Evolution of Religious Capacity in the Genus Homo

with Margaret Boone Rappaport and Christopher Corbally, "Evolution of Religious Capacity in the Genus Homo: Origins and Building Blocks"; Margaret Boone Rappaport and Christopher Corbally, "Evolution of Religious Capacity in the Genus Homo: Cognitive Time Sequence"; and Margaret Boone Rappaport and Christopher Corbally, "Evolution of Religious Capacity in the Genus Homo: Trait Complexity in Action through Compassion."

EVOLUTION OF RELIGIOUS CAPACITY IN THE GENUS HOMO: COGNITIVE TIME SEQUENCE

by Margaret Boone Rappaport and Christopher Corbally

Abstract. Intrigued by the possible paths that the evolution of religious capacity may have taken, the authors identify a series of six major building blocks that form a foundation for religious capacity in genus Homo. *Homo neanderthalensis* and *Homo sapiens idaltu* are examined for early signs of religious capacity. Then, after an exploration of human plasticity and why it is so important, the analysis leads to a final building block that characterizes only *Homo sapiens sapiens*, beginning 200,000–400,000 years ago, when all the other cognitive and neurological underpinnings gradually came together. Because the timing of cognitive evolution has become an issue, the authors identify the time periods for these building blocks based on findings from modern cognitive science, neuroscience, genomic science, the new cognitive archaeology, and traditional stones-and-bones archaeology. The result is a logical, and even a likely story 55–65 million years long, which leads to the evolution of religious capacity in modern human beings.

Keywords: aggression; ape; cognitive evolution; *Homo neanderthalensis*; HSP (highly sensitive person); moral capacity; parietal lobes; religious capacity; social tolerance; visuospatial reckoning

> [L]iving things appear to be designed to solve the problems confronting them in ways that are often ingenious, elegant and economical. . . . [A]n

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> evolutionary view of cognitive development leads one to expect the same economy and efficiency of design. . . .
> [W]hat is important is whether an adaptation reliably develops—i.e., the trait is reliably reproduced. . . . If this can be accomplished by exploiting the information structure of the environment, then there is reason to believe that natural selection would favor the use of such information. . . . A corollary of this view is that what often appears to be cognitive "flexibility" can, in fact, be the result of selection for developmental efficiency. Evolved mechanisms may be designed to tolerate some kinds of variation in developmental inputs. (Fiddick and Barrett 2001, 1–2)

This is the second in a series of three articles whose purpose is to describe the theoretical underpinnings for an evolutionary model of the biological emergence of religious capacity in the genus Homo. Once religious capacity is present, culture becomes fully involved in the further, biocultural evolution of religion in modern human beings, through cognitive feedback loops that we note here, and in the other articles of this series (Rappaport and Corbally 2018a, 2018c), and previously, in a model of *Homo erectus* as the first species with a rudimentary moral capacity (Rappaport and Corbally 2016, 2017).

We do not search for signs of religion in the archaeological record or in earlier species. Instead, we search for the evolutionary foundations for what became religious capacity on the human line. We concentrate on the timing of evolutionary "building blocks" that together constitute a foundation for religious capacity, because a central issue in cognitive evolution concerns timing (MacLean 2016). The first of our three articles (Rappaport and Corbally 2018a) fully defines the "building block."

Our underlying theme is that religious capacity has very ancient roots, and did not emerge suddenly or simply with a few genetic changes. It relied on evolutionary changes in many human biological systems, over many millions of years. Religious capacity remains one of our most elaborate, but one of the *least* uniformly expressed, phenotypic human traits. We infer from the work of Aida Gómez-Robles and Chet Sherwood (2016) that this lack of uniformity is, at least in part, the result of culture, including culture's shaping human cortical brain fold patterns (and other neurological structures). In humans, heritability is *low* for those patterns, although it is high in the chimpanzee, which emerged from the same ancestral ape population. Because of religious capacity's molding by strong cultural elements external to the individual, and because of the large number of brain capacities it likely draws upon, its phenotypic complexity is not unexpected. Religious capacity could be seen to challenge Laurence Fiddick and H. Clark Barrett's requirement for a "reliable" adaptation (2001; the leading quote for this article), because the trait is expressed variably and at a range of ages. In some children, religious capacity seems to begin showing itself around five or six years old, but in others it is expressed only in adulthood. In the case of religious capacity, "reliably produced" comes to imply a range of phenotypic expression, which Fiddick and Barrett suggest for human cognitive traits. For all these reasons, we saw the quotation we use from Fiddick and Barrett as especially relevant to this particular article.

Continuing our theme of variability in expression, this second article in the series (Rappaport and Corbally 2018b) discusses an important building block in religious capacity's foundation—plasticity—as a source of *phenotypic* variability in the genus Homo. When we delve into the research on plasticity, we see that plasticity is also a foundation for modern cognitive maturity, which flowers in late adolescence and early adulthood. It is difficult to imagine a species that was not very plastic evolving with religious capacity, because it is so variable in expression—variable, but again, reliably produced.

After examining plasticity in the genus Homo, key building blocks of our theoretical model are then identified, probed, and set in place, using findings from cognitive science, neuroscience, and genomic science. Added details from the article of the series, "Evolution of Religious Capacity in the Genus Homo: Origins and Building Blocks," are summarized briefly throughout. A third article in the series (Rappaport and Corbally 2018c) provides (1) an analysis of "compassion" using the temporal stages in our evolutionary model, (2) development of a theoretical approach to religious capacity using cultural neural reuse, and (3) a teaching tool in an example of "Religious Capacity in Action" in early *Homo sapiens*. This example frames religious capacity's phenotypic expression in our prehistoric past, and even now.

EARLIER BUILDING BLOCKS

Theoretical building blocks identified in the article of this series included a very ancient primate sociality, emerging 55–65 million years ago; and a basic ape model from a large and genetically variable population of Miocene apes, beginning around 19 million years ago, with the early ape Proconsul. From what flourished as a large, genetically diverse ape population throughout Eurasia, severely reduced populations of African apes and finally hominins emerged. Because the populations were small, we propose that both genetic drift and natural selection operated to create and limit genetic diversity. It will be important for our comprehension of the human line to see how genetic drift may have operated in small populations, to retain neutral and slightly deleterious genes.

From apes through early hominins to modern humans, there was a growing reliance on neurological plasticity, which was enabled by a steadily lengthening developmental trajectory, retention of paedomorphic traits in adulthood, and late cognitive development. The lineage of the genus Homo had increasingly large brains, higher protein diets of scavenged meat, and eventually intense social and emotional life, longevity, and morality with *Homo erectus* at 1–1.5 million years ago (Rappaport and Corbally 2016, 2017). We propose that religious capacity emerged with *Homo sapiens* 150,000 years ago (Bruner and Pearson 2013; Bruner et al. 2017), and give our reasons for this hypothesis below. We suggest, wherever possible, some of the types of genomic changes that may have supported evolutionary innovations undergirding religious capacity.

CLOSE, BUT NO CIGAR

Humans mature within an experiential learning environment where their brains respond to cultural input from their surroundings. Culture affects the way the brain develops, and the brain is ready for this input (Gómez-Robles and Sherwood 2016; Colagè 2015; Harris 2015). In the process, a very high level of human neurological plasticity becomes apparent. Not even our closest living relatives, the chimpanzees, have a brain structure molded quite so much by their environment; they show a high level of heritability in cortical organization. Humans are influenced morphologically by culture and have a lower level of heritability in cortical organization (Gómez-Robles and Sherwood 2016). Culture changes it. Culture fundamentally alters how our brains initially develop. There is evidence that the way our brains mature—specifically, the association areas—is related to a capacity for culture and level of intellect (Fjell et al. 2015). Plasticity, culture, and intellectual functioning are all bound together in human evolution, reflecting a single tendency to mature late and variably. Phenotypic variability is apparent especially in human religious thought and behavior, from one cultural group to another. The neurological foundation for highly variable phenotypic expression of religious capacity is firmly in place and has been for some time.

Still, the question remains: *When* did this difference evolve? When did humans become quite so "plastic" and when did religious capacity emerge? When did a biological substrate for culture flower and then engulf all of human sociality—a sociality that had already been present for perhaps fifty million years, functioning very nicely all by itself with no biological substrate for culture? We propose that at least some of the biological basis for culture has been present for 8–10 million years. This was the approximate time when we split from a population of ancient apes that would give rise to the chimpanzee line, which also shows culture, but weakly. Finally, *why* did plasticity, culture, and religious capacity expand on the human line, and were there important consequences of greater plasticity, late maturation, and increased intellect for the expression of religious capacity? Genomics scientist Svante Pääbo, of the Neanderthal Genome Project at the Max Planck Institute for Evolutionary Anthropology, in Germany, begins at the beginning, by discussing a colleague's work (Michael Tomasello 2010), and pointing to the human capacity called "theory of mind" as perhaps the first sign that a human baby is so very different from a chimpanzee baby of age one year. He writes,

> Mike has suggested that this compulsion to direct the attention of others is one of the first cognitive traits that emerge during childhood development that is truly unique to humans. . . . It is easy to imagine that the enormous human capacity for social activities, for manipulating others, for politics, and for concerted action . . . arise out of this ability to put oneself in another's shoes and manipulate that person's attention and interest . . . another potentially very important propensity that sets human children apart from ape youngsters: human children much more than apes, tend to imitate their parents . . . human children "ape" whereas apes do not "ape." (Pääbo 2015, 205–06)

We note the importance of comparing humans with our nearest living relatives, the chimpanzees, as others have done with thoughtful results (De Waal 2009). Still, chimpanzees are in another genus, Pan, while we are in the genus Homo. We now have a growing amount of information on relatives who are even closer to us, and in the genus Homo, although they are now extinct—the Neanderthals and Denisovans (another species of human found in Eurasia, probably a bit more closely related to Neanderthals than to modern humans). Neanderthals were living in Eurasia at the time that modern humans spread out of Africa to colonize this large area, and the world, 50,000–60,000 years ago. It is useful to remember that all these species are hominins who came from the same African roots, if one goes back far enough, at least 400,000 years ago, and probably closer to 800,000 years—a time when *Homo erectus* lived. Neanderthals and modern humans met again in Eurasia in prehistoric times, but the Neanderthals died out around 40,000 years ago (Roebroeks and Soressi 2016).

