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Review

From hominins to humans: how *sapiens* became behaviourally modern

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This paper contributes to a debate in the palaeoarchaeological community about the major time-lag between the origin of anatomically modern humans and the appearance of typically human cultural behaviour. Why did humans take so long—at least 100 000 years—to become 'behaviourally modern'? The transition is often explained as a change in the intrinsic cognitive competence of modern humans: often in terms of a new capacity for symbolic thought, or the final perfection of language. These cognitive breakthrough models are not satisfactory, for they fail to explain the uneven palaeoanthropological record of human competence. Many supposed signature capacities appear (and then disappear) before the supposed cognitive breakthrough; many of the signature capacities disappear again after the breakthrough. So, instead of seeing behavioural modernity as a simple reflection of a new kind of mind, this paper presents a niche construction conceptual model of behavioural modernity. Humans became behaviourally modern when they could reliably transmit accumulated informational capital to the next generation, and transmit it with sufficient precision for innovations to be preserved and accumulated. In turn, the reliable accumulation of culture depends on the construction of learning environments, not just intrinsic cognitive machinery. I argue that the model is (i) evolutionarily plausible: the elements of the model can be assembled incrementally, without implausible selective scenarios; (ii) the model coheres with the broad palaeoarchaeological record; (iii) the model is anthropologically and ethnographically plausible; and (iv) the model is testable, though only in coarse, preliminary ways.

Keywords: niche construction; behavioural modernity; hominins

1. DEVELOPMENTAL NICHE CONSTRUCTION

The theory of niche construction begins with the insight that agents individually and collectively shape their environment. Selection results in the adaptation of agents to their environments. But agents also adapt their environments to their own phenotypes. Termites flourish in the environments they experience in part because they experience environments they have built themselves [1,2]. Much work in niche construction focuses on the effects organisms have on their selective environment. But termite mounds and beaver complexes do not just modify the effects of the physical, social and biological world on adults. They also structure the environment in which the next generation develops. In modifying their own environment, many organisms also engineer the developmental environment of their offspring. As the effects of genes are often sensitive to their context [3], these effects on developmental environment influence the next generation's phenotypes. Thus, termites develop in a world built by and for termites, and so their developmental environment has been stabilized. Compared with their presocial ancestors, termite genes are expressed in a narrowed range of developmental environments, and hence the phenotypic effects of those genes are more predictable (see [4,5] on the importance of these environment–gene expression effects).

Developmental niche construction is of profound evolutionary significance. Indeed, there is a case for the idea that complex multi-celled animal life depends on intergenerationally engineered developmental environments. It is a truism of evolutionary theory that cumulative evolution depends on high fidelity inheritance, and high fidelity inheritance depends on sending developmental signals across the generation with high fidelity [6]. But complex multi-cellularity increases the demands on these mechanisms. Multi-celled organisms have evolved many times [7], but only in a few cases have these lineages generated impressive disparity and diversity. The evolution of complex multicellularity requires the evolution of a developmental cycle, and that in turn requires a major advance in mechanisms of inheritance. Protist genes never have to build the critical inner cellular structures of protists. The cell divides, but crucial intercellular structures do not have to be constructed from scratch in the descendant cells. Reproduction can largely be reduced to growth and fission. In contrast, organs and tissues do not exist in miniature in fertilized ova.

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Thus, one major transition in complex multicellularity is a transition from (largely) preformationist to epigenetic development. Complex multi-celled organisms exist only because there are developmental cycles in which key structures of adult organisms are rebuilt from scratch in the new generation. So, the problem of cross-generation fidelity is more pressing for macrobes than for microbes. It is likely that increased parental control of developmental environments was crucial to the Metazoan radiation. For genes to have stable phenotypic effects, they must be inserted into a structured and predictable developmental environment. Even if replication is of high fidelity, it is of no use to just make a new set of genes: the parental generation must build an environment in which those genes are used in the right way. The more complex the developmental pathways, the more the gene-reading environment is as important as signal quantity and fidelity. The egg is such a structured system; it is arguable that its invention is the major breakthrough that allowed the flow of genes across the generations to orchestrate development in a fine-grained and reliable way [8]. It is adapted both to function in an environment and to provide an initial set of triggers for gene expression. Whatever the fate of this specific suggestion, macrobe evolution depends on the evolution of increased developmental control.

