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How Our Ancestors Raised Children to Think as Modern Humans

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Abstract
This article argues that social selection pressures in recent human evolution were the driving force behind the emergence of modern cognition. These selection pressures took three specific forms: (1) Increased security and stability, which reduced allostatic load on developing children, thus releasing selection pressure against many executive functions, including working memory; (2) increased opportunities for mother–infant joint engagement, which created positive selection for more sophisticated forms of cognition; and (3) increased pressure on ritualized behavior associated with both mother–infant joint engagement and the construction and maintenance of an unprecedentedly complex adult social world. These pressures directly affected the development of the behavioral trait of effortful control in children. Effortful control is closely linked with executive functions, including working memory. Effortful control also shows characteristics that make it a prime candidate for rapidly spreading, culturally driven changes that were prevalent late in human evolution.

Keywords
allostatic load, effortful control, executive functions, modern cognition, ritual, working memory

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A compelling case can be made that modern cognition arose as the result of a modest but significant enhancement of working memory capacity. There are two aspects of this evolutionary change; however, that are often neglected: (1) Natural selection cannot operate on a mental capacity, only on the phenotypic expression of that capacity. (2) Greater working memory capacity does not arrive fully formed in an adult's head. Instead, it arises developmentally as the product of a naturally selected ontogenetic pathway. Thus, fully understanding the emergence of modern cognition requires identifying the selection pressure(s) that acted on behaviors associated with the ontogenetic pathway leading to enhanced working memory in adults.

This article argues that the selection pressures driving the emergence of enhanced working memory in our ancestors were primarily social. Beginning about 100,000 years before present (ybp), the social world of *Homo sapiens* changed dramatically, making it clearly distinct from that of other hominins. This world acted as a selective force on the behavioral trait of effortful control in hominin children. Effortful control is closely linked with executive functions, including working memory. The specific selection pressures of the *Homo sapiens*' social world were: (1) increased security and stability, which reduced allostatic load on developing children, thus releasing selection pressure against many executive functions, including working memory; (2) increased opportunities for mother–infant joint engagement, which created positive selection for more sophisticated forms of cognition; and (3) increased pressure on ritualized behavior associated with both mother–infant joint engagement and the construction and maintenance of an unprecedentedly complex adult social world. More demanding social rituals taxed areas of the brain associated with focused attention and working memory, especially the dorsolateral prefrontal cortex (DLPFC) and the anterior cingulate cortex (ACC). These same brain areas are critical to the development of effortful control in children.

Finally, given its high genetic heritability and sensitivity to gene–environment interaction effects, effortful control is susceptible to rapidly spreading, culturally driven evolutionary changes. Recent genetic evidence indicates that rapid, culturally driven evolutionary changes were very likely the key to the emergence of uniquely human cognitive and behavioral traits.

Enhanced Working Memory and the Evolution of Modern Cognition

In a series of recent papers, Coolidge and Wynn (2001, 2005; Wynn and Coolidge 2003, 2004, 2007) have built a strong case that the emergence of uniquely human cognition resulted from a modest but significant increase in working memory capacity. This increase made *Homo sapiens* better able to hold information in mind, especially information about behavioral procedures and intended goals, in spite of competing signals or response competition (Kane and Engle 2002). Thus, when confronting cognitive challenges, *Homo sapiens* were better equipped to resist mental sets and other prior habits of thought and behavior. This ability, Wynn and Coolidge (2003, 2004, **AQ1** 2007) argue, was essential for long-range planning, exploring novel relationships, innovative thinking, and creating and using symbols. This helps to explain why it was exclusively among Upper Paleolithic *Homo sapiens* that evidence of two unprecedented phenomena are found: an accelerating pace of innovation in tools and other artifacts, and abstract image-making, such as cave art, ornamental tools and weapons, and human/animal figurines.

For example, Wynn et al. (2009) analyzed the cognitive requirements for creating the 30,000-year-old Holenstein-Stadel (lion-man) artifact. They argue that the artisan needed to hold **AQ2** two disparate concepts (person and lion) in active attention while building an imagined superordinate category capable of uniting them (e.g., spiritual agent). This type of cognitive operation places great demands on working memory. As working memory capacity increases, more cognitive resources are directed to inhibitory processes (Kelly et al. 2006). These processes are essential for sustaining attention on a target task long enough to complete complex operations, such as those behind the making of the Holenstein-Stadel figurine. Willfully maintaining focused attention allows an organism to extract more information from a signal and relate that signal to more remote concepts. It is exactly this sort of cognitive process that is central to abstract thinking, long-range planning, creating symbols, and other forms of modern cognition.

Looking carefully at Coolidge and Wynn's argument, one can see that it is not so much greater working memory capacity per se that is crucial to modern cognition, but what it *allows for*: greater cognitive and behavioral control. This is critical because selective forces can only act on a phenotypically expressed trait, not on an internal mental capacity. Furthermore, no one simply arrives at adulthood with greater working memory capacity or greater cognitive control. These traits emerge over the course of ontogeny—in other words, they result from a certain developmental trajectory. Thus, to fully understand the emergence of modern cognition, one must identify the behavioral trait(s) that selective forces acted upon in order to propel ontogeny down a pathway leading to adults with greater working memory capacity.

Developmental studies have identified a key cognitive/behavioral trait central to a child's intellectual and social success: *effortful control*. In our ancestral past, ontogenetic selective forces (e.g., parents, social learning demands, developmental risk factors, etc.) could not have filtered infants and children for greater working memory capacity. However, they could have filtered them for greater effortful control and this would have resulted in adults with greater working memory capacity—and therefore the potential for modern cognition.

Effortful Control

Effortful control is defined as "the ability to inhibit a dominant response [so as] to perform a subdominant response, to detect errors, and to engage in planning" (Rothbart and Rueda 2005: 167). Effortful control is a major form of self-regulation—an important factor in social/cognitive development. Self-regulation refers to a child's ability to control reactions to stress, maintain focused attention, and interpret mental states in themselves and others (Fonagy and Target 2002). Effortful control allows children to more flexibly approach novel and anxiety-provoking situations by inhibiting emotion-driven reactions and/or prepotent responses that might be situationally suboptimal. Effortful control is an important predictor of social skill and academic success, as well as a range of social/cognitive abilities, including empathy, theory of mind, moral reasoning and behavior, and inferential reasoning (such as using contextual cues to disambiguate sensory signals). Deficits in effortful control are associated with an array of cognitive, emotional, social, and behavioral problems in children, where both externalizing (aggression, delinquency) and internalizing (anxiety, depression) reactions may be present (Rothbart et al. 1994, 2000; Eisenberg et al. 2001; Lengua 2003; Lengua et al. 2008).

Effortful control considerably overlaps with executive attention. Executive attention refers to the ability to willfully direct and sustain attention in spite of competing external or internal signals (Welch 2001; Kane and Engle 2002; Rothbart and Rueda 2005; McDonald 2008). Areas of the brain critical to executive attention and working memory are also implicated in the development of effortful control. These areas include the dorsolateral pre-frontal cortex (DLPFC) and anterior cingulate cortex (ACC; D'Esposito et al. 1999; Duncan et al. 2000; Curtis and D'Esposito 2003; Posner and Fan 2004; McDonald 2008). Brain imaging studies indicate that both of these cortical regions are active when psychological conflicts are confronted (Botvinick et al. 1999; Casey et al. 2001) or when prepotent, emotion-based responses must be suppressed in favor of more consciously controlled ones (Ingvar 1994; Beauregard et al. 2001; Richeson et al. 2003). While the ACC is important for identifying and monitoring conflict, the DLPFC is critical for conflict resolution.