Only modern humans survived. *Why* remains an issue that continues to this day to be somewhat unsettled. There has been a prevailing view in the literature (and in the field) that Neanderthals were somehow "less advanced" than *Homo sapiens*, and scholars today are actively reexamining whether, how, and to what degree this was true, and how much of it is a result of bias. Nevertheless, the conclusion is, for us, inescapable that Neanderthals did not have and use a level of visuospatial cognition that modern humans did and do have. That type of cognition affected not only the extent of the species' home range, but also, because the same brain areas control aspects of religious thinking, the likelihood of the presence of full-fledged religious capacity, complete with theologies. We propose that Neanderthals did not have this level of visuospatial reckoning and religious capacity, but early *Homo sapiens* did. The differences between the two species of Homo appear cognitive, developmental, and physical. The research findings on Neanderthal ritual are still mixed, and we must await further work in archaeology and genomics, which hopefully answer questions about Neanderthal ritual once and for all.

Some of the findings on cognitive differences between modern humans and Neanderthals are found in their relative plasticity (Gómez-Robles and Sherwood 2016), and other findings point to the extent of physical range the two species could conceive and master (Wynn and Coolidge 2012). We understand that the mastery of physical home range is a facility guided in part by the more fully expanded parietal lobes in modern humans, and connections between parietals and prefrontal lobes. While Neanderthals had both types of brain lobes, their fossil skull shape does not suggest a parietal expansion from front to back, involving the precuneus, which we do see in *Homo sapiens* (Bruner and Iriki 2016; Bruner et al. 2017). Neanderthal parietals only expanded laterally, side to side. When we look for the eventual full flowering of religious capacity in *Homo sapiens*, we look to expansion of parietals, and more specifically, the precuneus.

Here, we focus on two main features that differ between modern humans and Neanderthals: (1) neurological plasticity, which is well on its way to being demonstrated by Gómez-Robles and Sherwood (2016), and (2) full religious capacity in *Homo sapiens* but not in Neanderthals, which we feel is the logical inference from Emiliano Bruner and colleagues' analysis of the shape of the modern human skull versus the Neanderthal skull (Bruner and Pearson 2013; Bruner and Iriki 2016; Bruner et al. 2017). The two species seem so close, but they remain so different. To us, this is not surprising because the lines that led to these two species of Homo diverged hundreds of thousands of years ago, in Africa. The two species met again in Eurasia, much later, and what we can learn about them can help us understand what makes modern humans unique. Each species is ultimately unique, but humans have special cognitive traits that they share with no other species.

Whether Neanderthals evidenced ritual, as in "purposeful burials," is still a topic that is much debated, although a recent study by Rendu et al. (2014), of a burial at La Chapelle-aux-Saints, concludes, "These discoveries attest the existence of West European Neanderthal burial and the Neanderthal cognitive capacity to produce it" (81). We conclude that Neanderthals did have a cognitive ability to conduct burials, but we ask: What about other early members of the genus Homo? Did they have ritual? Our view is that ritual may well have existed in *Homo erectus* and *Homo heidelbergensis.* With an experiential learning context we call the "human hearth" (Rappaport and Corbally 2016) and, with full-time terrestrial existence (Coolidge and Wynn 2009), these species had the right setting, the right demography, and perhaps the right biology for early ritual. Neanderthals may well have had, too. Yet, in spite of some, still ambiguous evidence for ritual burials in *Homo neanderthalensis*, we see no evidence of the flowering of theories about relationships between humans and the supernatural. No species leaves clear evidence for theologies, except *Homo sapiens*. Perhaps evidence will emerge in the future. Still, the shape of the Neanderthal skull remains less fully expanded in the parietal areas, and this makes us, like others, wonder if they had the brain architecture to develop theologies.

There does seem to have been some Neanderthal borrowing of culture from *Homo sapiens*, at least in Europe, but this is often difficult to demonstrate. There was indeed some interbreeding. It may seem counter-intuitive that Neanderthal contributions to the modern human genome might be advantageous; however, they just might be. Cochran and Harpending (2010) suggest that an admixture of DNA from Neanderthals may have provided benefits, just because it was new DNA in different context. It is never certain how DNA is going to be expressed in the genomic context of another species. We do know that the repositioning of DNA segments in various "neighborhoods" of the human genome, itself, can have profound effects on phenotypic expression. Neanderthal DNA in the human genome might have provided advantages, and at least it augmented human genetic diversity. In small populations, that might have been a boon!

Before we delve into genomic differences between modern humans and Neanderthals, we should mention the very oldest archaeological finds that could signal some type of cognitive religious capacity, from a site near Herto, in Ethiopia. The reader should keep in mind that the fossils may only signal ritual, and religious capacity encompasses more than that. However, given Hublin et al.'s (2017) recent finds in Morocco, which view *Homo sapiens* as emerging gradually all over Africa from an approximate 400,000-year time horizon, we feel the notion is solid that the fossils at Herto, at 160,000 years ago, show ritual behavior, and maybe more. The major contribution of Hublin et al.'s work to our model is that religious capacity may have emerged more gradually, just as did our species' parietal lobe expansion and its globular skull. Bruner et al. (2017) find the parietal lobes and globe-shaped skull strongly and definitely present at 150,000 years ago.

What exactly is the evidence from Herto? Hominin fossils and artifacts were found by Tim White of the University of California Berkeley, at a site named Herto, in present-day Ethiopia (White et al. 2003). The hominin fossils unearthed at Herto may show evidence of some kind of ritual, at 160,000 years ago. Recall that the oldest fossils attributed to modern humans had been (until Hublin et al.'s recent discoveries) from Omo, another Ethiopian site, dated to around 195,000 years ago, quite near *what had been* the benchmark emergence of *Homo sapiens* at 200,000 years ago. White reports that the skulls had cut marks indicating they had been de-fleshed, perhaps in some kind of mortuary practice. The polishing of the skulls and the type of cut marks suggest this was not cannibalism, but a kind of ritual behavior. Ethnographic research shows this practice in some New Guinea societies where the skulls of ancestors are worshipped.

White et al. (2003) named the Herto remains *Homo sapiens idaltu*, and so, a member of our genus and species, but a different subspecies.

This appears to be a careful decision based on a substantial number of measured differences between the fossil remains and modern bones, which were submitted to two multivariate techniques. The factor plot of Factor 1 and Factor 2 shows the Herto skulls falling outside the range of modern humans, outside the range of Neanderthals, and outside the range of that other, fully upright but more ancient hominin, *Homo erectus* (White et al. 2003, 746, b). A plot of the first three principal components finds the Herto skulls again falling outside the range of modern humans (White et al. 2003, 746, c). Yet, an artist's rendition of *Homo sapiens idaltu* looks like a man we might meet on any subway car. "He looks like a linebacker," a colleague suggested. He is very close to us, but he is not us.

The Pliocene and Pleistocene epochs were a time for hominin radiation, just as the Miocene was a period of ape radiation (Rappaport and Corbally 2018a, 126, table 2). A variety of different hominin forms emerged. One should interpret neither period of radiation as "trying out new and different models," although it seems appealing. A better way to describe the process is that a successful model had evolved and was beginning to stabilize, and the question remained: Which refinements were most successful . . . or the luckiest? The process is random, until just about this point in human evolution. At the juncture where culture engulfs social life, where moral and religious capacities emerge and are used to support the social group, humans become actors in their own evolution. Cognition changes and feeds into the evolutionary process, in a feedback loop.

CONTROLLED COMPARISON

Because the fossil evidence is so sparse for our genus and species, one way to approach our questions about when, how, and why religious capacity evolved is to examine the fossil, cultural, and genomic evidence left by a related species that is closer than chimpanzees to modern humans, *Homo neanderthalensis*, our extinct relative. There is much we share with the Neanderthals, so it is useful to examine cultural differences and the small portion of our genome that is different. It is especially important to examine differences in regulatory genes, as well as protein-coding genes, of the two species of the genus Homo. We ask: If we compare humans with extinct Neanderthals, especially in areas relating to their cognition, could we get a better understanding of when humans became so very "plastic," so expert in manipulating culture, and when human religious capacity may have emerged?

The debate concerning the complexity of Neanderthal culture and cognition—including whether there are Neanderthal burials—has not abated (Rendu et al. 2014; Roebroeks and Soressi 2016). Neanderthals are now spoken of as our "sister lineage" that is being studied back into the Middle Pleistocene, and geographically, in places other than Europe

(Roebroeks and Soressi 2016). Still, the split with Neanderthals occurred much longer ago than once thought, so there has been considerable time for genetic differences on the two lines to accrue. A summary of the cultural, demographic, health, and genetic reasons for the Neanderthal extinction includes a wide variety of factors:

> [T]he Neanderthal demise appears to have resulted from a complex and protracted process including multiple factors such as low Neanderthal population density, interbreeding with some cultural contact, possible male hybrid sterility, and contraction in geographic distribution, followed by genetic swamping and assimilation by modern human immigrants. (Roebroeks and Soressi 2016, 6379)

Genomics has proven that there was some mixing of these two species of the genus Homo when they met again in Eurasia. Today, a revised estimate shows that about 2 percent of modern Eurasian DNA is Neanderthal (Prüfer et al. 2014; Harris 2015, 173–75). The Neanderthal species of early humans was very similar to modern humans, with a higher percentage of DNA in common with them, than the modern human and modern chimpanzee. Neanderthals and modern humans share almost 99 percent of their DNA, while chimpanzees and modern humans share about 96 percent.

The literature on Neanderthal fossils and cultural artifacts has always included a type of observation on plasticity—if not that exact word—a suggestion that Neanderthals do not seem quite as physically, behaviorally, or culturally as flexible as modern *Homo sapiens*. They were not as widely ranging, and some scholars believe their culture changed little until they encountered modern humans, from whom, it is postulated, they borrowed some ideas. Until genomics, this was just an interpretation, accompanied sometimes by unconvincing comparisons of artifacts. Neanderthals wore pendants, while modern humans wore beads.

With genomics, we can begin to form hypotheses about specific genes and their relationships with plasticity, and then compare modern humans and Neanderthals with respect to those genes. Not unexpectedly, plasticity appears to be determined by more than one gene. Gómez-Robles and Sherwood (2016) discuss a human-specific, protein-coding form of the FOXP2 gene, which is shared with Neanderthals and Denisovans. There is a variety of FOXP2 genes in other vertebrates and it is often involved in different types of communication. When the human form mutates, modern humans have a severe speech disability. Interestingly, Wolfgang Enard et al. (2009) have shown that the human FOXP2 gene increases plasticity in cortico-striatal circuits when expressed in mice. Simon Fisher and Constance Scharff also show that “Converging data indicate that FOXP2 is important for modulating the plasticity of relevant neural circuits” (2009, 166).