The evolution of complex form, then, depends both on high fidelity genetic inheritance and on the stability of the genotype–phenotype map. This stability depends, in part, on control by the adult organism of the environment of gene expression. But while genetic inheritance is the most fundamental system of inheritance, it is not the only one [9]. Intergenerational social learning is another, and while the overall importance of learning as a mechanism of inheritance is a matter of much debate, it is widely agreed to have been important in human evolution [10–12]. The core argument of this paper is, first, to show that the fidelity of social learning depends both on the intrinsic accuracy of cognitive learning mechanisms and on the control of the developmental environment and, second, to relate this idea to the gradually emerging but profound changes in human material culture; changes that emerged between 100 000 (or a little earlier) and 50 000 years BP.

I begin with the interactionist perspective on social learning. Human cultural life depends on our capacity to accumulate and transmit cognitive capital. Individually and collectively, humans act effectively in their economic, social and technological worlds largely because their lifeways are supported by information they inherit from the previous generation. Such transfer depends, in part, on specific cognitive adaptations for social learning (for example: language, imitation). But it also depends on adapted learning environments, on developmental niche construction. Humans accumulate cognitive capital through interaction between intrinsic, genetically canalized features of human minds and adaptively organized developmental environments. Thus, identifying the role of niche construction in human evolution is not an alternative to the dual-inheritance models that Stephen Shennan and others have been recently developing [13]. Rather, identifying the ways humans organize the developmental environment of the next generation helps explain the fidelity and bandwidth (the volume) of cultural inheritance, the features that make it central to human evolution.

Apprentice learning offers a helpful conceptual model of the synergy between organized learning environment and individual cognitive adaptation. Apprentice learning is a very powerful mode of social learning, making possible the reliable re-acquisition of complex and difficult skills. It is learning by doing. But it is learning by doing in an environment seeded with informational resources. These include raw materials processed, partly processed, unprocessed. In addition, full and partial templates of the final product are available to guide action. Moreover, there are many opportunities to learn by observing highly skilled practitioners. Often advice is available from both experts and peers, for learning is often social and collaborative. Apprentice learning depends on individual cognitive adaptations for social learning but it depends as well on adaptively structured learning environments. I will argue that this mode of social learning has deep roots in *sapiens* history.

The apprentice learning model has four important virtues. First: it identifies a form of learning that can be assembled incrementally. The reliable transmission of skill can begin as a side-effect of adult activity, without adult teaching or adaptations for social learning in the young. Once established, it then brings with it selection for cognitive and social changes that increase the reliability or reduce the cost of learning. But rudimentary and reliable skill transmission does not presuppose such adaptations [14]. Second, apprentice learning is known to support high fidelity, high bandwidth knowledge flow. Until recently, much technical competence in the industrial society depended on apprentice learning. Third, the model fits ethnographic data quite well. Formal educational institutions and explicit teaching are not prominent parts of traditional society. But many forager societies organize and enhance children's participation in economic activity, and this supports the transmission of traditional craft skills [15,16]. Finally, the model can be tested against the archaeological record, though only in a preliminary, suggestive, way.

One test depends on applying the model to a famous problem in palaeoanthropology: the origins of 'behavioural modernity'. That problem arises out of an apparent disjunction between the origin of our species and the archaeological record of our cultures. From about 50 kyr BP, the archaeological record seems to show human cultures that resemble foraging cultures known from historical records [17–20]. Those ancient members of our species often had a diverse, complex and regionally well-differentiated technology. They were ecologically flexible, exploiting a wide range of resources, responding appropriately to seasonal fluctuations, and able to penetrate quite demanding habitats. They were capable of crossing significant stretches of ocean in boats or rafts. Their lives were rich in the use of physical symbols. They stylized some of their technology. They made jewellery, and almost certainly used ochre to decorate their bodies and goods. They buried their dead.