Social Complexity and the Evolution of Effortful Control

Anatomically modern humans (*Homo sapiens*) emerged about 200,000 ybp in Africa (White et al. 2003; McDougall et al. 2005) and were one of at least four hominin species present at the time. There is no reason to suspect that effortful control differed substantially among these species. The emergence of *Homo sapiens* was marked by no dramatic change in the archeological record. Archaic hominins, such as Neanderthals, were expert toolmakers and highly proficient hunters whose technical skill and behavioral competence differed little from *Homo sapiens* (Sorensen and Leonard 2001; d'Errico et al. 2003; Grayson and Delpech 2003). Furthermore, the presence of worked beads, mineral pigments, sophisticated tools, and possibly representational art suggest that Neanderthals had some capacity for both symbolism and innovation (d'Errico et al. 2003: 19, 22–25; Marquet and Lorblanchet 2003; Langley et al. 2008). However, while hunting, tool making, and other subsistence activities may not have dramatically differed between *Homo sapiens* and other hominins, the same was not true of their social lives. Thus, if there were selection pressures on *Homo sapiens* capable of uniquely affecting effortful control, they were most likely social in nature (see McDonald 2008 for a similar conclusion).

The social worlds of archaics and *Homo sapiens* were quite distinct. Fossil evidence indicates that *Homo sapiens*' social groups were larger and more complex than Neanderthals. Relative to Neanderthals, European Cro-Magnon campsites were larger, more frequent, more intensely used and occupied, and (typically) more spatially structured (Dickson 1990: 84–92, 180–189; Stringer and Gamble 1993: 154–158; Bar-Yosef 2002; Hoffecker 2002: 129, 136). Many of these sites show evidence of seasonal aggregation, larger population density, and other signs of social complexity and stratification (Mellars 1996; Vanhaeren and d'Errico 2005).

Homo sapiens' groups were not just larger than those of Neanderthals, they were compositionally quite different as well. Increased longevity among *Homo sapiens* meant that their groups were composed of considerably more older adults relative to younger adults, adolescents, and children. Using dental samples, Caspari and Lee (2004) found evidence that the ratio of older to younger adults (older defined as $2 \times$ the average age of first reproduction) increased significantly in Upper Paleolithic modern humans compared to Austrolopiths, early *Homo*, and Neanderthals. In fact, it was only among modern humans that older adults outnumbered their younger counterparts. An increased supply of adults may have been important in allowing modern humans to adopt more clearly defined sex roles, with males hunting and females gathering (Kuhn and Stiner 2006). Sex role specialization appears not to have been the characteristic of Neanderthals.

Homo sapiens were also interacting with out-groups more frequently, resulting in raw material and (very likely) informational exchanges (Feblot-Augustins 1999; Gamble 1999; Adler et al. 2006). The emergence of shell beads sometime between 100,000 ybp and 70,000 ybp suggests that social marking was becoming increasingly important, as would be expected with a rise in inter-group interactions (Kuhn and

Stiner 2007). Furthermore, these shell beads are often found quite distant from their origin, suggesting the existence of expanded trading networks (Vanhaeren et al. 2006). The existence of expanded trade networks is further bolstered by the presence of tools made from "exotic" non-local raw materials in the Still Bay and Howieson's Poort tool industries, dated AQ3 to around 70,000–60,000 ybp (Ambrose 2002; Henshilwood 2007). Evidence of similarly extensive trade networks is lacking among archaic hominins.

Among its myriad impacts, the increasingly sophisticated social world of *Homo sapiens* would have had two ramifications relevant to the evolution of effortful control: (1) It would have created a more stable and secure rearing environment for children; and (2) it would have put unprecedented stress on social rituals.

Social Complexity and Ontogeny: Allostatic Load and Joint Engagement

Greater social organization provides a more secure and stable environment within which to raise children. The consistent presence of a sizable older generation among ancestral human groups meant more eyes to supervise and protect children and more hands to procure resources. Often these resources were being procured with increasingly effective technologies that reduced the physical burden on the user (such as lethal projectile hunting weapons). Male specialization in the most dangerous and strenuous activities meant that females could remain closer to camp, expending more energy on child rearing and protection. In addition, as males and females were collecting different food resources, scarcity in any one commodity (such as reduced numbers of large game) would not necessarily endanger survival. These factors, in conjunction with inter-group resource exchanging networks, resulted in a domestic world of *Homo sapiens* that was more buffeted against calamity compared to that of their archaic contemporaries. Life for *Homo sapiens* wasn't easy, but it was far less precarious than that of any other hominin.

Evidence for this can be found in the fact that Neanderthals and their children endured higher levels of stress and deprivation compared to *Homo sapiens*. The Neanderthal diet de- AQ4 pended heavily on big game (Boucherens et al. 2001, 2005; Marean 2007). Lacking projectile hunting weapons, Neanderthals regularly confronted large dangerous beasts such as mammoths and rhinos with spears designed to be thrust in at close range (Churchill 1993; Shea 1997). Unsurprisingly, this tactic produced extensive head, neck, and upper body trauma (Berger and Trinkaus 1995). The lack of sex role specialization meant that women and youngsters were very likely participating in big game hunts and sharing in the burdens.

The relative homogeneity of the Neanderthal diet also meant that their nutritional needs were more subject to stress when big game became scarce. Tooth samples show that Neanderthal children endured greater nutritional stress than Cro-Magnon children (Soffer 1994). Moreover, nutritional stress in general seems to have afflicted Neanderthals to a greater degree than Cro-Magnons (Stiner 1991; Stringer and Gamble 1993: 166). While evidence of cannibalism (presumably owing to nutritional stress) is present from Neanderthal sites (Defleur et al. 1993, 1999), similar evidence from Cro-Magnon sites is lacking (Klein and Edgar 2002: 198). Neanderthal morality rates were also extremely high—fewer than 10% of Neanderthals lived to over age 35 years. Among extant hunter–gatherer and tribal agriculturalists about 50% are over this age (Trinkaus and AQ5 Thompson 1987). Among the !Kung San of Southern Africa, although life expectancy at birth is only about 30 years, nearly 80% of the adult population lives to over the age of 60 years (Blurton Jones 2002: 314).

A more secure and stable domestic environment has positive effects on cognitive development. Neurocognitive studies have found that an impoverished upbringing detrimentally impacts brain systems associated with working memory, cognitive control, and executive functions in kindergarten and first graders (Farah et al. 2006; Noble et al. 2007). A key causal factor within the impoverished context is allostatic load (Evans and Shamberg 2009). AQ6 Allostatic load is a composite measure of stress endured during childhood that includes measures taken from blood pressure readings, overnight cortisol and catecholamine levels, and body mass index. Evans and Shamberg (2009: 6546–6547) AQ7 contend that allostatic load represents "an index of chronic stress" representing "the degree of cumulative wear and tear on the body during [the child's] early lifetime." Higher levels of allostatic load during childhood have damaging effects on numerous measures of intellectual performance, including working memory. The duration and degree of allostatic load incurred during childhood is a significant predictor of young adult's working memory capacity. Relatedly, a more disruptive and stressful home environment also adversely affects the development of effortful control (Eiden et al. 2001; Karreman et al. 2006; Lengua et al. 2007; Lengua AQ8 2009). AQ9

If allostatic stress during ontogeny is detrimental to the development of executive functions, including working memory and effortful control, then to the extent that the *Homo sapiens'* social/developmental environment reduced this stress, selection pressure against greater working memory capacity and effortful control would have been eased. However, a more stable and secure domestic world would have created positive selection pressure for these same cognitive/behavioral traits by virtue of greater opportunities for mother–infant joint engagement. Joint engagement refers to instances where mother and infant share attentional focus either on each other (dyadic) or together with a third object (triadic) such as a toy.

