census size (n_c), contra their claim. By way of illustration, one estimate of n_e for living humans is 622–10,437 individuals (Park 2011), whereas n_c is greater than 7 billion! More troubling to our hypothesis, as well as to more general models linking CTE to population density, is the finding that at the important site of Blombos Cave, MSA innovations appear in the context of what may have been low population density (based on shellfish remains). It may be that the MSA inhabitants of Blombos were part of a highly interconnected social network, which would thus allow for CTE (Powell, Shennan, and Thomas 2009) despite low population density. Certainly, an increased attention to the potential relationship between periods of cultural innovation and population growth (e.g., Jacobs et al. 2008) in the African MSA is needed to resolve this issue.

Wrangham raises a salient criticism of our model when he notes that available data for anthropoid primates do not support the assumption that higher population density leads to greater social tolerance. We admit that this presents an interesting, although not altogether damning, challenge to our hypothesis. When combined with Steele and Weaver's observation about apparent MSA population density at Blombos Cave, it suggests that population packing is neither necessary to CTE nor sufficient to promote the evolution of social tolerance. As noted above, CTE may accelerate in the absence of high population density given a high degree of interconnectivity of social groups. We note that recent foragers tend to live in relatively small social groups and at relatively low population densities but within extensive social networks (Hill et al. 2011). What is unique about these groups, compared to other primates, is that they are characterized by relatively low levels of genetic relatedness (Hill et al. 2011) and high levels of affinal relationships, especially between unrelated adult males (Chapais 2010). We postulated that increased population density in the late MSA was the driving force behind increased social tolerance, but it is equally (and perhaps more) likely that a need for greater male-male tolerance in the context of enhanced social networking provided the selective environment for a shift in human temperament (along these lines, it would be useful to examine the macaque data in terms of group size and number of adult males per group, since population density data may be saying more

about the carrying capacity than the actual "local" population density experienced by the animals themselves). Wrangham himself may have also provided part of the answer in noting that language, and the coalitionary behavior that it promotes, may have been a major factor in selection against less tolerant individuals (we focused on the reproductive benefits of greater tolerance: Wrangham offers the flip side of the same coin in delineating the potential reproductive costs of intolerance). Thus population packing per se may be insufficient to promote tolerant temperaments in most primates, yet will do so in language-bearing early modern humans.

Much more work remains to be done on the physiological and neurological underpinnings of modern human behavior and its evolutionary history, but we hope we have at least suggested some avenues that might merit further research. Again, we thank the commentators for their useful and constructive thoughts.

—Robert L. Cieri, Steven E. Churchill, Robert G. Franciscus, Jingzhi Tan, and Brian Hare

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