There is as yet no clear evidence of music, but that may well reflect limits on preservation rather than limits on these ancient cultures. In short, they were 'behaviourally modern'.

Modernity does not, however, coincide with the first appearance of our species (or any other). Anatomically modern humans—our species—seem to have appeared in Southern Africa at some stage during the period 200–150 kyr BP [18,21]. But those first humans do not seem to have been behaviourally modern. Their technology seems to have been less diverse; their ecology less flexible; their cultural lives less mediated by physical symbols. It was once thought that this ensemble of contrasts between behaviourally modern and early *sapiens* arose abruptly in hominin history, 50–60 kyr BP. This saltationist model is still sometimes defended, but there seems to be good evidence that the modern cultural ensemble arose gradually in Africa, and that its abrupt appearance in the European record is the signature of migration (and perhaps indigenous response) rather than rapid biocultural evolution [20,22–24]. Even so, there seems to be a contrast between the more recent *sapiens* cultures and those of the first two-thirds of the history of the species, and this has led to a vigorous debate in palaeoanthropology about the identification of behavioural modernity, its significance and how its origin is to be explained. I will first review this debate, and then show that niche construction theory enables us to develop a satisfying solution to the puzzle that is supposedly at its heart.

2. BEHAVIOURAL MODERNITY

It can be reasonably doubted whether there is a qualitative difference between the earliest *sapiens* cultures and those that established in Africa, Europe, the Middle East, Asia and the Sahul 50 000 years ago or so. Perhaps the supposed cultural difference is a result of our imperfect record of the cultural and cognitive life of the earliest *sapiens*. Moreover, Peter Hiscock and Sue O'Connor point out that rare technologies are less well preserved when we look deeper into the past. The record is not just imperfect, it is biased, showing us less of the most ancient cultures [25,26]. Moreover, we would expect a smaller and geographically restricted set of populations to have a less varied material technology than larger and more widespread populations, even if their fundamental cognitive capacities and social organization are the same. Even so, in archaeology and palaeoanthropology, the prevailing orthodoxy holds that there is a qualitative difference, and I shall accept that consensus in this paper. The nature of that qualitative difference, though, is a matter of great dispute, and this section and the next identify the change to be explained.

On one view, behavioural modernity is a cluster of cognitive capacities that are both critical in themselves to contemporary human culture and which leave a detectable signature in the historical record. Perhaps, the most influential paper in this genre is Sally McBrearty and Andrew Brooks' *The Revolution That Wasn't* [24]. As the authors see it, these cognitive competences are: behavioural and technological innovativeness; abstract thinking (the capacity to think about the elsewhere and the elsewhen); the ability to plan as an individual and to coordinate with others; and the ability to make and use physical symbols. And they suggest potential archaeological signatures of all of these capacities. The most obvious are technological signatures of innovation. Innovation is signalled by any or all of: new stone technologies (blades, microblades, backing); the increasing use of new materials like bone and antler; a larger toolkit (e.g. projectiles); and an increased control of fire. Likewise, they argue that planning and coordination can be detected in the historical record, for example, in the expansion of the human range into challenging environments. Moreover, the capacity to hunt large and dangerous animals without excessive risk is the evidence of planning, cooperation and coordination, and not just of technological ability. Symbolic behaviour, too, they argue, leaves a detectable signature. The most obvious is self-adornment with beads and ornaments, but it is also evident in the use of pigment, in decorated objects, in burying the dead and in the imposition of style on utilitarian objects.

Of course, these crucial human capacities are not instantly recognizable in the human record: they are recognizable only when they have been magnified by history and culture. An innovation will only be recognizable once it has established and spread. We do not see origins in the record, but the cultural effects of innovations as their effects accumulate. We do not see the first instance of an innovation; we see it once it has become a routine feature of the community toolkit. But over time and place, these elements of the 'modernity suite' will leave traces. The physical traces of behaviourally modern humans will be different from those left by their more technologically and ecologically constrained ancestors.