The greater number of adults present in *Homo sapiens*' groups meant more help was available to the mother, allowing her to devote more time tending to a young infant as opposed to actively gathering or processing resources. By contrast, the high level of skeletal robusticity found in Neanderthal females suggests that mothers (and their children) were highly active, working hard for a living (Lieberman and Pearson 2001; Lieberman et al. 2001). Reduced physical demands on *Homo sapiens* mothers would have left more time and energy for childcare and more opportunities for joint engagement. More frequent and extended bouts of joint engagement would have enhanced both the social and cognitive development of infants and children.

Socially, it is through joint engagement that critical social/emotional bonding occurs between infants and adult caregivers (Hobson 2004; Reddy 2008). If *Homo sapiens'* mothers had unprecedented opportunities for mother–infant joint engagement, then we could expect that the degree of social/emotional bonding between them also reached never-before-seen levels. This would have had important effects on the development of effortful control. Parenting strategies high in warmth, constructive limit-setting, support for autonomy, and consistent disciplining (especially during the pre-school years) foster greater effortful control in children (Eiden et al. 2001; Karreman et al. 2006; Lengua et al. 2007; Lengua, 2009). Conversely, as has been mentioned earlier, inconsistent parenting and domestic and environmental stress negatively impact effortful control.

Cognitively, infants demonstrate a number of mental skills in the context of joint engagement that are either absent or less sophisticated outside of this context. For example, joint engagement has been found to facilitate word learning and vocabulary development (Tomasello and Todd 1983; Tomasello and Farrar 1986; Baldwin 1991). Furthermore, within joint engagement, children show more sophisticated organizational abilities, more advanced forms of play, and an enhanced understanding of other's mental states (Ratner et al. 2002; Tomasello and Haberl 2003; Bigelow et al. 2004; Moll et al. 2007). One possible reason for these cognitive enhancements is that joint engagement heightens cortical activity in infants' brains (Striano et al. 2006).

In summary then, as the *Homo sapiens*' child-rearing world increasingly became one characterized by reduced levels of allostatic stress and increased levels of mother–infant joint engagement, a context conducive to the development of greater effortful control in children was increasingly created. Given the numerous positive social/cognitive outcomes associated with greater effortful control (greater empathy, self-control, reasoning ability, etc.), children higher in effortful control would have been generally easier to deal with, more popular with peers and adults, and endowed with a host of other developmentally relevant, fitness-enhancing qualities compared to other children.

Building Greater Social Complexity: Social Rituals

Evidence reviewed earlier indicated that *Homo sapiens*' social groups were larger, more complex, and included more intergroup interactions compared to Neanderthals. But by what mechanism is such a social world constructed? Throughout the animal world, when careful communication is required, ritualized behavior is present. In the current context, ritual refers to a rule-governed and generally invariantly sequenced pattern of behavior that is attention-getting and formalized (Bell 1997: 138–169; Rappaport 1999: 24).

For example, consider a common ritual used for social bonding among male baboons called "scrotum-grasping." Two males wishing to signal friendship will take turns holding each other's testicles (Smuts and Watanabe 1990; Whitham and Maestripieri 2003). Grabbing and ripping at the genitals is common when primates fight. Thus, the "scrotum-grasp" can be understood as a ritualized version of this fighting action. However, the "scrotum-grasp" is a formalized or more restricted form of the action (i.e., a momentary grasp rather than an aggressive grabbing and ripping). The act itself is undoubtedly attention-getting (it's hard to ignore someone handling your genitals); and it follows a rule-governed, relatively invariant sequence: one baboon strides up to another using a rapid, straight-legged gait. As he approaches, he looks directly at the other baboon making affiliative gestures, such as lip-smacking, flattening back of the ears, and narrowing of the eyes. The other responds in like fashion, and then after a quick hug they each present their hindquarters and the fondling begins.

As highly social animals, it is not surprising that primates have an extensive array of social rituals designed to build trust, promote group harmony, and reinforce social relations (Goodall 1986; van Roosmalen and Klein 1988: 515). For example, when bonobo, chimpanzee, and spider monkey foraging groups reunite, they engage in a number of rituals of welcoming and social reaffirmation, such as mutual embracing, kissing, group pant-hooting, and grooming. Among chimpanzees, reconciliation between combatants is signaled by bowing and begging gestures (on the part of the loser) followed by kissing and embracing (by the winner; de Waal 1990).

The wealth of social rituals present among our primate cousins indicates that our hominin ancestors were preadapted for using ritualized behavior as a means of regulating their social lives. Thus, faced with the challenge of constructing and managing larger and more complex social groups, and communicating carefully and effectively to suspicious out-group members, our ancestors would have naturally turned to rituals, very likely extending and elaborating on their use as demanded by circumstances.

Among traditional societies, social rituals are often physically and mentally demanding, requiring great behavioral discipline and cognitive control. They frequently require one to inhibit reflexive, prepotent responses in order to show commitment to group norms or a willingness to adhere to rules of reciprocity (for a more in-depth discussion, see Rossano 2009). Looking across a number of traditional societies, three types of social rituals are commonly used for establishing and maintaining intra- and inter-group trust and cohesion. These ritual types are (1) rituals of trust-building and reconciliation, (2) rituals of initiation, and (3) shamanistic healing rituals. While detailed discussion of these ritual types is beyond the scope of the current article (see Rossano 2009), an example or two from each category is enough to make the point that these rituals are acutely taxing on executive functions, especially working memory and cognitive control.

Rituals of Trust-Building and Reconciliation A truce among the Amazonian Yanamamo can only be achieved after warriors show they can resist the taunts, threats, insults, and brandished weapons of their rivals (Chagnon 1968). Disputes among the Ammassalik of Greenland are often addressed using a traditional "drum match," where the aggrieved parties face each other and drum and sing about how the other has injured them and about the other's many personal and familial faults (Mirsky 1937). Tradition dictates that the listener remains frustratingly indifferent to the singer's derisions and accusations. In our ancestral past, those best able to successfully complete these rituals would have very likely achieved a fitness advantage by virtue of greater inclusion in intra- and inter-group resource exchange networks.

Rituals of Initiation Adolescent rites of passage occur in over 70% of traditional societies (Lutkehaus and Roscoe 1995; Alcorta 2006). Rites of initiation common among traditional people often require the initiate (both males and females) to endure isolation, deprivation, intimidation, psychological stress, and physical pain resulting from tooth removal, scarring, genital cutting, exhaustive dancing, and other forms of "hazing" (Catlin 1867; Whitehouse 1996; Power 1998: 122–125; Glucklich 2001). Possibly the most dramatic of these initiations was the famous Mandan Indian Sun Dance ceremony where young males were suspended from the top beam of a large ceremonial enclosure with ropes attached to skewers embedded in their chests (Catlin 1867). They might remain there for hours or days as dancing and chanting went on below them. Successful completion of rigorous initiation rituals would have offered a fitness advantage through group acceptance and enhanced social status.