Equally fascinating details emerge on a second gene, SRGAP2, which is involved in human neocortical development. Gómez-Robles and Sherwood (2016) believe it may also be involved in human plasticity. They explain that the gene had two duplications after divergence from the chimpanzee line and one duplication, SRGAP2C, combines to form a dimer with ancestral SRGAP2, which inhibits its function. "This inhibition underlies certain human-specific neural developmental changes that are related to brain plasticity, including neoteny during spine maturation" (2016). They cite Dennis et al. (2012) who write that the duplication occurred 2–3 million years ago, near the emergence of the genus Homo. In addition to modern humans, Neanderthals and Denisovans also carry these duplications. Again, this shows that what we call "human" began emerging long ago, in this case, when the gene duplication occurred, around the time our genus Homo evolved and well before our species emerged. Furthermore, we are not the only "humans" to have this genetic feature; we share it with earlier humans.

Using additional findings from Dennis et al. (2012), Gómez-Robles and Sherwood (2016, 6, figure 4) illustrate the independent assortment of the human, protein-coding FOXP2 and the human regulating FOXP2 (note that a nonhuman regulatory form of FOXP2 is found in Neanderthals and Denisovans), and finally SRGAP2C—all of them genes emerging from an ancestral hominin population that had *all* of these versions except human regulatory FOXP2. That regulatory gene is the one that sets modern humans apart.

As with so many human traits, we see that plasticity has multiple coding and regulatory genes that guide its functioning phenotypically. Evolution frequently follows a conservative path of change, where the same genomic material is duplicated or changed slightly, thereby creating an entirely new phenotype. We see in this example the importance of regulatory genes in phenotypic expression. The human regulatory FOXP2 is our species' alone, although modern humans share the human *protein-coding* FOXP2 with Neanderthals and Denisovans. One is tempted to point to regulatory FOXP2 as the source of a very important difference, which affects language, but also plasticity for modern humans.

Unfolding from these details is the suggestion that human evolution has involved a variety of mechanisms so that we can now achieve what is so important: A longer developmental path in which some juvenile characteristics are perpetuated into adulthood.

Why this trajectory is so important is surely related to late adolescent and early adult maturation, when cultural, moral, and religious capacities emerge fully and combine. The lengthening of the human developmental course appears to us to be a basic underlying function of plasticity—both cause and result, at once. We propose that the slower developmental course of humans and retention of some juvenile characters is essential for the attainment of modern human cognitive maturity. While this proposal may appear contradictory on the surface, the longer path allows modern human adolescents and young adults time to practice the use of variable capacities, such as moral capacity and the very different religious capacity, and to integrate them fully into their various cultures—those cultures, themselves, providing the proper stimulus for their development.

Some observers have commented that modern culture is somehow "less religious" now than in the past. Our reply would be that, to an extent, it matters little. The capacity remains in our species as a strong trait with a 55–65-million-year evolutionary foundation, whether it is used now or not. There may be lengthy periods of time in the future for humans when they come to rely strongly on religious capacity to keep hope and faith in the future alive. The capacity will still be available then to *Homo sapiens*.

A MODEL FOR THE EMERGENCE OF RELIGIOUS CAPACITY IN THE GENUS HOMO

Building Blocks: Sociality and a Basic Ape Model

Our theoretical model for the emergence of religious capacity on the human lineage rests ultimately on two very solid foundations: (1) primate sociality that emerged 55–65 million years ago (and that humans and the higher apes share with the lesser apes, monkeys, and lower primates), and (2) a basic species model from the Miocene ape radiation. The latter was a population that was large in size, number of species, had great genetic variability, and already showed signs of an expanding brain. We shall peg the emergence of the basic ape model to Proconsul, at 19 million years ago, although more advanced apes came along afterwards.

The sociality of the order Primates has always allowed a natural mutual defense and good access to partners for mating. That ability to live and act in groups would flower on the human line to heretofore unknown dimensions. The Miocene ape radiation suggests a good level of population quality. Even if most of those species became extinct, one survived to found the African anthropoids, including modern gorillas, chimpanzees, bonobos, and humans. Their genomes carried enormous assets, especially genetic material that would be able to mutate and provide even more energy to a brain that would continue to enlarge until it met the natural constraints of maternal energy expenditure and/or anatomy of the birth canal. At that point, the complexity of the brain continued to rise through cortical folding, development of expanded neural connections, division of labor between parts of the brain, and of course, plasticity.

In identifying the ancestral ape population common to us all, our goal is to find the underpinnings of religious capacity for a specific line that emerged from that population—the human line. Our subspecies, *Homo sapiens sapiens,* may not be the only subspecies emerging from this ancestral ape population to show some early signs of religious capacity. *Homo neanderthalensis* may have had burials with grave offerings (Solecki 1975; Rendu et al. 2014), suggesting perhaps some belief in an afterlife. We believe it is quite possible that *Homo erectus*, *Homo heiedelbergensis*, and *Homo neanderthalensis* had some types of ritual. However, early modern humans in Europe, and even in the Levant at 100,000 years ago, had burials and offerings that were more elaborate than those of the nearby Neanderthals. Generalizations about the two sets of offerings suggest that *Homo sapiens* made more finely fashioned gifts, of greater variety, and more symbolic and "artistic" (Vanhaeran et al. 2006; Stringer 2012). We do not see all of these observations from so many researchers as the result of bias.

Did these two early species of human believe in an afterlife, and so provisioned the dead with items they might need on their journey to it? And, what are we seeing when we interpret grave offerings as more symbolic and artistic? Surely it must be that we see more of ourselves in them. That is our view after studying Bruner and colleagues' paleoneurological evidence for parietal expansion in fossil skulls. We are convinced that Neanderthal skulls were not shaped quite right for the parietal expansion we see in *Homo sapiens*, and more specifically, expansion of the precuneus (Bruner and Iriki 2016, Figures 5 and 6; Bruner et al. 2017).

Building Block: Realignment of the Senses

We add to a foundation of primate sociality and ape strength an important series of evolutionary changes in sensory perceptual abilities that accrued over millions of years, especially an enhancement of vision and hearing. Some of these gains and losses characterized the primates as a group, and other changes were specific to the human line. Primates, like cetaceans, have lost olfactory senses in their evolution. Humans have lost olfactory receptor genes in our recent evolution, and experienced upgrades in both vision and hearing. Next to many mammals, humans have poor senses of smell and taste, although Rob DeSalle and Ian Tattersall point out that humans still come equipped with around 900 genes for olfactory receptors, and about 25 genes for taste reception (2008, 181). However, this represents a reduction in taste and olfaction, and it may be related to human cultural abilities to identify the species in their environment that could provide harm, food, or shelter. Ethnomedicine continues to provide fascinating examples of the cultural classification of useful plant and animal species.

Humans have good vision, which apparently coincided with the loss of olfactory genes in primates, so humans share this feature with many other members of the order Primates. Yoav Gilad et al. write, "Our findings suggest that the deterioration of the olfactory repertoire occurred concomitant with the acquisition of full trichromatic color vision in primates" (2004, 120). Our view is that taste and smell have been reduced in humans, and vision enhanced, in response to arboreal life during much of our evolution. Unlike the canines, for example, early members of the genus Homo were dependent more on good vision to find food and avoid predators, and less on the fine detection of smells on the ground. We remained at least partially arboreal through the evolution of *Homo habilis*, who may have scavenged for meat on the ground, but probably slept in trees at night (Coolidge and Wynn 2009, 129–30). The latest finds from our genus, Homo, peg our last arboreal ancestor's emergence at 2.8 million years ago (Villmoare et al. 2015). This was either *Homo habilis* or some other very early member of our genus. If *Homo habilis*, the species lasted until 1.4 million years ago—rather recent.

Turning to a living near-relative, Aylwyn Scally et al. (2012) remind us that 30 percent of the gorilla genome is closer to human or chimpanzee than the latter are to each other. Eugene E. Harris (2015, 25–35) provides an outstanding explanation of how human, chimpanzee, and gorilla gene trees can conflict with each other, and with species trees, giving a "fuzzy" quality to data on the population ancestral to the three genera (Gorilla, Pan, and Homo). In spite of this technical uncertainty, what is clear, when Scally et al. considered pairwise parallel evolution among these species, is that humans and the gorilla have undergone some parallel evolution in the senses. They write, "A comparison of protein coding genes reveals approximately 500 genes showing accelerated evolution on each of the gorilla, human and chimpanzee lineages, and evidence for parallel acceleration, particularly of genes involved in hearing. . . . [E]ar morphology is one of the few external traits in which humans are more similar to gorillas than to chimpanzees" (Scally et al. 2012, 169, 173). This parallel evolution is not surprising, since they all came from the same ancestral ape population.

We conclude that upgraded sensory abilities in the human line were essential for their adaptation over many millennia, in various environments and different sociocognitive niches. Harris notes that "Genes in . . . categories like chemosensation and olfaction are also in direct interaction with changing environmental agents such as dietary compounds and smells" (2015, 90). This was especially true for species that were bipedal, mobile, and acquiring improved visuospatial abilities to maneuver the increasingly large landscapes they colonized. Nevertheless, the human senses that excel remain vision and hearing.

While the original function of improved senses for vision and hearing might have been to identify food sources, master the landscape, and avoid predators, the eventual use of those perceptions became important in ways culturally constructed. With the emergence of *Homo erectus*, we hypothesize that the intense learning context called the "human hearth" was tailor-made for sensual experiences, including early rituals and artistic forms like dance and chanting. With the advent of *Homo sapiens* and the full emergence of religious capacity, sensory perceptual abilities were used to heighten religious experience, create the symbols of religious belonging, encourage recruitment to religious groups, use religious expression in common rites of passage, and guide worship, prayer, and deep meditation (a hypo-excited state). They were used at the other end of the excitement scale to allow encounters with the supernatural through trance, which is a hyperexcited state (Bourguignon 1973). Psychoactive drugs have been used in religious expression by individuals in societies ranging from hunting and gathering groups to cults in modern nation-states.

