

benefits of cooperation [8]. Bacteria also cooperate to kill. They secrete bacteriocin molecules that kill unrelated bacteria, and so reduce competition for their clonemates, who are immune to the bacteriocins [9].

Males and females join together to raise offspring, but each can be selected to contribute differently to parental care [10]. And there is conflict between these parents and their offspring over how much care to give the offspring [11]. For example, while a foraging bird could be favoured to share its food between its chicks, each chick would like to receive a greater share of that food. And they would be favoured to obtain an even greater share when they are less related to their siblings, and hence have less aligned interests [12].

One of the most exciting aspects of conflict within cooperative societies is that we can often make very clear predictions about when it would occur and the form it should take. Combined with elegant empirical studies, this has led to work on conflict providing some of the greatest success stories of the social evolution literature. For example, the workers in colonies of ants, bees and wasps have been shown to adjust the sex ratio of larvae being reared in the colony with extreme precision, towards the worker optimum, and away from the queen optimum [4]. Social insect workers may be sterile helpers, but they do not blindly help the queen — they still look after their own interests.

An appreciation of this potential for conflict and cooperation has led to a much more nuanced understanding of societies. Except in extreme cases, like clonal groups, assuming that individuals are behaving ‘for the good of the group’ will lead to error [2,13]. Instead, we see individuals trying to maximize their fitness, which can sometimes involve cooperation, but sometimes involve conflict.

The papers in this special issue show where the study of conflict and cooperation is heading. They provide a range of fascinating examples, from genes to complex animal societies, which are fast becoming tomorrow’s success stories. Furthermore, by bringing this work together, this collection of papers illustrates how different study systems offer different advantages to understanding the

evolution of conflict and cooperation. For example, with multicellular systems we can more easily record individuals’ behaviours in a group to study cooperation and conflict, while the search for the underlying genes driving these behaviours is more complex. Whereas microbes offer tractable systems in which we can more easily detect the mechanisms underlying the behaviours and when they are driven by gene loss or acquisition, gene mutations, changes in the genomic architecture or regulation [14]. The papers review how we have exploited advances in technology to study sociality in much greater depth, detecting the mechanisms underlying cooperation and conflict at a much finer scale, to determine how the tension between conflict and cooperation plays out in the real world.

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Feature

Uncovering the roots of religion

Religious beliefs can inspire collaboration on enormous scales, as witnessed by monuments like ancient cathedrals and mosques. At the same time, they are also known to fuel conflicts which haunt us to this day. The most powerful and pervasive ‘big god’ beliefs appear to be a relatively late-occurring phenomenon in the evolution of complex societies, as a comprehensive new study suggests. **Michael Gross** reports.

The fire that destroyed the roof and the spire of Notre Dame cathedral in Paris on April 15 united people around the world in their shock and grief at the damage to — and narrowly avoided loss of — an icon of global cultural heritage. The cathedral meant many different things to the many thousands of visitors it attracted. It was a place of worship for some, an architectural marvel for others, and the mascot of a Disney movie as well as a Victor Hugo novel for many.

The design of gothic cathedrals where the weight of the roof and upper walls is channelled outwards by the buttresses implies that the destruction of the roof could have very easily caused the entire cathedral to collapse like a house of cards. The sheer implausibility of people erecting such a gravity-defying monument with the mechanical tools available in the 13th century reminds us that religion is a very strong motivator that can get large numbers of people to cooperate and achieve amazing results.

While Notre Dame is closed for repairs, there are half a dozen other gothic cathedrals around northern France inviting visitors to ponder the question of just how ardently people must have believed in their cause to erect stone arches in the sky with their bare hands.

The project to build Notre Dame was launched around 1163, and construction completed around 1300. During that same timeframe, the same religion also inspired a very different kind of endeavour, namely the crusades against the Muslims in the Middle East. From the Third Crusade (1189–1192)

through to the Ninth Crusade (1271–1272), the major Christian powers of Europe spent an inordinate amount of effort trying to conquer what they called their Holy Lands from people whose only fault was that they worshipped a different god.

Clearly the strong religious feelings in mediaeval Europe were able to inspire constructive cooperation as well as conflict. Both can be described as two sides of the same coin, the strong group identity provided by a powerful religion. But where did this particularly strong religiosity, matched by the Muslim Arabs, but not, for instance, by pre-colonial high cultures in the Americas, come from?