Shamanistic Healing Rituals The ubiquity of shamanistic practices among traditional societies coupled with possible evidence of shamanism in the archaeological record suggest that it is humanity's oldest form of religion, possibly predating the Upper Paleolithic (Winkelman 1990, 2002; Guenther 1999; Townsend 1999; Vitebsky 2000; Lewis-Williams 2002; Hayden 2003). Central to shamanism is the use of ritual to achieve an altered state of consciousness, wherein spirits are encountered and healing energy is directed. For example, the Kalahari !Kung conduct "healing dances" about every two weeks, where shaman healers dance about frenetically, laying hands on and transmitting healing power to all present. These dances are considered essential to the health and vitality of the !Kung, both individually and as a community (Katz 1982). It is not hard to imagine our late Pleistocene ancestors engaging in similar rituals around a blazing campfire. Recent neuroscience evidence confirms that ritualized meditative practices, such as those common in shamanism, activate areas of the brain critical to focused attention and working memory, including the dorsolateral prefrontal cortex (DLPFC) and the anterior cingulate cortex (ACC) (see Rossano 2007 for discussion). Furthermore, in our ancestral past, those most capable of achieving altered states would very likely have gained a fitness advantage in the form of psychophysical healing effects (McClenon 2002; Rossano 2007).

The critical point about these social rituals is that they would have placed great demands on the ability to inhibit prepotent responses while maintaining mental focus on the need to complete the ritual in order to achieve a highly valued social goal (e.g., acceptance in the group, an alliance between groups, connection to spiritual power, etc.). Cognitive neuroscience research shows that this ability taxes two parts of the brain integral to executive functions and working memory—the dorsolateral prefrontal cortex and anterior cingulate cortex (Beauregard et al. 2001; Cunningham et al. 2004; Hester et al. 2004; Kelly et al. 2006). Furthermore, increased working memory capacity allows for greater cognitive resources to be dedicated to conscious inhibitory processes (Kelly et al. 2006). This suggests that in our ancestral past, those with greater working memory capacity would have had an advantage over others in their ability to successfully complete demanding social rituals. This in turn would have translated into fitness benefits.

Baby Rituals Ritualized behavior connects the development of effortful control in infants and children with the demands of adult social life. Mother–infant joint engagement is, in fact, an early form of social ritual that presages later adult rituals. All the elements of ritual—attention-getting, formalization, rule-governance, invariant sequencing—are found in the earliest bouts of joint engagement between infants and their caregivers, engagements pivotal to the development of social/cognitive skills.

Attention-getting Human infants are designed to attract and hold the attention of their adult caregivers using imitation.

Infants less than an hour old imitate facial expressions, such as tongue protrusion, mouth opening, and eye blinking (Meltzoff and Moore 1977; Field et al. 1982; Kugiumutzakis 1988). The creative and effortful nature of these imitative behaviors indicate that they are more than just reflexive; they are provocative—specifically intended to attract and engage adults in social interactions (Nagy and Molnar 2004; see also Reddy 2008: 52–55). As children get older, "showing off" and "teasing" join imitation as mechanisms for attracting attention and initiating social exchanges (Reddy 2008: 136–140, 211–214).

Invariant sequencing Evidence for neonatal imitation is present in other primates (Myowa-Yamakoshi et al. 2004; Ferrari et al. 2006). By two or three months of age, however, human infants demonstrate a range of social competencies that surpass their primate cousins. Chief among these is the ability to engage in extended "back and forth" reciprocal social exchanges with adult caregivers. These exchanges follow a strict sequence (Tronick et al. 1979):

1. Initiation—where either participant engages the attention of the other.
2. Mutual orientation—where the infant's initial excitement calms and mother's vocalizations become soothing.
3. Greeting—characterized by the infant smiling, moving his/her limbs, and mother becoming more animated.
4. Play dialogue—where mother and infant take turns exchanging sounds and gestures. This turn-taking has been called "protoconversation" because it follows the same social conventions as adult vocal conversation (Keller et al. 1988).

Rule-governance It is in protoconversation that the third aspect of ritual, rule-governance, is apparent. Infants seem to innately understand the rules of taking turns in social interaction and become distressed when they are violated. Experiments with the "still face" provide evidence of this (Tronick et al. 1978; Ross and Lollis 1987; Tronick 2003; see also Reddy 2008: 72–77). In these experiments, after some protoconversation with their infants, mothers unexpectedly become unresponsive, offering an emotionally neutral face. The effect is dramatic. The infant will often look away, then attempt to re-engage mother with a wary smile. For a time the infant alternates looking away with glances back at mother to see if she "snaps out of it." Eventually the infant gives up, disengaging entirely. The still-face is distressing to the infant both because of mom's unexpected unresponsiveness and because it violates conversational rules.

Formalization The fourth element of ritual, formalization, is easily seen when protoconversations expand into social games, the most well known of which is peek-a-boo. The peek-a-boo gestures are restricted forms of the actions they represent. One does not actually hide the face in peek-a-boo, but represents it by just placing the hands over the eyes.

Thus, well before a child's second birthday, he or she has had considerable experience with ritualized social interactions. In fact, these are the primary means by which the infant enters into the human social world, and it is from within that world that social/cognitive development proceeds.

Ritual and Effortful Control

Ritual's role in development matches to a great extent the role it plays in adulthood—that of providing a framework that promotes self-regulation. It does this in at least two ways. First, early social rituals create a context for interpreting the intentions behind actions. Within the context of peek-a-boo, for example, what otherwise might be frightening (pushing one's face at an infant and saying "boo") becomes playfully arousing (Bruner 1975). The ritualized nature of the game creates a security and predictability that helps youngsters constructively regulate defensive reactions—an integral element of effortful control.

Second, early social rituals further encourage emotional self-regulation through social referencing. Social referencing is when infants and children use adult caregivers as anchors for their own emotional states. Mother–infant social turn-taking involves eye-to-eye gazing during which the infant harmonizes his/her emotional state with that of mom. If mom smiles, the infant responds with joyful expressions. If mom is sullen, the infant reduces its activity and becomes more subdued. It is through this social/emotional referencing that infants learn to regulate their emotional states so that they can participate in increasingly extended and attentionally demanding social interactions. Furthermore, this emotional regulation is critical in dealing with novelty, allowing them to explore new environments and situations without becoming unnecessarily defensive and fearful—another critical aspect of effortful control (Haviland and Lelwica 1987; Hobson 2004: 37).

There is evidence that mothers vary in their ability to successfully engage in extended bouts of joint engagement with their infants. Mothers with a history of greater sensitivity to their infant's emotional state and to the rules that govern social interaction are more successful at re-engaging their infants after the still-face disruption. These more "ritually capable" mothers engage their infants in longer, more productive, and more satisfying social exchanges. Caregivers who are too directing or controlling actually impair the social/cognitive development of their infants (Tomasello 1988; Trevarthen and Aitken 1994; Kogan and Carter 1996). Just as it does today, variance in mother's ritual competence would have had important implications for the social/cognitive development of infants in our ancestral past.

By way of summary, the connection between ritual in development and adulthood can be stated thusly: In infancy

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and childhood, ritual *facilitates* the development of effortful control and working memory. In adulthood, ritual *requires* effortful control and working memory. In our ancestral past, the youngsters who more effectively participated in ritualized social interactions during the course of their development grew into adults more capable of engaging in ritual and reaping the fitness advantages it offered.