Building Blocks: Downregulation of Aggression, Emergence of Secondary Altriciality, Social Tolerance, and an Upgrade in Intellect

Like the FOXP2 and SRGAP2C profiles analyzed by Gómez-Robles and Sherwood (2016), in which brain plasticity seems to emerge from the interaction of at least two different genes (which themselves affect other biological processes), there are examples, perhaps less researched, in which we can see humans and our evolutionary relatives inheriting different assortments of genes through both mutation and independent assortment (the redistribution of different genetic characters in sex cell production, something like shuffling cards to produce different "hands" to play). After all, the three members of the genus Homo that Gómez-Robles and Sherwood examined (modern humans, Neanderthals, and Denisovans) emerged from the same evolutionary population. That common ancestor was probably an African hominin who was less advanced, perhaps *Homo heidelbergensis* and maybe *Homo erectus*. Going further back, all these members of the genus Homo shared a common ape ancestor.

A later, reduced ancestral ape population is what we turn to now, and three species that emerged from it: chimpanzee, bonobo, and human. In the first article of this series, "Evolution of Religious Capacity in Genus Homo: Origins and Building Blocks," that ancestral ape population was *not* the very large ancient ape population common to all apes and humans. The smaller population we refer to now had gone through reductions in census population, as well as effective population size (theoretical size of the breeding population), and consequently genetic diversity. The biggest change was a drop from the ancestors of all great apes to the African great apes only, and then, there were two additional drops from the African great apes to the ancestral population common to chimpanzees, bonobos, and humans (Schrago 2013, 43). In the reduced ancestral ape population common to all three, we search for an important foundation of religious capacity: the downregulation of aggression and emergence of social tolerance. We propose that they evolved together, and are both critical in the biological evolution of religious capacity in modern humans.

Because we address the topic of aggression, and we find one of religious capacity's most important building blocks the downregulation of aggression, we should restate our conviction that religious capacity (religious thinking), as a biological trait, is essentially prosocial and its main purpose is to support the social group. We note, yet again, that the misuse of religious capacity (the trait) is possible, as well as the expedient coercion of religious organizations for nefarious political and economic purposes. However, for example, we cannot condemn Christianity in its entirety, because Hitler's Third Reich used it to protect itself politically. That it was able to do so does not nullify the essentially prosocial quality of the human biological trait, religious capacity.

While religious capacity is a strong human trait, it cannot always fend off wayward purpose. We ask: Is religious capacity therefore a "weak" trait? First, we are not convinced there is such a thing as a "weak trait," except in relation to a specific econiche. If the trait did not support the social group in some ecological niche, there is a likelihood it would vanish—although some deleterious genes do survive. We do not see religious capacity as weak, but in the face of stronger economic and political social forces it can be corrupted. This corruption is sometimes very unfortunate, and the possibility of it paints anything but sanguine or saccharine picture of nonaggression as an essential foundation for the emergence of religious capacity. It almost guarantees that social organizations of a religious sort will always be, potentially, squarely in the middle of the political and economic action. History proves it.

There were real dangers for apes when nonaggression and social tolerance emerged. As noted, pervasive social tolerance is unusual for adult mammals, unless they have been domesticated (a biological breeding process). Therefore, nonaggression was not completely without risk for our ancestral apes, nor is it in their descendants—us. In ever more complicated circumstances, humans are required to determine *when* to be tolerant and *when* to be aggressive.

We naturally ask: *When* did the aggression/tolerance changes occur? When did our ancestral line change from a more aggressive ape to a less aggressive ape who was our human ancestor? Our view is that it occurred in the reduced ancestral ape population common to chimpanzees, bonobos, and humans, and therefore, at a time preceding the chimpanzee and human lineage divergence 7–8 million years ago. Harris describes the circumstances this way:

> [I]t might help if you imagine this ancient ancestral species—before gorillas split off the species tree—distributed throughout large regions in Africa and also being quite genetically and anatomically diverse. A widely spread species might very well have consisted of various different subpopulations in which slightly different features existed. Perhaps in one of these ancient subpopulations, human features were already evolving. (2015, 57–58)

Our view is that some genetic features that would support human traits of nonaggression and social tolerance in some subpopulations would also support them among bonobo ancestors. Humans and bonobos became very different, but in the downregulation of aggression and emergence of social tolerance, they became similar. This hypothesis emerges from fascinating details on bonobos.

We were drawn to a 2012 study by Brian Hare, Victoria Wobber, and Richard Wrangham, to consider an extension of their analysis of bonobos and chimpanzees to include the human lineage. These authors do not go so far as to compare humans to bonobos and chimpanzees. Instead, they remind us that traits we now see in the bonobo include features that they share with domesticated animals. However, these features can be viewed as strikingly similar to some human features, too.

> [J]uvenile levels of aggression could explain the cascade of behavioural, physiological and morphological traits typical of juveniles that tend to be retained in adults of the descendant domesticated species . . . serotonin levels are generally higher in the brains of immatures than in the brains of adults, and . . . increased serotonin leads to decreased impulsive aggression . . . less reactive temperaments in domesticated animals may be related to the fact that dopamine, adrenaline and melanin have the same biochemical precursor while dopamine is thought to inhibit the hormone that stimulates pigment cells to produce melanin . . . change in an animal's stress response might lead to changes in pigmentation patterns via effects on shared biochemical pathways. (Hare et al. 2012, 4)

Changes include "variations in body coloration, cranial shape, dentition, brain size, activation of the hypothalamic-pituitary-adrenal (HPA) axis and problem-solving abilities" (Hare et al. 2012, 1). When the bonobo is compared to domesticated animals, they both show a "multitrait behavioural syndrome" including less aggression, so reduced reactivity of the HPA axis, more frequent reproductive cycles, increased prosocial behavior, play including nonreproductive sexual play, shortening of the face, reduction in tooth size, depigmentation of some body parts, and reduction in sexual dimorphism (2012, 1, 3). These are paedomorphic, juvenile characters that persist into adulthood. The traits have made domesticated animals easier for humans to handle and to breed. Now, with these descriptions, we must ask: Have humans evolved with some version of this complex of traits, too?

The chimpanzee, *Pan troglodytes*, is relatively aggressive in comparison to *Pan paniscus*, the bonobo. Members of the species *Pan troglodytes* often have difficulty feeding next to one another without fighting, and sex often involves threats and sometimes violence. There are no female "parties" (foraging groups that socialize), as there are among the bonobos (Hare et al. 2012, 7). Bonobos are more docile and less aggressive in comparison to chimpanzees, which may have been originally the result of occupying a niche in which there was less competition for food. However, bonobos are not as cognitively sharp as chimpanzees. The more aggressive chimpanzees

Table 1. Hypothesized independent assortment of one-to-many genes for aggression and cognitive abilities in the descendants of the ancient ape population ancestral to the hominins

Species	Aggression		Cognitive ability	
Chimpanzee		High		High
Bonobo	Low		Low	
Human		Variable		Very high

score higher cognitively than bonobos. Hare et al. (2012, 8) provide these details:

> V. Wobber, E. Herrmann, B. Hare, R. Wrangham and M. Tomasello (unpublished data) . . . using a large cross-sectional sample of bonobos and chimpanzees that were tested on a cognitive test battery . . . found that bonobos also demonstrate delayed development in tasks pertaining to their understanding of the physical world. Bonobos developed these abilities more slowly and never reached the level of competence observed in adult chimpanzees on tasks examining their spatial memory, their use of tools and their understanding of causality (similar to findings of Gruber et al. 2010).

What stands out from these authors' findings is that cognitive ability does *not* appear to vary with aggression. Research on bonobos gives a first impression that "They're just like humans!" After further thought, we see that in some ways they are, but in other ways they are not. Our view is that there are two main dimensions of difference (among many others): (1) cognitive skills, and (2) aggression. Given the complexity of these two dimensions, we can assume that they are both determined by a number of different genes, including many regulatory genes. When the human lineage is added to the bonobo–chimpanzee comparison, we see a hypothesized independent assortment of genes for cognition and aggression, similar to the independent assortment of the FOXP2 and SRGAP2C genes in humans, Neanderthals, and Denisovans (Gómez-Robles and Sherwood 2016). Table 1 diagrams the two dimensions for the three species.

Given that these three species emerged out of the same ancestral ape population—one that had already been twice-reduced in size and genetic variability—we begin to see that the genomic regulation of both aggression and cognition may have taken some of the same paths in these three descendant species. Because of the conservative nature of genomic change, it is altogether likely that complexes of genes (like the genes described for domestication) evolve together. It is worthwhile, at minimum, to search out similarities in traits and how they may have mutated in the same ways. One can imagine that the downregulation of aggression in the bonobos led to their diminished cognitive capacity, but that is probably not right because we have a human species that is high in cognitive ability, but variable in aggression.

What we can learn from our comparison of the three species is that there was the potential in this ancestral ape population for mutations to make big differences in both aggression and cognition. There is no question that humans have an "altricial" developmental path, or "secondary altriciality" according to biologists Ajit Varki and Tasha Altheide (2005, 1747). There is also no question that the human aggression profile is not uniformly passive or aggressive, and in this, they are different from both the bonobos and the chimpanzees. Our view is that humans are, and are not, aggressive. It depends on the circumstance, so the question becomes what regulates the level of human aggression at the genomic level, which is an enormously complex topic, even in comparison with other complex genomic questions, given the confounding influence of culture.

Our conclusion is that human aggression has been downregulated as part of a complex of paedomorphic traits, but that other regulators are operating so that human aggression can be turned on instantaneously when necessary for either self-defense or aggression in hunting. Furthermore, humans are cognitively sharp, so whatever downregulation of aggression occurred, it did not affect our ability to solve problems, develop excellent spatial memory, or make and use tools.

An intriguing line of research has emerged since the bonobo genome was sequenced. Kay Prüfer et al. write,

> We find that more than three percent of the human genome is more closely related to either the bonobo or the chimpanzee genome than these are to each other. These regions allow various aspects of the ancestry of the two ape species to be reconstructed. (2012, 527)

Sequencing surely will *not* show a pattern where bonobo and chimpanzees sequences are uniformly more closely related to each other than to humans. In other words, the gene trees and species trees will not always agree with each other, and the gene trees will give variable results. The issue gave rise to the gene tree–species tree conflict that was eventually sorted out, showing that humans are closer to chimpanzees than gorillas (Harris 2015). This puzzle is analogous. Prüfer continues,

> Although they are similar in many respects, bonobos and chimpanzees differ strikingly in key social and sexual behaviors, and for some of these traits they show more similarity with humans than with each other. (2012, 527)

Research on the three-part split of humans, chimpanzees, and bonobos, and on the 3 percent of the human genome Prüfer notes above, may well point toward some of the genomic basis for behavioral differences among the three species.