Birth of big gods

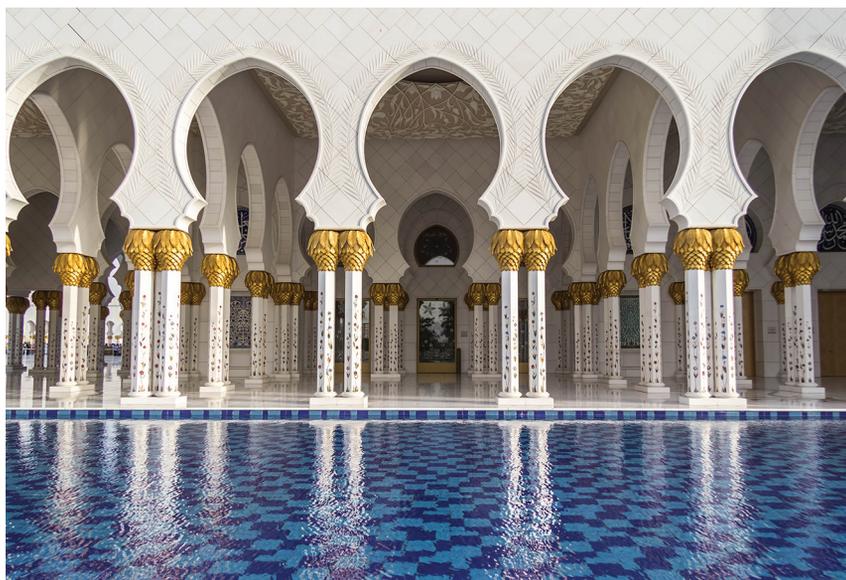
To people of Christian or Muslim background it may appear the norm that an omnipotent deity makes rules about how they should live their lives. However, these so-called moralising high gods or, more colloquially, ‘big gods’ were the exception in many parts of the world before Arab conquests and European colonialism spread Islam and Christianity far and wide.

In pre-colonial times, the Americas, for instance, had religious rituals and deities of many forms, but there is no evidence suggesting that any of these cultures believed in gods that were concerned with the interactions among mere mortals.

History suggests that the less demanding ‘nature religions’, where rituals and offerings to deities were thought necessary to avert extreme weather events and natural disasters, gave way to the more stringent big god religions as societies grew larger and more complex.

The big question is which of these changes is the cause and which the effect. Did complex societies give rise to moralising high gods, or did conversely the cultures that happened to have big gods have an advantage in evolving to higher complexity? Several attempts to answer this question, each based on a sample covering a limited number of populations, have yielded contradictory results.

To help provide a definitive answer to this much-debated question, Harvey Whitehouse, Pieter François, and Patrick Savage from the University of Oxford, UK, led efforts to use a new big-data



Religion reflected: Ambitious architecture of sacred buildings has long reflected the strong beliefs and the spirit of cooperation inspired by major religions. This photo shows the modern Sheikh Zayed Grand Mosque at Abu Dhabi, United Arab Emirates, combining a variety of influences from across the Islamic world. (Photo: Andrew Moore/Flickr (CC BY-SA 2.0).)

tool, the Seshat Global History Databank (seshatdatabank.info), to examine the evolution of religion and complex societies in 414 polities (independent political units) in 30 regions around the world (*Nature* (2019) 568, 226–229).

Seshat’s director, Peter Turchin from the University of Connecticut at Storrs, USA, who co-founded the database with Whitehouse and François in 2011, also contributed to the new study. “Our multidisciplinary project integrates the expertise of historians, archaeologists, anthropologists, social scientists as well as data scientists into a state-of-the-art, open-access database,” Turchin explains. “The databank relies on the work of dozens of experts around the world who helped to assemble detailed data on social complexity and religious beliefs and practices from hundreds of polities, beginning with Neolithic Anatolians (today Turkey) in 9600 BCE.”

“Seshat allows researchers to analyse hundreds of variables relating to social complexity, religion, warfare, agriculture and other features of human culture and society that vary over time and space,” Pieter François notes. “Now that the database is ready for analysis, we are poised to test a long list of theories about human history.”