Gene-Culture Coevolution and Rapid Evolutionary Change

There is yet another reason to focus on the development of effortful control as a key evolutionary factor behind the emergence of modern cognition—it is a prime candidate for the rapid evolutionary changes associated with gene-culture coevolution. There is considerable evidence that humans have undergone recent rapid evolutionary changes. For example, Pollard et al. (2006) identified over 200 sites in the human genome where rapid evolutionary change has been ongoing over the course of human evolution (called human accelerated regions, or HARs). These regions are highly conserved in other species, suggesting that strong selection pressure against evolutionary changes was reversed in our hominin ancestors. The five HARs showing the greatest change have up to seven times more substitutions relative to analogous sites in chimpanzees. Other genetic evidence indicates that the most recent 40,000 years of hominin evolution have seen a one to two orders of magnitude increase in the rate of adaptive mutations, and a 100 times increase since the Neolithic (Hawks et al. 2007). Finally, uniquely human variants of two genes important in regulating brain growth—microcephalin (MCPH1) and abnormal spindle-like microcephaly (ASPM)—have arisen in just the past 40,000 and 6000 years respectively (Evans et al. 2005; Mekel-Bobrov et al. 2005).

Earlier, evidence was presented indicating that the most significant factors distinguishing our ancestors from other hominins were social/cultural. Culture can produce rapid evolutionary changes. For example, the emergence of dairying in the last 10,000 years created a potent selective advantage for those adults capable of metabolizing milk sugar. Today, the allele responsible for this can be found in up to 90% of the population of some European countries. However, DNA analysis of Neolithic skeletons shows that as recently as 6000 years ago this allele was nearly absent in the European population. This genetic change has then occurred rapidly within only the last few thousand years (Burger et al. 2007). This provides a powerful example of where a human-created cultural selection pressure produced a very quick evolutionary change. Archeological evidence suggests that the emergence of enhanced working memory, and with it modern cognition, was also a relatively late and rapid evolutionary change (Coolidge and Wynn 2009: 222–236, 244–245).

Effortful control has a strong genetic basis and is subject to significant gene–environment interaction effects. Repeated studies comparing effortful control in monozygotic (MZ) versus dizygotic (DZ) twins have consistently found higher MZ correlations with heritability factors ranging from roughly 30% to 80% (Goldsmith et al. 1997; Gagne and Saudino 2005; Yamagata et al. 2005; Lemery-Chalfant et al. 2008; see review in Gagne et al. 2009). A particular gene, D4 receptor (DRD4), appears to play a key role in the development of effortful control in humans (Fan et al. 2001). This gene is important in the expression of dopamine in the ACC and is vital in many processes associated with executive attention. There is also evidence that this gene has been under recent positive selection pressure (Ding et al. 2002).

Genetic inheritance alone, however, is only partially responsible for one's phenotypic expression of effortful control. As discussed earlier, domestic stability and parenting styles have significant effects on the development of effortful control. At the same time, however, a child's pre-existing level of effortful control serves to mediate the degree to which the home environment produces positive or negative behavioral outcomes. For example, children high in effortful control have been found to be significantly less at risk for externalizing and internalizing problems despite exposure to multiple contextual risk factors, such as neighborhood crime, lack of services, maternal depression or substance abuse, and household insecurity and stress (Lengua et al. 2006). All of this makes it highly plausible that cultural factors and inherited levels of effortful control coevolved and amplified each other, producing rapid changes. While social selection increasingly targeted effortful control, higher levels of effortful control in a population could in turn produce even more intense cultural selection pressure.

The Evolutionary Scenario

Evidence for trading networks in the form of beads and exotic microliths can be found as far back as 100,000–70,000 ybp, although dental-based evidence indicating greater longevity is closer to the Upper Paleolithic (about 35,000 ybp). This suggests a rough sequence in the social/cultural changes leading to modern cognition. The first important change exerting selection pressure on our hominin ancestors was the emergence of increasingly demanding social rituals. More demanding social rituals helped to create greater social complexity, including inter-group resource exchange networks. This in turn led to increased longevity, more adults in social groups, sex role specialization, and greater heterogeneity in resource procurement. These factors ultimately produced generally greater security and stability in the human evolutionary niche.

More demanding social rituals filtered humans for greater working memory capacity and cognitive control. Furthermore, more "ritually-capable" adults would have become parents (mothers mostly) better able to sustain extended, cognitively enriching bouts of joint engagement with their infants. Initially, however, opportunities for these encounters would have been limited. As human existence became increasingly stable and secure, these opportunities increased and selection pressure against greater increases in working memory and effortful control eased. These changes had the effect of opening up an ontogenetic pathway, whereby mothers with greater skill at joint engagement and infants with greater capacity to benefit from those engagements could work together to expand effortful control abilities in developing children. As children with ever-increasing abilities in effortful control grew into adults, ritual behavior could become increasingly demanding, thus intensifying ritual selection pressure for greater executive control and working memory. Ultimately, it was this feedback loop between adult social rituals and ritualized mother–infant joint engagements that produced both modern cognition and the extreme forms of social rituals often seen in traditional societies.

Testing the Model

An advantage of the model being proposed is that a number of testable hypotheses flow from it. Many of these hypotheses have been discussed in more detail in another publication (Rossano 2009), and only a few brief examples will be presented here. Archeologically, the current model predicts a necessary link between evidence of social complexity and modern cognition. Where we find archeological evidence of modern cognition—image-making, elaborate burials, rapid innovation—we should also find evidence of social complexity (e.g., trading networks; larger, spatially structured settlement sites). If, for example, evidence of modern cognition was found among Neanderthals without comparable evidence of social complexity, then this would be damaging and potentially falsifying to the current model. Psychologically, this model would predict that ritual behavior facilitates cognitive control, especially under stressful conditions. Already, evidence of this link can be found in athletic competition, where ritualizing certain behavior patterns (such as a basketball player's free throw routine) often facilitates performance (see Rossano 2009 for examples).

References

Adler DS, Bar-Oz G, Belfer-Cohen A, Bar-Yosef O (2006) Ahead of the game: Middle and Upper Paleolithic hunting behaviors in the Southern Caucasus. Current Anthropology 47: 89–118.

Alcorta CS (2006) Religion and the life course: Is adolescence an "experience expectant" period for religious transmission? In: Where God and Science Meet, Vol. 2 (McNamara P, ed), 55–79. Bridgeport, CT: Praeger.

Ambrose SH (2002) Small things remembered: Origins of early microlithic industries in Subsaharan Africa. In: Thinking Small: Global Perspectives on Microlithic Technologies (Elston R, Kuhn S, eds), 9–29. Archaeological papers of the American Anthropological Association #12. Arlington, VA: American Anthropological Association.

Baldwin D (1991) Infants' contribution to the achievement of joint reference. Child Development 62: 875–890.

Bar-Yosef O (2002) The upper paleolithic revolution. Annual Review of Anthropology 31: 363–393.

Beauregard M, Levesque J, Bourgouin P (2001) Neurocorrelates of conscious self-regulation of emotion. Journal of Neuroscience 21(RC 165): 1–6.

Bell C (1997) Ritual: Perspectives and Dimensions. Oxford: Oxford University Press.

Berger TD, Trinkaus E (1995) Patterns of trauma among the Neandertals. Journal of Archaeological Science 22: 841–852.

Bigelow AE, MacLean K, Proctor J (2004) The role of joint attention in the development of infants' play with objects. Developmental Science 7: 518–526.

Blurton Jones N (2002) The lives of hunter-gatherer children: Effects of parental behavior and parental reproductive strategy. In: Juvenile Primates: Life history, Development, and Behavior (Pereira ME, Fairbanks LA, eds), 309–326. Chicago, IL: University of Chicago Press.