In our research, we have noted that several primate classification diagrams now place bonobos closer to humans than to chimpanzees in a species tree of the three. Eventually, the genetic proximity of these three very closely related species (chimpanzee, bonobo, and human) will be sorted out, and the results may have the added advantage of allowing us to link genome segments to behavioral differences. Which behaviors are "old," belonging to the ancestral ape population common to all three, and which are "derivative" will be most interesting to discover.

To return to our central task of identifying the building blocks leading toward the biological evolution of religious capacity, we therefore add to primate sociality, a basic ape model, improved senses in vision and hearing, and intensification of learning contexts through heightened sensory perceptions, an important foundation that we call "social tolerance." It is most often seen in other animals as a paedomorphic trait that disappears upon reaching adulthood. As described above, it is a morphological complex of more juvenile traits that are retained into adulthood, and regulated culturally. Human religious capacity rests on all these essential underpinnings, and on others. Without them, religious capacity would be different, or nonexistent, as a human trait.

We note in our article on the emergence of a rudimentary moral capacity in *Homo erectus* (Rappaport and Corbally 2016) that the emergence of moral capacity could have occurred more than once during the species' long tenure on Earth. We add this notion to our model here: The emergence of nonaggression might have occurred more than once in the subpopulations leading to humans, bonobos, and chimpanzees (in whom it was not perpetuated). If it did so, it is very likely that it occurred, at minimum, at this evolutionary stage, because the effective population size of the ancient ape ancestral population giving rise to humans, chimpanzees, and bonobos was larger in effective population size than any of the populations of bonobos, chimpanzees, or humans that would follow, so there was a greater likelihood that mutations would arise that led to nonaggression. There was simply more variable genetic material at this presplit stage.

In its current version in modern *Homo sapiens*, religious capacity always involves some form of nonaggression, noncompetition, sharing, and/or gift-giving. It is true that wars have been fought for so-called "religious reasons," but we doubt, along with Karl Peters (1986), simplistic explanations, as well as the notion that religion is at the core of warmongering. Instead, we see economic reasons that should be considered first. That debate is for others to finish. Let us simply say that human religious capacity, as it is expressed widely and variably, involves some type of accommodation of other adult humans. Cultures are highly variable in terms of which types of individuals and groups they protect with religious behavior or in religious organizations. Nevertheless, *someone* is brought near and tolerated in every single phenotypic expression of religious capacity. This is not usual among adult mammals, except for reproductive purposes. It is new, but we see its shadow genetically and behaviorally in our relative, the bonobos, who came from the same ancestral gene pool of ancient apes.

Evan MacLean reminds us that the reduction in human aggression may not have come all at once, but in waves of selection that followed changes in niche. He writes that since *Homo sapiens* emerged, aggression may well have been reduced further. He writes,

> [A]dditional changes in human craniofacial morphology raise the intriguing possibility of a second wave of selection against aggression that coincided with the emergence of behavioral modernity (Klein 1995). Specifically, Cieri et al. documented increased feminization of human crania from the Middle Pleistocene through the present—evidenced by a reduction in brow ridge projection and a shortening of the upper facial region (2014). These anatomical changes are hypothesized to result from a reduction in androgen activity and are consistent with the well-documented effects of testosterone on craniofacial masculinization. Given that testosterone is linked to dominance and aggressive behavior in men (Mazur and Booth 1998), these changes may reflect a more recent wave of selection for increased social tolerance that allowed humans to work productively with conspecifics in new ways (Hill et al. 2014), as suggested by the proliferation of cultural artifacts 20–70 thousand years ago (Klein 1995; Powell et al. 2009; Derex and Boyd 2015). (MacLean 2016, 6350–51)

These findings suggest different and later factors involved in the downregulation of aggression in early, anatomically modern humans (AMHs). The bonobo model suggested an earlier mechanism for the downregulation of aggression and increased tolerance while feeding. It is quite likely that the human line underwent repeated bouts in the downregulation of aggression, especially later, as the effectiveness of decision-making skills improved to regulate aggression both up and down. This could well be how the human species ended up with aggression, social tolerance, and sharp cognitive skills—all three. The efficacy of improved decision-making skills provided a mechanism by which aggression could be turned on in specific circumstances for particular reasons (e.g., to protect home and hearth). One could interpret this as humans ending up with the best combination of aggression and tolerance. However, it is interesting to note that a sequence of bouts of genomic regulation of aggression makes most sense if social tolerance emerges first. Intuitively, it appears less logical if aggression comes first with needed add-ons in terms of social tolerance. Eventually, it will be extremely interesting to see genomic results on the sequence of changes related to social tolerance and aggression. The answers are written in the human genome, and perhaps also in the genomes of our closest relatives.

It has been worthwhile to examine features that must have emerged from the reduced ancestral ape population common to bonobos, chimpanzees, and humans—but in different combinations and/or different proportions. One of those combinations made adult social tolerance highly likely on both the human and bonobo lines. If side-by-side feeding is the measure, then humans are certainly tolerant. They rarely fight over food (if not starving), often share food as a form of social reciprocity and conviviality, and the only individual who is, cross-culturally, ritually avoided at meals is a man's mother-in-law, following what is widely known in cultural anthropology as the "mother-in-law taboo." Even this taboo falls away in the modern world.

It is true: There are many, many examples of human intolerance, so sifting through the likely emergence of social tolerance on the human line is not clear or easy. Data are fuzzy and random genetic drift has perhaps allowed unusual features to persist on our line, due to reduced population size and inbreeding. The bonobos make it easier to recognize social tolerance. Humans may have inherited a similar profile of juvenile features—tolerance, play, more frequent reproductive cycles, and the lessening of differences between males and females. However, humans remain very cognitively sharp.

Therefore, we find the foundations of religious capacity that emerge from our comparison of humans, chimpanzees, and bonobos to be the downregulation of aggression, rise in social tolerance, but also an intellect that made us sufficiently self-aware and other-aware to determine *when* to be aggressive and when to be tolerant. All three features are essential for religious capacity. Yet, in the ancestral ape subpopulations in which secondary altriciality and social tolerance first appeared, there was a new problem: *when* to be aggressive. Our ancestors solved that problem in a number of ways, but they had a major challenge. Clearly it was indeed solved because the first known member of our genus—*Homo habilis* at around 2.8 million years ago, if that fossil find holds (q.v. Villmoare et al. 2015)—is known for both tool use and aggressive scavenging of meat (Coolidge and Wynn 2009, 106). The species was cognitively sharp, but aggressive when necessary.

When social tolerance and intellect are added to the special human sensitivities that we explore next, and, as well, to a rudimentary moral capacity that we see emerging after *Homo erectus* was able to control fire and a learning context called the "human hearth" emerged at 1–1.5 million years ago (Rappaport and Corbally 2016, 2017), we sense we are edging closer and closer to a satisfying outline of the foundations that support religious capacity in the genus Homo, in the past and even today.

We next consider sensitivity on the human line, both general and emotional. When others are brought close after aggression recedes, life becomes complicated and our ancestors needed heightened sensitivities to manage all that information and all those decisions. Robin Dunbar has suggested that brain size continued to grow in response to the burgeoning requirements of social relationships (1998). We shall now look at some human features whose early versions may have aided in the task of keeping them all straight. The reader should remember that, while we examine two traits for sensitivity, there are probably many more such traits guided by both protein-coding and regulatory genes.

Building Block: Sensitivity

We now consider what humans do once others are brought near and tolerated, and that leads us to another foundation of religious capacity: an upgrade in sensitivity. It also suggests an important foundation of religious leadership—from the medicine man among hunters and gatherers, to the local pastor, to the Pope. In performing their cultural functions well, a generous level of sensitivity (however defined) is required. It is important to note that we could have written that nonaggression involves "someone brought near, tolerated, and comforted," but that is not what the downregulation of aggression does. Separate, additional, steps are required once aggression is gone and tolerance is present. Without aggression, there are new opportunities to sense other members of the group more completely, but there are also new dangers, so decision making lingers as an important issue.

An upregulation of sensitivity on the human line is suggested by new neurological and cognitive findings, which are sure to join additional research results in the future. It may be that one or more of the genetically based features we describe represent a phenotype that has not yet reached fixation, like some other traits, for example, protection against diabetes (Cochran and Harpending 2010). Or, it may be that sensitivity genes are in balanced polymorphisms and will not spread throughout the human population. At the present, our understanding of human sensitivity is incomplete. Yet, we can glimpse how complex that group of genes is, even now. Multiple genes and regulators are guiding the nature and level of human sensitivity. They did not all emerge at once, but probably over millions of years of social living in groups. And yet, we firmly believe that the downregulation of aggression in at least some subgroups of the ancient ape population giving rise to chimpanzees, bonobos, and humans created circumstances in which improved sensitivity became important and was genetically retained for present, and what became future, use by humans.

The reader will note that there are "downsides" to sensitivity. We are not suggesting that finely tuned human sensitivity is always a blessing, or that it is shared equally by everyone. However, the variety and extent of genetic regulators of sensitivity suggest that some capacities were found useful and perhaps necessary on the human lineage. Not surprisingly, the first findings we review are of a trait shared with other animals. We note that, as with the FOXP2 gene, humans appear to use a type of genomic material widely found in other animals, but their own version of it. This reminds us how closely we are all linked to common ancestors who lived long ago.

Most interesting among the findings on sensory processing sensitivity (SPS) is that—for at least one gene and its phenotype—it exists by itself as a measurable trait that can operate without the amygdala, an important emotion center in the brain (Acevedo et al. 2014, 590). We know that visual sensory perception has been enhanced on the human line, so we expect visual images to excite emotions in humans, but things are not quite that simple. Bianca Acevedo et al. write, "Theory and research suggest that sensory processing sensitivity (SPS), found in roughly 20 percent of humans and over 100 other species, is a trait associated with greater sensitivity and responsiveness to the environment and to social stimuli" (2014, 580). The phenotype for SPS does not emerge in everyone. Because of its downsides, it may not be advantageous for everyone to be a highly sensitive person (HSP).