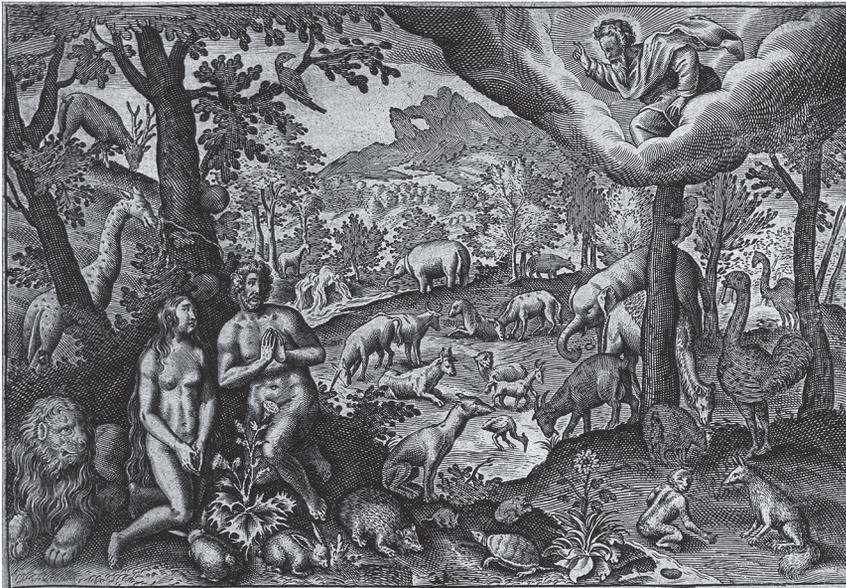
To address the question about big gods and complex societies, the research team coded 55 variables,

including 51 describing the complexity of a society, which they condensed to a single principal component, and four that described the religious belief system prevalent in a society, such as the belief in moralising high gods and/or in broad supernatural punishment. The Buddhist idea of karma is an example of the latter, more general idea of sanctioning human behaviour.

Of the 30 geographic regions covered by the study, ten showed no evidence of big god religions in pre-colonial times, including all six regions in the Americas, and a few in Asia and Oceania.

Among the 20 regions where big gods did emerge, the authors identified 12 that had data of sufficient complexity concerning the times before and after emergence of big god beliefs to construct a timeline and address the question of which came first. If big gods were the catalysis that helped societies to grow in complexity, one would expect to see a rapid increase in complexity after the appearance of big god beliefs. However, the authors could find no evidence of this sequence of events in any of the 12 regions for which they have established timelines.

Conversely, in ten of the 12 regions studied, they found that the belief in moralising gods was established within 100 years after society reached a certain



Big god: High gods setting moral standards and policing them are a relatively recent phenomenon in the evolution of human societies. This line engraving of Adam and Eve facing an angry God was made as an illustration for a printed Bible. (Image: Wellcome Collection (CC BY 4.0).)

threshold of complexity described as a megasociety. This complexity threshold is typically reached when a population exceeds a size of about one million.

It is also worth noting that the evolution of writing (Curr. Biol. (2012) 22, R981–R984) typically preceded moralising high gods by four centuries. This finding rules out the alternative explanation that the age of big god religions might be underestimated for a lack of written documentation. “Historical evidence suggests that writing evolved first as a method of accounting and standardisation for large-scale societies, their ritual practices, and taboos regarding human–divine interactions,” explains Patrick Savage from Keio University, Japan, the corresponding author of the paper. “Only later it was used to standardise specifically pro-social moralising doctrines regarding how humans should treat one another as societies became even more complex.”

Causing conflict

The onset time of belief in moralising high gods has been the focus of severe criticism of the *Nature* study. Does the absence of evidence for such big gods count as evidence of their absence? Bret Beheim from the Max-Planck-Institute for Evolutionary Anthropology at Leipzig, Germany, and colleagues

have argued in response to Whitehouse *et al.* that this assumption produces a ‘forward bias’ shifting the onset time of big gods forward with respect to the measured complexity increase (<https://psyarxiv.com/jwa2n>).

Using the Seshat data, Beheim and colleagues shifted the onset time for big gods back by only one century to account for the possibility of data loss in the early phase of a big god religion. Under this assumption, they come to the opposite conclusion, namely that moralising high gods precede the rapid rise in social complexity — in line with the finding of the original study that the gap between the two was less than a century.

A group of historians involved with the Database of Religious History (DRH; religiondatabase.org) and led by Edward Slingerland from the University of British Columbia at Vancouver, Canada, has also criticised the study and warned that it neglected established scholarship in the history of religion. Their comment is due to be published in the *Journal of Cognitive Historiography*. Clearly, the capacity of religion to cause conflict is undiminished.

Big gods may not have had much of a role in early city states, but they became an important part of historical events when conquering

kingdoms turned into empires. As the Islamic and Christian conquests have demonstrated, the belief in an all-powerful deity can provide a shared sense of identity to a patchwork of populations with different cultures and languages.

This sense of identity defined by the belief in the ‘right’ god has proven the most powerful motivator for cooperation with and compassion for other people who are not blood relations and may not even speak the same language. It has also motivated the proliferation of aggression against other people who also believed in a big god, but, unfortunately, in a different one.