One crucial problem with the project of reading ancient minds from ancient behaviours is that technology and resource use reflect the local economic landscape as well as cognitive capacity. The techniques used and the resources exploited depend on agents' abilities but also on relative costs and benefits. These relativities depend on environment and demography. Haim Ofek, for example, suggests that fire keeping was probably the first technical specialization, and points out that such specialization is only possible once market size—a function of demography—reaches a threshold [27]. So if we do not see the systematic exploitation of hard-to-process foods (birds, fish, grain), this might just show that those humans had no need to impose those burdens on themselves, not that they were incapable of carrying them. The 'broad spectrum revolution'—the extension of the human ecological base to birds, fish, grain—may well be a response to the exhaustion of more valuable resources as populations expanded, signalling new needs, not new capacities [28].

For this reason, it is sometimes thought that symbolic behaviour leaves a more reliable trace in the record than do the capacities for innovation and flexibility. In contrast to these technical competences, symbol use is not a response to immediate environmental demands. Moreover, symbolic behaviour seems to be distinctive

of a specifically human form of social life. People do not just belong to groups. They recognize themselves as a member of a group; and often treat that fact as a central feature of their lives. Individuals identify with their communities, and identity with their distinctive norms and customs. When agents use symbols that are insignias of their group, or of their place in that group, we know that agents are aware of and identify with their groups. Thus, physical symbols have been identified as the benchmark of behavioural modernity (hence the very recent excitement generated by João Zilhão's claim to have discovered indisputably indigenous Neanderthal shell jewellery [29]). Symbol use is a sign of a cultural revolution; a transition from coexistence with others to identifying oneself with others. Moreover (the idea goes), the archaeological record suggests that this is a recent development, and so distinctive of recent *sapiens* populations (and possibly those of our large-brained sister species). Thus, McBrearty and Stringer clearly thinks of symbols as forging a new form of social life when they write:

> 'The ability to manipulate symbols is considered an essential part of modern human cognition and behaviour, although definite traces of symbols in the archaeological record are difficult to recognize and are often obscured by the ravages of time. All humans today express their social status and group identity through visual clues such as clothing, jewellery, cosmetics and hairstyle. Shell beads, and haematite used as pigment, show that this behaviour dates to 80 000 years ago in coastal North and South Africa' [30, p. 793]

Thus, archaeologists have come to focus on material symbols as the distinctive signature of the modern mind, both because symbol use is important in itself and because it is more reliably detected than other elements of the modern cognitive suite.

I am sceptical. Insignias of identity and role are not archaeologically transparent. Consider, for example, recent arguments that insignia symbols have quite a deep African history, long pre-dating the Upper Palaeolithic [31–34]. The most systematic early examples of possible 'symbolic behaviour' are burial of the dead and the use of ochre. But while there is evidence of fairly systematic burial of the dead [24], the significance of this practice is not clear. It is one thing not to treat as refuse the corpse of your father, sister, daughter. It is another to construct a magical narrative about their ongoing significance. In the absence of grave goods, there is no evidence of magical narrative. In short, while burial of the dead is evidence of emotional attachment, it is not evidence of anything else. Ochre, too, is ambiguous in its significance. Ochre may have purely utilitarian purposes: as a preservative, insect repellent or ingredient of glue. But suppose, in some cases, such mundane uses can be excluded. It does not follow that the use of ochre is symbolic, either in the sense of displaced reference, or in the sense of social marking. It could, for example, be used in signal enhancement: making a face, a shield, a person more visible, startling or threatening. Imagine, for example spooking animals by suddenly emerging from cover in a game drive. Signal enhancement would make such a tactic much more effective. Kuhn & Striner [35] make a somewhat similar suggestion in the context of interpersonal interactions. Camouflage is another possibility: for example, using ochre to break up contours. This suggestion seems especially relevant given recent reports of Neanderthal use of dark ochres.