There has always been chemosensory perception in animals, beginning with one-celled creatures and flatworms, which needed chemical sensitivity to give clues as to which way to travel—to or from noxious chemicals, to or from sources of food. There has been something like social sensitivity in many mammals, especially primates, who live in well-structured troops. And, emotion was part of much communication. Among apes, emotion warned of predators and saved lives; it gave mothers motivation to take all the trouble necessary to tend to infants born immature. Emotion also made the fabric of society more complex. Emotions, those pesky feelings with deep roots in the older parts of our brains, had to be taken into account so often. They have always been with our line, but they changed during human evolution. How they changed is emerging tentatively from recent research.

Using functional magnetic resonance imaging (fMRI) scans, Acevedo et al. (2014, 580) report that SPS shows up in activation of brain regions used in awareness, integration of sensory information, empathy, and action planning (e.g., cingulate, insula, inferior frontal gyrus, middle temporal gyrus, and premotor area). However, when subjects viewed "emotionally evocative photographs, SPS does not necessarily engage limbic emotional processes" (Acevedo et al. 2014, 590). HSPs had "stronger activation of brain regions involved in awareness, empathy, and self-other processing" (Acevedo et al. 2014, 580). The HSP is adept at attention, awareness, and readiness for action (2014, 589–90). It is interesting that "empathy" is not part of the emotional repertoire handled (at least in this case) by the amygdala. Results suggest that, at least for this trait, empathy is something other than an emotion—something perhaps more like an aspect of awareness. Readers should keep this distinction in mind when we explore parietal expansion and the emergence of religious capacity in *Homo sapiens* below, and when we analyze a much more complicated human feature, compassion, in the third article of this series.

Acevedo et al. (2014) report that the brains of HSPs are "alert and ready to respond," but also empathetic and adept at integrating sensory information. They write that, "results suggest that highly sensitive individuals 'feel' and integrate sensory information to a greater extent in response to their close others' affective states, in particular positive emotional states" (2014, 590–91). HSPs show the same pattern in response to sad and happy images of people close to them, as well as strangers in happy images, but not stranger images that are sad. Results suggest a neurological basis for those who view empathy as biased against strangers. Therefore, these findings become part of the discussion on "Is Empathy Immoral?" (Peterson 2017; Deane-Drummond 2017).

SPS is interpreted as "an innate trait associated with greater sensitivity to environmental and social stimuli (e.g., Aron, Aron, and Jagiellowicz 2012). Behaviorally it is characterized by more elaborate processing of stimuli and, to facilitate this, 'pausing to check' before approaching novel situations" (Acevedo et al. 2014, 588–89). HSPs show "stronger activations in response to close others and to positive social stimuli, including activation in the ventral tegmental area, a dopamine-rich area well-known for involvement in reward processing" (2014, 589).

The authors conclude that SPS is perhaps advantageous from an evolutionary perspective, but metabolically costly, so selective attention to those who are close may be a way to conserve energy:

> [I]ndividuals with greater SPS appear to be reducing their reactions to negative emotional information that may not be particularly salient, as for strangers versus close others. This is consistent with behavioral evidence of highly sensitive individuals reporting that they tend to avoid negative overstimulation (such as loud sirens, horror movies, and having too much to do at once) and needing recovery time after viewing arousing stimuli. (Acevedo et al. 2014, 591)

Elaine Aron et al. (2012) review the research on components of high sensitivity, including inhibition of behavior; sensitivity to stimuli; depth of processing (expressed often as amount of time); and emotional/physiological reactivity. The strongest association was with a component called "ease of excitation" (2012, 14).

People scoring high on a HSP scale are more likely to carry the short, low-expressing variant of the serotonin transporter polymorphism, 5-HTTLPR. Those people not scoring high on sensitivity view stimulating material with greater equanimity, and they are more likely to carry the long allele of this gene in the homozygous state (Beevers et al. 2009). Yet more recent research illustrates that genes can determine sensitivity to emotional information. Some people experience "emotionally enhanced vividness," making it more likely that they will remember the images they see. These people are called "ADRA2B deletion carriers." The effects of the ADRA2B (adenoreceptor alpha 2B, a protein-coding gene) deletion are to prevent braking of the neurotransmitter norepinephrine, so individuals with this genomic variant have an increase in visual experience of emotional images.

In contrast to 5-HTTLPR, viewing emotional images by all test subjects increased activity in the lateral amygdala, which is important in emotion processing. Test subjects with the ADRA2B deletion had added input from the ventromedial prefrontal cortex, which is connected to the processing of internal emotional experience (Brookshire 2015; Todd et al. 2015). The term HSP has also been applied to individuals with deletion of ADRA2B. Not surprisingly, this genetic condition is linked to susceptibility to traumatic memory (Todd et al. 2014). Work on this and other neurotransmitter variants has been useful in treating post-traumatic stress disorder.

The second set of findings takes us from general sensitivity to emotional sensitivity. In commenting upon Rebecca Todd et al.'s 2015 study of "the ADRA2B deletion," neuroscientist Vladimir Miskovic (quoted in Brookshire 2015) remarks, "Certainly more neurotransmitters are involved, and of course to make our lives more complicated, they all interacting [sic] with one another." It is not surprising, given that humans are the most socially complex of all organisms, that many genome segments are involved in sensitivity regulation. Sorting them all out will take us well into the future.

The multiplicity of genes involved in human sensitivity, by itself, lends credence to our assertion that an upregulation in sensitivity occurred on the human lineage. Furthermore, since religious capacity is involved in some of the most complex social and emotional experiences known to humans, it is very likely that multiple genes are involved in regulating human sensitivity responses during religious rituals, rites of passage, religiously motivated beneficence ("charity"), and in, for example, lengthy, socially complex religious group gatherings.

Our view is that it is only logical to interpret sensitivity among those features that are *sine qua non* for religious capacity. Religious teachings and activities may well function to modulate and make cultural sense of various reactions within the scope of human sensitivity. The human capacity for heightened sensitivity can be a mixed blessing, especially for humans who are susceptible to overstimulation. The capacity for overstimulation can be physically and emotionally managed by group members in religious contexts (exorcism, voodoo, and cult-based worship). Overstimulation can also be a *qualification* for religious practitioners. In some tribal societies, a shaman may enter into altered states of consciousness to interact with the supernatural realm on the group's behalf. Even major, modern religions have ceremonies in which some people react excessively and must be assisted until they are recovered.

We propose that there must have been adaptive group functions in having some individuals who carry sensitivity genes in early human populations. The fact that some of them "paid a price" in terms of overstimulation might have been worth it for the social group. We propose that the timing of a human upgrade in sensitivity coincides with the downregulation of aggression. It was the loss of aggression that allows more advanced apes and early hominins to approach each other as adults more closely, be tolerated, learn from them, and engage in joint action. While chimpanzee "gangs" are well known for their aggression, we suggest that this is not cooperative hunting or foraging, as in *Homo erectus*. Sensitivity to others' movements, vocalizations, signals, and smell can assist group hunting in ways incongruent with chimpanzee gangs.

We shall strive to separate sensitivity from common terms for human-to-human beneficence like "compassion," "kindness," and "charity." Sensitivity appears to be a separate human trait complex, which does not necessarily imply any of these arguably defined activities. Sensitivity varies on its own set of scales. Note "compassion" is analyzed in the third article of this series.

Building Block: Morality Emerges, only to Be Overtaken

Our model of morality's emergence in *Homo erectus*—around 1–1.5 million years ago when the species learned to control fire—encompassed a cognitively based, decision-making capacity that operated along a timeline, with a valence of good to bad, and with an emergent form of the modern left hemisphere interpreter (LHI) and early decision-making loops to help make evaluations and decisions (cf. Rappaport and Corbally 2016, 2017). Here, in this exploration of the emergence of religious capacity, we propose that the moral capacity that emerged in *Homo erectus* was overtaken, once *Homo sapiens* emerged, in large measure by religious behavior and institutions, which then became the most common (but not the only) mechanism for applying morality. Together, they produced a strong, variable, but reliable, biocultural capability to support a variety of human social groups.

We have written of the demography, lifeway, cognitive sophistication, and likely language abilities of *Homo erectus*, in forming our hypothesis that a rudimentary morality emerged in this early, but not the earliest member of our genus (Rappaport and Corbally 2016, 2017). The species had a fully upright posture and gait, and was mobile, ranging widely in a home territory that could have been as much as ten square miles. Eventually, *Homo erectus* became the first of our genus to leave Africa and populate Eurasia. The species was likely a scavenger of meat, which was necessary to feed a brain that was much enlarged in comparison to ape precursors to our genus, or even the earliest member of our genus, *Homo habilis* (likely the first tool maker), or other (partially) bipedal apes, such as the australopithecines.

Homo erectus was long-lived, and sexual dimorphism was much reduced. As with *Homo habilis*, the proportions of the limbs were human-like, not ape-like. Females may have required almost as much energy as males, and were probably active in providing food to children, and perhaps grandchildren (cf. the "grandmother hypothesis," Opie and Power 2008). Our conclusion was that this early hominin was in an evolutionary position to have developed a rudimentary moral decision-making capacity after the species learned to control fire, at around 1–1.5 million years ago, and a learning context we called the "human hearth" emerged. In the context of a communal fire, childhood lengthened along with an overall developmental trajectory and prefrontal maturation came increasingly late, so that it would not impede convention learning (cf. Thompson-Schill, Ramscar, and Chrysikou 2009, 259). Moral learning took advantage of late cognitive maturation, so that definitions of what was "real" and "true" and "right" were conveyed early, with little questioning.

In our formulation of human phenotypic morality in *Homo erectus*, and its application, we listed the following features: a mental step both back and up; an arbitration mechanism that operates along a timeline; an evaluation using a valence from good to bad; a regretfully dispassionate reasoning; a tentativeness in a mental balancing act; a sad rejection of "wantonness"; a capacity for empathy with someone receiving moral judgment; the experience of a burden; resolution on the part of the group; and hope and faith in the future, on the part of the group. All of these cognitive and social steps were eventually subsumed under religious capacity when it emerged in *Homo sapiens*, and so these steps also become part of religious expression in humans. Every religion includes some method for determining "good" versus "bad" behavior, and dealing with it.