Beliefs before moralising gods

The pre-colonial cultures of the Americas provide several examples of complex societies that evolved writing but no moralising gods. “The Americas are interesting in this regard because there are multiple writing systems in Mesoamerica — without the appearance of the kind of moralising gods that were believed to promote prosociality among humans,” explains Alan Covey from the University of Texas at Austin, who is also a co-author of the *Nature* paper. “The Incas (and probably Wari) had a non-written system that performed elements of accounting and narrative management that are seen in other early writing systems, also without moralising gods.”

It is impossible to tell, Covey suggests, whether or not American civilisations might have come up with moralising gods if Europeans had left them alone a few centuries longer. Perhaps there was not enough time, but then again, Covey notes that there are many other cultural differences, for instance that “in the Inca world you don’t see the kind of emphasis on a soul or metaphysical self that can be rewarded or punished in an ultimate sense.” So it is conceivable that humans, even in complex societies, can live just fine without moralising gods — as countless communities of hunter-gatherers have always done.

Further back in time, before the advent of agriculture, history can’t help much and archaeology can only provide circumstantial evidence to the origins of religion, such as burial rites. However, if religious beliefs evolved and spread

like genetic traits, as has been shown for languages and fairy tales (Curr. Biol. (2018) 28, R679–R681), it might be possible to trace a phylogenetic tree based on hunter-gatherer societies that were observed in modern times.

Hervey Peoples from the University of Cambridge, UK, and colleagues have used this approach based on the religious beliefs of 33 hunter-gatherer societies recorded in the 20th century (Hum. Nat. (2016) 27, 261–282). The authors coded data available for these societies to capture the presence of five separate kinds of religious beliefs, including animism (defined as “the belief that all ‘natural’ things such as plants, animals, and even such phenomena as thunder, have intentionality (or a vital force) and can have influence on human lives”), belief in an afterlife, shamanism (defined as “the presence in a society of a ‘shaman’ (male or female), a socially recognized part-time ritual intercessor, healer and problem solver”), ancestor worship, and high gods. Additional parameters covered the question of whether or not the deceased ancestors or high gods were active in that they could influence people’s lives.

From their phylogenetic analyses, Peoples and colleagues concluded that animism, which was present in all societies studied, was the earliest kind of religious belief. They suggest that animistic thinking is a natural consequence of the evolution of the human ‘theory of mind’ — the tendency to attribute intentions and thoughts to other humans and by extension also to animals and objects. As such, animism may have arisen early in hominin evolution, even before the origins of language. In this case, it would also have been present in our closest hominin relatives, the well-studied Neanderthals and the newly emerging Denisovans (Curr. Biol. (2019) 29, R105–R107).

The belief in an afterlife was the next step to evolve, but did not appear in all societies. This is an important interdisciplinary nexus, as archaeologists can provide evidence from burial sites, and linguists studying the origins of human language have noted that emerging rituals such as burials may have shaped the early forms of language.

The phylogenies indicate that shamanism arose after the belief in an



Multi-functional: The Pancaraksa (five protections) is a Buddhist text written in Sanskrit. This copy in Ranjana script dates from 1653 CE. (Image: Wellcome Collection (CC BY 4.0).)

afterlife. The authors suggest that the sense of being watched by the spirits of the dead created the need for a shaman to manage relations with the spiritual realm. In the sample studied there is only one exceptional case where shamanism is present without the belief in an afterlife.

The worship of ancestors, naturally, also depends on the belief in an afterlife and appears to have evolved after the other religious traits already discussed. Especially in its stronger form, where dead ancestors can influence the living, it is quite rare among surviving hunter-gatherer societies.

High gods, who may be worshipped as creators, for instance, are the most recent trait to evolve in the phylogenies of Peoples and colleagues. Especially in the stronger variant where they may influence the living, they are quite rare among hunter-gatherer societies.

In an earlier investigation of the moralising high gods hypothesis as discussed above, covering complex societies in Austronesia, Joseph Watts from the University of Auckland, New Zealand, and colleagues also used

phylogenetic trees derived from the study of the language families in that region (Proc. R. Soc. B (2015) 282, 20142556). These authors found that moralising high gods follow political complexity, but that a more general concept of supernatural punishment may precede it.

Analysing correlations between, for instance, religious beliefs and other kinds of cultural and societal elements in human societies is complicated by the fact that all humans alive today have shared ancestry and are thus not independent of each other. Phylogenetic analyses of such traits have the advantage of taking common roots into account. Moreover, separate phylogenetic studies based on genes, languages, religious beliefs and other cultural expressions provide opportunities for researchers from these different fields to compare notes and to trace back the lineages leading not just to the origins of religion but to the origins of our species.

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