Botvinick MM, Nystrom LE, Fissell K, Carter CS, Cohen JD (1999) Conflict monitoring versus selection-for-action in anterior cingulate cortex. Nature 402: 179–181.

Boucherens H, Billiou D, Mariotti A, Toussaint M, Patou-Mathis M, Bonjean D, Otte M (2001) New isotopic evidence for dietary habits of Neandertals from Belgium. Journal of Human Evolution 40: 497–506.

Boucherens H, Drucker DG, Billiou D, Patou-Mathis M, Vandermeersch B (2005) Isotopic evidence for diet and subsistence pattern of the Saint-Cesaire I Neanderthal: Review and use of multi-source mixing model. Journal of Human Evolution 49: 71–87.

Bruner JS (1975) The ontogenesis of speech acts. Journal of Child Language 2: 1–19.

Burger J, Kirchner M, Bramanti B, Haak W, Thomas M G (2007) Absence of the lactase-persistence-associated allele in early Neolithic Europeans. Proceedings of the National Academy of Sciences of the USA 104: 3736–3741.

Casey BJ, Durston S, Fossella JA (2001) Evidence for a mechanistic model of cognitive control. Clinical Neuroscience Research 1: 267–282.

Caspari R, Lee SL (2004) Older age becomes common late in human evolution. Proceedings of the National Academy of Sciences of the USA 101: 10895–10900.

Catlin G (1867) O-kee-pa: A Religious Ceremony and Other Customs of the Mandans. London: Trubner.

Chagnon N (1968) Yanamamo: The Fierce People. New York: Holt, Rinehart.

Churchill SE (1993) Weapon technology, prey size selection, and hunting methods in modern hunter-gatherers: Implications for hunting in the Palaeolithic and Mesolithic. In: Hunting and Animal Exploitation in the Later Palaeolithic and Mesolithic of Eurasia (Peterkin GL, Bricker HM, Mellars PA, eds), 11–24. Archeological Papers of the American Anthropological Association #4. Arlington, VA: American Anthropological Association.

Coolidge FL, Wynn T (2001) Executive functions of the frontal lobes and the evolutionary ascendancy of *Homo sapiens*. Cambridge Archaeological Journal 11: 255–260.

Coolidge FL, Wynn T (2005) Working memory, its executive functions, and the emergence of modern thinking. Cambridge Archaeological Journal 15: 5–26.

Coolidge FL, Wynn T (2009) The Rise of *Homo Sapiens*: The Evolution of Modern Thinking. New York: Wiley.

Cunningham WA, Johnson MK, Raye CL, Gatenby JC, Gore JC, Banaji M (2004) Separable neural components in the processing of Black and White faces. Psychological Science 15: 806–813.

Curtis CE, D'Esposito M (2003) Persistent activity in the prefrontal cortex during working memory. Trends in Cognitive Science 7: 415–423.

D'Errico F, Henshilwood C, Lawson G, Vanhaeren M, Tillier A-M, Soressi M, Bresson F, Maureille B, Nowell A, Lakarra J, Backwell L, Julien M (2003) Archaeological evidence for the emergence of language, symbolism, and music: An alternative multidisciplinary perspective. Journal of World Prehistory 17: 1–70.

D'Esposito G, Kirkby BS, van Horn JD, Ellmore TM, Berman KF (1999) Context-dependent, neural system-specific neurophysiological concomitants of ageing: Mapping PET correlates during cognitive activation. Brain 122: 963–979.

Dickson BD (1990) The Dawn of Belief. Tucson, AZ: University of Arizona Press.

Ding YC, Chi HC, Grady DL, Morishima A, Kidd JR, Kidd KK, et al. (2002) Evidence of positive selection acting at the human dopamine receptor D4 gene locus. Proceedings of the National Academy of Sciences of the USA 99: 309–314.

Defleur A, Dutour O, Valladas H, Vandermeersch V (1993) Cannibals among the Neanderthals. Nature 362: 214.

Defleur A, White T, Valensi P, Slimak L, Cregut-Bonnoure E (1999) Neanderthal cannibalism at Moula-Guercy, Ardeche, France. Science 286: 128–131.

de Waal FBM (1990) Peacemaking among Primates.Cambridge, MA: Harvard University Press.

Duncan J, Seitz RJ, Kolodny J, Bor D, Herzog H, Ahmed, A, Newell FN, Emslie H (2000) A neural basis for general intelligence. Science 289: 457–460.

Eiden RD, Leonard KE, Morrisey S (2001) Paternal alcoholism and toddler noncompliance. Alcoholism: Clinical and Experimental Research 25: 1621–1633.

Eisenberg N, Cumberland D, Spinrad TL, Fabes RA, Shepard SA, Reiser M, et al. (2001) The relations of regulation and emotionality to children's externalizing and internalizing problem behavior. Child Development 72: 1112–1134.

Evans PD, Gilbert SL, Mekel-Bobrov N, Vallender EJ, Anderson JR, Vaez-Azizi LM, Tishkoff SA, Hudson RR, Lahn BT (2005) Microcephalin, a gene regulating brain size, continues to evolve adaptively in humans. Science 309: 1717–1720.

Fan J, Wu Y, Fossella J, Posner MI (2001) Assessing the heritability of attentional networks. BioMed Central Neuroscience 2: 14.

Farah MJ, Shera DM, Savage JH, Betancourt L, Giannetta JM, Brodsky NL, Malmud EK, Hurt H (2006) Childhood poverty: Specific associations with neurocognitive development. Brain Research 110: 166–174.

Feblot-Augustins J (1999) Raw material transport patterns and settlement systems in the European lower and middle Paleolithic: Continuity, change, and variability. In: The Middle Paleolithic Occupation of Europe (Roebroeks W, Gamble C, eds), 193–214. Leiden, Netherlands: University of Leiden Press.

Ferrari PF, Visalberghi E, Paukner A, Fogassi L, Ruggiero A, Suomi, SJ (2006) Neonatal imitation in rhesus macaques. PLOS Biology 4: e302.

Field TM, Woodson R, Greenberg R, Cohen D, (1982) Discrimination and imitation of facial expressions by neonates. Science 218: 179–181.

Fonagy P, Target M (2002) Early intervention and the development of self-regulation. Psychoanalytic Quarterly 22: 307–335.

Gagne JR, Saudino KJ (2005) A behavioral genetic analysis of inhibitory control at 24 months of age. Behavior Genetics 35: 801.

Gagne JR, Vendlinski MK, Goldsmith HH (2009) The genetics of childhood temperament. In: Handbook of Behavior Genetics (Kim Y-K, ed), 251–267. New York: Springer.

Gamble C (1999) The Upper Paleolithic Societies of Europe. Cambridge, UK: Cambridge University Press.

Glucklich A (2001) Sacred Pain. New York: Oxford University Press.

Goldsmith HH, Buss KA, Lemery KS (1997) Toddler and childhood temperament: Expanded content, stronger genetic evidence, new evidence for the importance of environment. Developmental Psychology 33: 891–905.

Goodall J (1986) The Chimpanzees of Gombe. Cambridge, MA: Harvard University Press.

Grayson DK, Delpech F (2003) Ungulates and the middle-to-upper Paleolithic transition at Grotte, XVI (Dordogne, France). Journal of Archaeological Science 30: 1633–1648.