When we consider the building blocks of our model of religious capacity—those that came before moral capacity's emergence in *Homo erectus*—we can conceive a rightful place for ritual within the context of the human hearth, where stories were enacted for all to see, and all could understand the lessons learned. If the species was able to reason with a rudimentary morality, then this would be a natural place for instruction. The envisioning of ritual in the life of *Homo erectus* should not be understood as the full flowering of religious capacity, but it did in all likelihood make use of many of the evolutionary changes described in our model to this point: sociality, improved perceptions in vision and hearing, the downregulation of aggression and an intellectual ability to decide when to be aggressive, the emergence of secondary altriciality, an upgrade in sensitivity, and with *Homo erectus* a moral sense and application of it among group members. Ritual that is lit by a communal fire would naturally take advantage of improved (and improving) senses of vision and hearing. Drama, dance, and chanting could have aided instruction. Social tolerance was the substrate for this type of group learning. It emerged long before, from the reduced ape population that gave rise to chimpanzees, bonobos, and humans.

We do acknowledge some overlap of moral and religious capacities, and eventually, in practice, they overlapped almost entirely in *Homo sapiens*.

While ritual was very likely useful in *Homo erectus* groups (especially for socialization), ritual by itself is not religious capacity. If we stick by our definition—that religious capacity includes the construction of theories (theologies) about the relationships between humans and the supernatural, then there is no evidence suggesting this occurred before the expansion of the parietals, especially the precuneus (cf. Bruner and Iriki 2016; Bruner et al. 2017). The fossil evidence showing progressively globular skulls from around 200,000–400,000 years ago is naturally varied. The finds do not consist of *uniformly* globular skulls, nor is there strict uniformity even at 200,000 years ago, nor even today, caused by variable expansion of the precuneus (cf. Bruner and Iriki 2016). We note again, throughout these three articles, that our "building blocks" do not have hard and fast boundaries. As in most biological systems (not just our genomes) there is a fuzziness to generalizations. Still, there is a good argument for moral capacity with *Homo erectus*, but there is no evidence to suggest an ability to engage in theology construction in that species. That appeared in *Homo sapiens* alone, when the expansion of the precuneus and a globular skull shape stabilized, around 150,000 years ago (Bruner and Pearson 2013).

Building Block: Expansion of Parietal Lobes

When we first wrote on human phenotypic religious capacity, we listed traits that we knew did not apply to every human (Corbally and Rappaport 2013). However, they appeared to be an accurate set of features that spanned human religious experience, from spirit beliefs among hunters and gatherers, to formally developed theological faiths among people in modern nation-states. The ordering of the traits we described was important, from the most basic to the least basic, and they remain useful in framing the cognitive, emotional, and behavioral features that describe human religious behavior and experience: awe and wonder; belief in supernatural spirits or beings; adoration; reverence; obedience; endowing ritual with symbolic meaning; alignment, or continual comparison with a moral code, and planning one's life according to that code; introspection and meditation; the habit of prayer; religious transformation, or an ability to achieve a deep selflessness and be filled with a supernatural presence; and achieving an ecstatic state (an altered state of consciousness) to interact with the supernatural (Rappaport and Corbally 2015). Yet, for every human cultural group, some applied and some did not. The common feature was that they all made use of an advanced type of thinking that imagined the supernatural and manipulated those imaginings with a creativity that was guided and supported human culture.

Here, we approach the task of characterizing human phenotypic religious capacity again, as a reliably produced, human, biologically based trait founded on specific neurological and cognitive building blocks that emerged over millions of years. Like moral capacity, not everyone expresses the trait, but then, not everyone has blue eyes. Not everyone engages in religious thinking or behavior, but this does not disprove the trait. Its foundational building blocks go back too far, their integration is too old, and the trait's integration into cultural life is too widespread, too deep, to suggest it had, has, and will have no adaptive nature. However, religious capacity does go awry, in tribal groups to modern nation-states, but we are not convinced that it is religious capacity, itself, that is antisocial, only its use to further wayward political and economic goals. We see the human religious trait as discrete and separable from human moral capacity.

On the surface, religious thinking does not seem very advanced, but our view is that it is. Religious thought expresses (and we propose, combines) *types of thinking for which there is no evidence in other animals*, even those closest to us. For some, religious capacity does not appear advanced or intellectual because it is often emotional, experiential, stylized, ritualistic, and/or dramatic. Religious practitioners engage in events and activities in settings that are set apart and away from normal interaction. We saw the same feature in the emergence of moral capacity (Rappaport and Corbally 2016, 2017), and suggest this is part of what religious capacity takes from moral capacity, and uses in its own way. The goals are different. Religious behavior is set apart with the purpose of interacting with the supernatural, but that is tightly bound together with the cultural identification and use of special places, set apart because of their beauty, or symbolism, or importance in mythologies.

We titled our initial efforts to address the emergence of religion in early humans "Crossing the Latest Line" (Corbally and Rappaport 2013), and philosophers commenting upon chimpanzee studies have made a good attempt at defining what that line was and what it remains (Kitcher 2009; Korsgaard 2009). Religious capacity is still with us as a species, whether we profess religious beliefs or exhibit religious behavior or not. Religious capacity remains in some large proportion of humans in the continued presence of the cognitive and neurological underpinnings described in this article. What will become of this type of thinking in our evolutionary future can be imagined, but it may take our descendants to take religious thinking to new levels. It is quite possible that the evolution of religious capacity, and religious thinking, is still in mid-stream. After all, 150,000 years in evolutionary terms is a very short span indeed. Religious capacity may change, and we may be either able or unable to imagine the result at the present.

Our focus has been on religious thinking, not necessarily what we see as the overt results of religious thinking, that is, religious behavior or religious organizations. We were committed to an approach that would cover *all* religions, at all times, from the prehistoric to the modern, even into the future. We thought again and again about misnamed "primitive religions," tribal religions, Eastern religions, and Western religions. They all had to fit, even something that is as aberrant (to some) as voodoo, Santería, condomblé—those had to fit, too, because we are one species, only one, and our thesis is that we all have what we call "religious capacity," whether it is used or not. There are cultures, too, around the globe that are not "very religious," in which religious thinking and behavior does not play a big role. One of the best examples was described by Fredrik Barth in *Nomads of South Persia* (1961). It is a good example of a nonmodern society whose level of religious expression is muted. Does that mean these people cannot call on human religious capacity? No. It is still there, used or not.

Nevertheless, our main task here has been to describe the timing of sequential, evolutionary changes that are responsible for religious thinking in modern humans. To this point, we have described changes without which religious capacity would not exist, or it would be very different. These are very basic components of a system that tops out with a rather sophisticated type of thinking that we call religious thinking in modern humans. Where did it come from? Which biological systems were involved in its emergence?

With the expansion of the parietal areas of the brain, and the interaction of the parietals and prefrontal cortex, we finally arrive at a human evolutionary development that has no equivalent in earlier hominins, so we are left with fossil evidence, cognitive and neurological findings on today's anatomically modern humans, and extrapolation of today's scientific theory backward to explain fossil changes. Coolidge and Wynn were among the first to highlight the importance of parietal expansion in the emergence of modern thinking (2009, 209, 222). They, like we, have gone on to follow the work of paleoneurologist Emiliano Bruner and his colleagues (Bruner and Iriki 2016; Bruner at al. 2017). While this section focuses upon the parietals, the reader is reminded that other genetic changes were accruing concomitantly on the human line, including perhaps another bout of the downregulation of aggression (MacLean 2016, 6350–51).

Expansion of the parietal areas is a modern human trait found in East Africa as far back as 195,000 ± 5,000 years ago (Fleagle et al. 2008). More recent finds in Morocco (Hublin et al. 2017) suggest that *Homo sapiens* and the species' globular skull emerged more gradually than we first thought. The date of 200,000 years ago is still useful because human mitochondrial DNA coalesces at around 200,000 years (Garrigan et al. 2005; Templeton 2005). The more recent date suggests that a solid model was almost in place for *Homo sapiens*. In the first draft of this article, we wrote that other finds may change this date somewhat, although it is clear that important evolutionary changes were occurring between 200,000 and 400,000 years ago, all over Africa. In Bruner et al.'s 2017 publication, it became clear that an even more recent time horizon made the best sense for stabilization of the precuneus expansion and fixation of the globular skull (Bruner and Pearson 2013). Therefore, 150,000 years is the time horizon that we adopt for full-fledged theological thinking.

The presence of a mixture of both "archaic" and "modern" *Homo sapiens* features in the Omo fossil finds have, themselves, given us a snapshot that demonstrates, like Hublin et al.'s (2017) finds, that a model was becoming fixed and stable. Paleoneurologists Bruner and Atsushi Iriki write about this type of process, which may well have attended the emergence of *Homo sapiens*:

> Once a novel, alternative, and bistable state is associated with increased fitness, additional resources will be invested to stabilize the system, probably generating further redundancy. Humans can induce such a loop directly and actively, shaping a more comfortable environmental niche. Indeed, human-specific cognitive characteristics seem to be subserved mainly by these "expanded" parietal areas. . . . Subsequently, triggered by extra-genetic or epigenetic factors embedded in such an environment, the corresponding neural niche in the brain could be reinforced further, generating a recursive intentional niche construction. (Bruner and Iriki 2016, 103)

These authors address a critical loop in cognitive evolution, a version of which we have described for *Homo erectus* and the emergence of moral capacity (Rappaport and Corbally 2016, 857–58; 2017); and another cognitive loop in the process of cultural neural reuse in the stabilization of religious capacity in *Homo sapiens* (Rappaport and Corbally 2018c, the third article in this series). That type of feedback loop—no doubt multiple versions of it—must eventually be implicated in the genetic and phenotypic integration of the sets of features we identify in our model for religious capacity. That integration could not have occurred before the expansion of the parietal areas of the brain, the invention of human theologies, and the application of theologies to human cultural functioning. It had to "work for us," and it did, in group after group and theology after theology. The trait is omnipresent in human cultural groups, if not in each and every member of them.

Let us take a closer look at some of Bruner and colleague's analysis of the expansion of the parietal areas to achieve the globular skull of our species, *Homo sapiens*. There were other changes that came with expanded parietals: smaller teeth, smaller jaws, more pronounced chins, smaller upper faces (including noses and brow ridges), and faces that are rotated under the cranium. These paleoneurologists suggest that *Homo sapiens* has enhanced visuospatial reckoning because of expanded parietals, which also serve to integrate information with sensory data from hands, eyes, and memories of relevant episodes. On the other hand, our nearest relatives, the Neanderthals, did not have the same "praxis and body interface" that *Homo sapiens* had because of the expansion of the parietals in that species. Both species had lateral bulging, but only *Homo sapiens* had longitudinal bulging that created the globular shape of the skull (Bruner and Iriki 2016, 104–05).