Moreover, there is good reason to think that the fabrication and use of physical symbols, like other material technologies, is sensitive to demography, economics and social organization. In itself, it is not a direct reflection of social cognition. In an important discussion, Kuhn and Stiner compare ochre and shell-based beads as signalling systems. Ochre significantly precedes the use of shells as beads in the archaeological record; ochre use may be as early as 280 kyr BP [29]. As we have seen, ochre has uses other than human-to-human signalling. So perhaps its use was established before humans regularly altered their bodies and garments to send social signals, and was then exapted as an existing technology to send signals. That may explain why shell-beads, which have no use except as signals, arrive later in the record. However, Kuhn & Stiner show that ochre and shell-based beads have different properties as signals. They suggest that shell-based systems are well-suited for within-group signals. Shells can be standardized and compositionally organized. Their pattern and placement can itself be a signal, and one that can be duplicated or systematically varied. Having (say) three rows of shells rather than two around one's neck can be a discrete, regular and repeated signal. As a consequence, shell-bead systems have the capacity to encode precise information about rank, role, age, status, gender or even individual identity, just as ornithologists use the sequence of colour bands on a bird's leg to identify individual birds. But while being potentially precise and rich, such signals have low amplitude: the precise pattern is difficult to see at any distance. Moreover, if the comparison with symbols of rank or identity is apt, the system is both somewhat complex and arbitrary. The significance of a particular array will be obvious only to insiders. In contrast, ochre has a high amplitude. A shield, a face or a garment coloured in a distinctive way is visible and recognizable at a distance. In contrast to shell-bead signals, ochre-based signals would be well-designed to signal group membership or identity to another group. While such signals are arbitrary, they are neither part of a complex system, nor are they displaced in space and time from their referents. They are like national flags, and as with flags, their role could be learned simply and quickly by individuals in other groups.

If these considerations are persuasive, the appearance of ochre, beads and the like in the archaeological record is an effect of demographic change. Signals and symbols are not just information: symbols of rank sometimes serve to assert and reinforce hierarchy, not just signal an agent's place in a hierarchy. But to the extent that material symbols are information-sending systems, in simple social environments they have no function. There are no strangers to inform. This demographic suggestion is supported by the fact that physical symbol making

emerges at different times in differing *sapiens* groups [19]. According to the population-structure hypothesis, the appearance of physical symbols of group membership in the archaeological record does not mark the first appearance of people thinking of themselves as members of groups. Rather, it is the invention of advertising. Members of a group only needed to badge their identity—to wear insignias—once their social world became dense. After that threshold, they regularly met others who did not know them as individuals located in a specific network. That transition selected for physically advertising group membership [36–38]. Beads and similar low amplitude, short-range signals appear later, as groups become more internally complex, more differentiated and perhaps more hierarchical. Physical symbols, then, are just one fallible indicator of cultural richness. There is no palaeoanthropological golden spike, no material trace left when and only when agents live in social worlds that fall within the modern range. Thus, McBrearty's approach, treating modernity as a syndrome of capacities, is preferable to one that focuses on material symbols. However, the syndrome is a proxy for a more fundamental cognitive and social phenomenon, or so I shall argue in the next section.

3. A SAPIENT PARADOX?

> 'if the genetic basis of the new species (i.e. of *Homo sapiens*) is different from that of earlier hominids, and of decisive significance, why is that new inherent genetic capacity not more rapidly visible in its effects, in what is seen in the archaeological record? That rather puzzling question may be termed the sapient paradox. It has significant consequences. They become even more obvious if the transition to *Homo sapiens* is set earlier and relocated to Africa' [34, p. 72]

It is one thing to identify socio-cultural differences between the first *sapiens* and those living 150 kyr later. It is another to think that this difference poses a profound explanatory puzzle. Colin Renfrew thinks the puzzle is so profound that it amounts to a paradox: the paradox of explaining why it took 100 000 years for humans to behave like humans. This is a paradox only if it is conjoined with a 'simple-reflection model' of the relations between cultures, minds and genes: a model in which cultures reflect the intrinsic capacities of human minds, and these in turn reflect our evolved genetic endowment.