Guenther, M. (1999). From totemism to shamanism: Hunter–gatherer contributions to world mythology and spirituality. In: Cambridge Encyclopedia of Hunters and Gatherers (Lee RB, Daly R, eds), 426–433. Cambridge, UK: Cambridge University Press.

Haviland JM, Lelwica M (1987) The induced affect response: 10-week-old infants' responses to three emotional expressions. Developmental Psychology 23: 97–104.

Hawks J, Wang ET, Cochran GM, Harpending HC, Moyzis RK (2007) Recent acceleration of human adaptive evolution. Proceedings of the National Academy of Sciences of the USA 104: 20753–20758.

Hayden B (2003) Shamans, Sorcerers and Saints: A Prehistory of Religion. Washington, DC: Smithsonian Institution Books.

Henshilwood CF (2007) Fully symbolic sapiens behaviour: Innovation in the Middle Stone Age at Blombos Cave, South Africa. In: Rethinking the Human Revolution (Mellars P, Boyle K, Bar-Yosef O, Stringer C, eds), 123–132. Cambridge, UK: McDonald Institute for Archaeological Research.

Hester R, Murphy K, Garavan H. (2004) Beyond common resources: The cortical basis for resolving task interference. NeuroImage 23: 202–212.

Hobson P (2004) The Cradle of Thought. Oxford, UK: Oxford University Press.

Hoffecker JF (2002) Desolate Landscapes: Ice-Age Settlement in Europe. New Brunswick, NJ: Rutgers University Press.

Ingvar DH (1994) The will of the brain: Cerebral correlates of willful acts. Journal of Theoretical Biology 171: 7–12.

Kane MJ, Engle RW (2002) The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. Psychonomic Bulletin & Review 9: 637–71.

Karreman A, van Tuijl C, van Aken MAG, Dekovic M (2006) Parenting and self-regulation in preschoolers: A meta-analysis. Infant and Child Development 15: 561–579.

Katz R (1982) Boiling Energy: Community Healing Among the Kalahari !Kung. Cambridge, MA: Harvard University Press.

Keller H, Scholmerich A, Eibl-Eibesfeldt I (1988) Communication patterns in adult–infant interactions in western and non-western cultures. Journal of Cross-Cultural Psychology 19: 427–445.

Kelly AM, Hester R, Foxe JJ, Shpaner M, Garavan H (2006) Flexible cognitive control: Effects of individual differences and brief practice on a complex cognitive task. NeuroImage 31: 866–886.

Klein RG, Edgar B (2002) The Dawn of Human Culture. New York: John Wiley.

Kogan N, Carter AS (1996) Mother–infant re-engagement following the still-face: The role of maternal availability in infant affect regulation. Infant Behavior and Development 19: 359–370.

Kugiumutzakis G (1988). Neonatal imitation in the intersubjective companion space. In: Intersubjective Communication and Emotion in Early Ontogeny (Braten S, ed), 63–88. Cambridge, UK: Cambridge University Press.

Kuhn SL, Stiner MC (2006) What's a mother to do? The division of labor among Neandertals and humans in Eurasia. Current Anthropology 42: 953–980.

Kuhn SL, Stiner MC (2007) Body ornamentation as information technology: Towards an understanding of the significance of early beads. In: Rethinking the Human Revolution (Mellars P, Boyle K, Bar-Yosef O, Stringer C, eds), 45–54. Cambridge, UK: McDonald Institute for Archaeological Research.

Langley MC, Clarkson C, Ulm S (2008) Behavioural complexity in Eurasian Neanderthal populations: A chronological examination of the archaeological evidence. Cambridge Archaeological Journal 18: 289–307.

Lemery-Chalfant K, Doelger L, Goldsmith HH (2008) Genetic relations between effortful and attentional control and symptoms of pathology in middle childhood. Infant and Child Development 17: 365–427.

Lengua, LJ (2003) Associations among emotionality, self-regulation, adjustment problems and positive adjustment in middle childhood. Journal of Applied Developmental Psychology 24: 595–618.

Lengua LJ, Bush NR, Long AC, Kovacs EA, Trancik AM (2008) Effortful control as a moderator of the relation between contextual risk factors and growth in adjustment problems. Development and Psychopathology 20: 509–528.

Lengua LJ, Honorado E, Bush N (2007) Cumulative risk and parenting as predictors of effortful control and social competence in preschool children. Journal of Applied Developmental Psychology 28: 40–55.

Lewis-Williams D (2002) The Mind in the Cave. London: Thames & Hudson.

Lieberman DE, Devlin M, Pearson OM (2001) Articular surface area responses to mechanical loading: Effects of exercise, age, and skeletal location. American Journal of Physical Anthropology 116: 266–277.

Lieberman DE, Pearson OM (2001) Trade-off between modeling and remodeling responses to loading in the mammalian limb. Bulletin of the Museum of Comparative Zoology 156: 269–282.

Lutkehaus NC, Roscoe PB (1995) Gender Rituals: Female Initiation in Melanesia. London: Routledge.

Marean CW (2007) Heading north: An Africanist perspective on the replacement of Neanderthals by Modern humans. In: Rethinking the Human Revolution (Mellars P, Boyle K, Bar-Yosef O, Stringer C, eds), 367–379. Cambridge, UK: McDonald Institute for Archaeological Research.

Marquet J-C, Lorblanchet M (2003) A Neanderthal face? The proto-figurine from La Roche-Cotard, Langeais (Indre-et-Loire, France). Antiquity 77: 661–670.

McClenon J (2002) Wondrous Healing: Shamanism, Human Evolution and the Origin of Religion. DeKalb, IL: Northern Illinois University Press.

McDonald KB (2008) Effortful control, explicit processing and the regulation of human evolved predispositions. Psychological Review 115: 1012–1031.

McDougall I, Brown FH, Fleagle JG (2005) Stratigraphic placement and age of modern humans from Kibish, Ethiopia. Nature 433: 733–736.

Mekel-Bobrov N, Gilbert SL, Evans PD, Vallender EJ, Anderson JR, Hudson RR, et al. (2005) Ongoing adaptive evolution of ASPM, a brain size determinant in *Homo sapiens*. Science 309: 1720–1722.

Mellars P (1996) The Neanderthal Legacy. Princeton, NJ: Princeton University Press.

Meltzoff AN, Moore MK (1977) Imitation of facial and manual gestures by human neonates. Science 198: 75–78.

Mirsky J (1937) The Eskimo of Greenland. In: Cooperation and Competition Among Primitive Peoples (Mead M, ed.), 51–86. New York: McGraw-Hill.

Moll H, Carpenter M, Tomasello M (2007) Fourteen-month olds know what others experience only in joint engagement with them. Developmental Science 10: 826–835.

Myowa-Yamakoshi M, Tomonaga M, Tanaka M, Matsuzawa T (2004) Imitation in neonatal chimpanzees (*Pan troglodytes*). Developmental Science 7: 437–442.

Nagy E, Molnar P (2004) Homo imitans or homo provocans? The phenomenon of neonatal imitation. Infant Behavior and Development 27: 57–63.

Noble KG, McCandiliss BD, Farah MJ (2007) Socioeconomic gradients predict individual differences in neurocognitive abilities. Developmental Science 10: 464–480.

Pollard KS, Salama SR, King B, Kern AD, Dreszer T, Katzman S, Siepel A, Pedersen JS, Bejerano G, Baertsch R, Rosenbloom KR, Kent J, Haussler D (2006) Forces shaping the fastest evolving regions in the human genome. PLoS Genetics 2(10): e168. DOI: 10.1371/journal.pgen.0020168.