Psychologist Frederick L. Coolidge and paleoanthropologist Thomas Wynn have rightly commented that "a near myth has been perpetuated that frontal lobes have been solely responsible for the creation of the modern mind" (2009, 236). At the very same time, anthropologists going back to Raymond Dart in the 1920s have noted a difference in shape of the parietal areas of, for example, the skulls of early humans versus the australopithecines. Bruner and Iriki write that "an actual bulging of the upper parietal surface was the main feature characterizing the globularity of the modern brain, when compared with all the . . . extinct human species" (2016, 102). They quantify and visualize three-dimensionally the geometric expansion of the parietals and flattening of the face, to illustrate how the globular skull shape of *Homo sapiens*' skull was and is achieved (2016, figure 5). Bruner and Iriki report the specific location of that expansion:

> [A] recent shape analysis . . . in adult humans revealed some important information: the main source of individual variability associated with the brain geometry is due to the proportions of the precuneus, with a pattern which is surprisingly similar to that observed in the distinction between modern and non-modern human species . . . The resemblance between the two patterns suggests that the precuneus may be a major factor accounting for the morphological changes associated with the evolution of the modern human brain geometry. (2016, 102)

The precuneus is part of the superior parietal lobe in front of the occipital lobe. Its functions have been identified with mental imagery of the self and visuospatial imagery.

When one attempts to understand parietal expansion in the lifeway of early humans, it stretches our credulity to imagine that religious capacity was initially adaptive to the point that, by itself, it immediately became part of a feedback loop of the type described above. How could survival have depended so very much on imagined inner spaces and beings?—Perhaps eventually, in a role that religious capacity came to assume, but not at its initial appearance. However, parietal expansion did not bring religious thinking alone. It came along with other abilities. The parietal areas of the human brain impart the advantages of visuospatial reckoning and synthesis (Bruner and Iriki 2016, 98), sensory integration (especially body and spatial awareness, and the sense of touch), spatial sense and navigation, action planning, goal-oriented behavior, and acknowledgment of other people's actions. Bruner and Iriki describe the parietal cortex as a "brain-environmental interface through the eyes and hands" (2016, 100; cf. Bruner et al. 2017). It is no wonder that we humans can so easily distinguish the finely made tools of fossil *Homo sapiens* versus the more crudely made tools of *Homo neanderthalensis*.

Mastery of one's surroundings with improved visuospatial abilities, and an ability to envision stalking and hunting animals in specific locales, with a certain terrain, with a certain number of people helping, at a certain time of the day, so in certain types of light and weather—*that* could well have been sufficiently advantageous to secure parietal expansion and its connections to the prefrontal cortex as an adaptive trait. An ability to envision where to strike a predator in the head, where to slice its throat, how to grab the animal so it cannot move, and then how many people it will take to bring down a large bull, or a wounded female, or a small calf—all that would have been so advantageous to survival it could well have impacted early humans immediately, oneself and one's family (some of whose members shared the genes guiding these changes). Life itself depended on imagining the use of these skills, and practicing them in vivid detail and with increased accuracy. It was a fundamental upgrade from the mental imaging thought to be characteristic of *Homo erectus* and responsible for the species' ability to maneuver larger home territories and leave Africa. Ariane Burke writes of the feedback between visuospatial abilities and the social use of them, leading to further changes in cognition:

> The development of a modern hunting and gathering way of life could have conferred an adaptive advantage. . . . It may also have fostered the development of cognitive differences between AMHs and Neanderthals. The challenge of maintaining complex, spatially extensive social networks, implying heightened mobility and spatial awareness, requires the deployment of specific cognitive skills related to wayfinding, stimulating the development of spatial abilities that could eventually lead to changes in spatial cognition. (Burke 2012, 232)

Although Bruner and colleagues do not mention genetic drift in small populations as a possible source for changes in the parietal areas, a mutation could have arisen in a small population and been retained through inbreeding. Perhaps, just as Daniel Matute's (2013) work on genetic drift and fixation of traits suggests, early humans who were restricted to small bands could well have had advantageous, neutral, and slightly deleterious mutations that were retained because of inbreeding, and then, as he also suggests, some changes might require natural selection to fix them in a population. Skills sharpened by parietal expansion would be supremely useful for early humans who progressively expanded their territories. We see the absence of front-to-back parietal expansion and the absence of abilities to manage wider territories in the Neanderthals, and we add that to our knowledge that the parietals are responsible (along with the prefrontal lobes) for visuospatial reckoning. While an earlier member of our genus, *Homo erectus*, migrated out of Africa to Eurasia, he must have been challenged far more than *Homo sapiens*. By the time anatomically modern humans reached more northern climates, they would distinguish themselves (if they had not already in the Levant) by mastering expanding territories, unlike their "sister lineage," the Neanderthals, who tended to restrict their home territories.

The capacities that early *Homo sapiens* enjoyed would be similar to what we have today—a sense of space, of our bodies and hands in that space and interacting with objects, and an ability to imagine and manipulate all of this, through interaction with the prefrontal cortex. Our modern human abilities deriving from parietal expansion are programmed and captured by the app that summons our Uber ride. It allows us to model in full color and three dimensions whether an asteroid that seems to be headed for Earth will strike it, or not. It allows pilots to train in flight simulators with virtual reality runways. While they were probably not thinking of these functions when they wrote the following, Bruner and Iriki's words are directly applicable: "We suggest that changes in the visuospatial integration functions and in the parietal areas may have represented an essential component for enhancing embodiment capacity. . . . Visuospatial integration, within the perspective of extended cognition, may have had a major influence in establishing current human intellectual abilities and social patterns" (2016, 98).

While the discussion to this point suggests that religious capacity "came along with" other more critical capacities, this, in our view, is placing the emphasis incorrectly. Those other, visuospatial abilities certainly cemented changes in the parietal areas as reliable adaptations, ones that would be faithfully produced again and again to help early humans survive. This argues strongly for an innate quality to religious capacity, which is fundamentally bound to ways of thinking that allow us enjoy roller coasters, solving three-dimensional puzzles, spelunking, and space walks. Expansion of the parietal areas of the brain is ultimately the reason *Homo sapiens* colonized the globe, and now the Moon and Mars. Yet other human capacities may assist our expansion to the rest of the solar system, and on to other star systems.

Eventually, the forms of thinking that came to be defined as part of religious capacity functioned in ways that were strongly patterned through time by culture. Those cultural patterns, in conjunction with moral capacity, served to motivate, organize, validate, and support the social group. Activities relying on improved visuospatial abilities, which determined whether early humans lived or died, received an added boost. They became rationalized through religious cultural beliefs—in yet a different type of cognitive feedback loop. To call visuospatial reckoning the "initial adaptation" and religious capacity "the add-on" would overlook the previous 55–65 million years of underpinnings, which made something like religious capacity, very likely, extremely useful, and a source of human comfort in the face of unsolvable problems and unanswerable questions. By the time religious capacity came along, human beings were already examining their own thoughts. That would set us apart from all the rest of nature, itself, and never let us stop asking the questions—what, how, where, when, and why?

Finally, we should think carefully about the importance of abilities imparted by the parietal areas, specifically for religious capacity. One feature of all religious belief systems (i.e., cultural products, rather than the genomic and neurological substrate they are reliant upon) is the imagining of other spaces and places of supernatural importance. Mythologies have their own landscapes and diagrams of layers, sections, phases, and specially designated places that have gates, doors, openings in the ground, and other ritual access mechanisms that mimic landscapes on Earth. Supernatural beings populate these imagined realms, and maps are common, visual or verbal, in which we can see the fine work of the expanded parietal lobes in conjunction with prefrontal association areas.

Religious capacity and religious thinking make special use of the entire gamut of visuospatial processing abilities in imagining and eventually believing in spiritual worlds and beings. The concept of autonoetic consciousness finds a place here. It refers to the human ability to mentally place oneself in the past, future, or in counterfactual situations, and then to examine our own thoughts in these situations. Recall that the human LHI constantly cranks out explanations about the way things work. It does not matter whether an explanation is based in science or rationality, the LHI simply makes up explanations (Gazzaniga 1999). The operation of the parietal lobes in religious thinking is akin to mental time travel. It is also related to "a theory of mind," only in this case human understanding is extended to what spirits or gods think, or "what God wants for us." Out of all these abilities, humans develop theories about the relationships between humans and supernatural beings. These theories, or theologies, are cultural products but strongly dependent on neurological foundations described in these three articles.

In parietal expansion, we have some of the needed pieces for religion as a social institution: imagined spaces, and interpretations of the actions, intentions, and goals of others, including spirits, gods, and other supernatural beings. With the expansion of the parietals, the evolutionary stage was set for the development of human theologies composed of structured and integrated theories of the relationships between humans and the supernatural. In that enormous task, religious capacity would draw heavily from moral capacity, and use yet uncounted brain capacities to accomplish the task.

Sequential Timing of the Emergence of Religious Capacity, and Looking Forward

A benefit of definitions and time periods for the foundational building blocks undergirding religious capacity is that it gives us a framework for analysis of those aspects of human life that we now define as fundamentally "religious," such as compassion and charity. One could examine each of these concepts, and many others, by looking at each layer of development: primate sociality at 55–65 million years ago; a basic ape model from about 19 million years ago, in the Miocene; a realignment of some senses with improvements in vision and hearing; a downregulation of aggression; increase in social tolerance; and an uptick in intellect to control aggression at 8–10 million years ago; an upregulation in sensitivity (environmental, social, and emotional); the emergence of moral capacity with *Homo erectus*, after the species controlled fire at 1–1.5 million years ago; and finally, expansion of the parietal areas (especially the precuneus), giving modern humans the necessary brain structure to construct theologies, along with excellent skills in visuospatial reckoning.

A third article of this series will extend the theoretical model presented in the first and this, the second article in the series, by providing an example of the type of analysis described above, focused on "compassion." This will bring our viewpoint well up to the present day. Then, we shall provide a teaching tool about early *Homo sapiens* and very early religious thinking and behavior. Only with *Homo sapiens* do evolutionary trends come together that began emerging 55–65 million years ago in order to produce the human biological trait of religious capacity.

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