Posner MI, Fan J (2004) Attention as an organ system. In: Topics in Integrative Neuroscience: From Cells to Cognition (Pomerantz JR, Crair MC, eds), 31–61. Cambridge, UK: Cambridge University Press.

Power C (1998) Old wives' tales: The gossip hypothesis and the reliability of cheap signals. In: Approaches to the Evolution of Language: Social and Cognitive Bases (Hurford JR, Studdert- Kennedy M, Knight C, eds), 111–129. Cambridge, UK: Cambridge University Press.

Rappaport RA (1999) Ritual and Religion and the Making of Humanity. Cambridge, UK: Cambridge University Press.

Ratner HH, Foley MA, Gimpert M (2002) The role of collaborative planning in children's source monitoring errors and learning. Journal of Experimental Child Psychology 81: 44–73.

Reddy V (2008) How Infants Know Minds. Cambridge, MA: Harvard University Press.

Richeson JA, Baird AA, Gordon HL, Heatherton TF, Wyland CL, Trawalter S, Shelton JN (2003) An fMRI investigation of the impact of interracial contact on executive function. Nature Neuroscience 6: 133–1328.

Ross HS, Lollis SP (1987) Communication within infant social games. Developmental Psychology 23: 241–248.

Rossano MJ (2007) Did meditating make us human? Cambridge Archaeological Journal 17: 47–58.

Rossano MJ (2009) Ritual behavior and the origins of modern cognition. Cambridge Archaeological Journal 19: 243–256.

Rothbart MK, Ahadi SA, Evans DE (2000) Temperament and personality: Origins and outcomes. Journal of Personality and Social Psychology 78: 122–135.

Rothbart MK, Ahadi SA, Hershey KL (1994) Temperament and social behavior in childhood. Merrill–Palmer Quarterly 40: 21–39.

Rothbart MK, Rueda MR (2005) The development of effortful control. In: Developing Individuality in the Human Brain: A Tribute to Michael I. Posner (Mayr U, Awh E, Keele S, eds), 167–188. Washington, DC: American Psychological Association.

Shea J (1997) Middle Paleolithic spear point technology. In: Projectile Technology (Knecht H, ed), 79–106. New York: Plenum.

Smuts BB, Watanabe JM (1990) Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). International Journal of Primatology 11: 147–172.

Soffer O (1994) Ancestral lifeways in Eurasia—the Middle and Upper Paleolithic records. In: Origins of Anatomically Modern Humans (Nitecki M, Nitecki D, eds), 101–109. New York: Plenum.

Sorensen MV, Leonard WR (2001) Neandertal energetics and foraging efficiency. Journal of Human Evolution 40: 483–495.

Stiner, MC (1991) The faunal remains at Grotta Guattari: A taphonomic perspective. Current Anthropology 32: 103–117.

Striano T, Kopp F, Grossman T, Reid VM (2006). Eye contact influences neuralprocessing of emotional expressions in 4-month-old infants. Social Cognitive and Affective Neuroscience 1: 87–94.

Stringer C, Gamble C (1993) In Search of the Neanderthals. London: Thames & Hudson.

Trevarthen C, Aitken KJ (1994) Brain development, infant communication and empathy disorders: Intrinsic factors in child mental health. Development and Psychopathology 6: 599–635.

Trinkaus E, Thompson DD (1987) Femoral diaphyseal histomorphometric determination for the Shanidar 3, 4, 5, and 6 Neandertals and Neandertal longevity. American Journal of Physical Anthropology 72: 123–129.

Tomasello M (1988). The role of joint attentional processes in early language development. Language Sciences 10: 69–88.

Tomasello M, ;arrar MJ (1986) Joint attention and early language. Child Development 57: 1454–1463.

Tomasello M, Haberl K (2003) Understanding attention: 12- and 18-month olds know what's new for other persons. Developmental Psychology 39: 906–912.

Tomasello M, Todd J (1983). Joint attention and lexical acquisition style. First Language 4: 197–212.

Townsend JB (1999) Shamanism. In: Anthropology of Religion (Glazier, SD, ed), 429–469. Westport, CT: Praeger.

Tronick EZ (2003) Things still to be done on the still-face effect. Infancy 4: 475–482.

Tronick E, Als H, Adamson L (1979) The structure of face-to-face communicative interactions. In: Before Speech (Bullowa M, ed), 349–370. Cambridge, UK: Cambridge University Press.

Tronick E, Als H, Adamson L, Wise S, Brazelton TB (1978) The infant's response to entrapment between contradictory messages in face-to-face interaction. Journal of the American Academy of Child and Adolescent Psychiatry 17: 1–13.

Vanhaeren M, d'Errico F (2005) Grave goods from the Saint-Germain-la-Riverere burial: Evidence for social inequality in the upper Paleolithic. Journal of Anthropological Archaeology 24: 117–134.

Vanhaeren M, d'Errico F, Stringer C, James SL, Todd JA, Mienis, HK (2006) Middle Paleolithic shell beads in Israel and Algeria. Science 312: 1785–1788.

van Roosmalen MGM, Klein LL (1988) The spider monkeys, genus *Ateles.* In: Ecology and Behavior of Neotropic Primates (Mittermeier R, Rylands AB, Coimbra-Filho AF, da Fonesca GAB, eds), 445–537. Washington, DC: World Wildlife Fund.

Vitebsky P (2000) Shamanism. In: Indigenous Religions (Harvey G, ed), 55–67. London: Cassell.

Welch MC (2001) The prefrontal function and the development of the executive function in childhood. In: Handbook of Brain and Behavior in Human Development (Kalverboer AF, Gramsbergen A, eds), 767–790. Dordrecht, Netherlands: Kluwer Academic.

White TD, Asfaw B, DeGusta D, Tilbert H, Richards GD, Suwa G, Howell FC (2003). *Homo sapiens* from Middle Awash, Ethiopia. Nature 423: 742–747.

Whitehouse H (1996) Rites of terror: Emotion, metaphor and memory in Melanesian cults. Journal of the Royal Anthropological Institute 2: 703–715.

Whitham JC, Maestripieri D (2003) Primate rituals: The function of greetings between male guinea baboons. Ethology 109: 847–859.

Winkelman M (1990) Shamans and other "magico-religious" healers: A cross-cultural study of their origins, nature, and social transformation. Ethos, 18: 308–352.

Winkelman M (2002). Shamanism and cognitive evolution. Cambridge Archaeological Journal, 12: 71–101.

Wynn T, Coolidge FL (2003) The role of working memory in the evolution of managed foraging. Before Farming 2: 1–16.

Wynn T, Coolidge FL (2004) The expert Neanderthal mind. Journal of Human Evolution 46: 467–87.

Wynn T, Coolidge FL (2007) Did a small but significant enhancement in working memory capacity power the evolution of modern thinking? In: Rethinking the Human Revolution (Mellars P, Boyle K, Bar-Yosef O, Stringer C, eds), 79–90. Cambridge, UK: McDonald Institute for Archaeological Research.

Wynn T, Coolidge F, Bright M (2009) Hohlenstein-Stadel and the evolution of human conceptual thought. Cambridge Archaeological Journal 19: 73–83.

Yamagata S, Takahashi Y, Kijima Y, Mackawa H, Ono Y, Ando J (2005) Genetic and environmental etiology of effortful control. Twin Research and Human Genetics 8: 300–306.

Queries

AQ1: Author: Please confirm the change made in text citation as "Wynn and Coolidge (2003, 2004, 2007)."
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