Obviously, no-one thinks that the intrinsic structures of the mind determine fine-grained features of culture: they define a range of variation. The particular funeral practices of a group will reflect its idiosyncratic history. But *having funeral practices* of some kind (rather than, say, letting mum rot where she drops) is part of what it is to be in a human culture. We do not treat the remains of our fellows as debris, and that reflects the intrinsic structure of the human mind. This simple reflection model is explicit in Mark Hauser's recent opinion piece exploring potential parallels between Chomsky's theoretical linguistics and theoretical morphology [39]. As Hauser [40] sees it, both research programmes aim to identify innate constraints on individual developmental mechanisms. These in turn define a space of possible variation. Theoretical linguistics characterizes a space of possible human languages. That space is larger than the actual variation but it excludes many readily describable, apparently possible, languages. Likewise, theoretical morphology characterizes (for example) a space of possible skeletons. That space includes many skeletons never found in nature. But it also excludes many that can readily be imagined. Hauser suggests a similar but broader programme for cognitive science: that of characterizing a space of possible human societies—a 'culturespace', a space of social organizations compatible with the innate structure of the human mind [39, p. 195]. The simple reflection model is never explicit in palaeoanthropology, but it is often implicit in much palaeoanthropological theorizing. For example, there is an important strand of work on Neanderthal extinction which presupposes that Neanderthal displacement by *sapiens* must have been owing to some important sociocultural difference between Neanderthal and *sapiens* groups, and that this sociocultural difference, in turn, was due to an intrinsic cognitive difference between *sapiens* and Neanderthal minds. For example, Steven Mithen and others have argued that the Neanderthals lacked full human language [21,41–43].

Indeed, the simple reflection model is implicit in the claim that the *sapiens* paradox is, indeed, a paradox. If ancient *sapiens* and recent *sapiens* were genetically similar (as their morphological similarity suggests), and if genetic similarity implies cognitive similarity, which in turn implies cultural similarity, the cultural contrast between our recent and our more ancient ancestors is indeed surprising. Something has to give. One response, guided by the reflection model, is to try to identify a small but important genetic-cognitive difference between behaviourally modern humans and their early *sapiens* ancestors (perhaps, a difference in cognitive fluidity or language [20,22,44]).

However, it is also possible to reject the reflection model: the complexity and organization of human culture is not sharply constrained by innate features of the human mind. Humans act on their material environment. But they also act on their informational environment, and this informational engineering often has important consequences for cognition and culture. In acting on their informational environment, humans sometimes enhance individual cognitive capacity. The invention of numerals, and of systems of numerical notation, enabled humans to think about quantity in ways that were previously impossible [45–47]. Material symbols enhance memory, as do various other external prompts [48]. Many important cognitive capacities are like literacy: they exist only in environments in which they are supported. So, individual cognitive capacities often depend on cultural resources that amplify learning capacities. Moreover, informational labour can be divided: in cooperative environments, agents serve as memory and expertise stores for one another, and so individual capacity—innate or acquired—does not sharply constrain cultural complexity. Perhaps the most powerful example is that of the natural sciences themselves. Individuals organized

and connected in the right way, and only in that way, are a self-improving, accelerating engine of discovery. Science has been made possible in part by making individual scientists smarter (by providing them with cognitive tools), and in part by organizing their collective effort, at and across time, in the right ways.

The social amplification of individual capacity is important to adult capacity. But children profit immensely from adult organization of their learning environment. Behavioural modernity is a real and important phenomenon. But it was not a new and especially bright light being turned on in human minds by a sudden but subtle genetic shift in *sapien*s genomes. Rather, it represents the cumulation of a long trend in hominin evolution. The capacity to retain, and ultimately to amplify, the cognitive resources inherited from the preceding generation became increasingly important. Behaviourally modern humans control, and depend on controlling, impressive amounts of information about their local environment, local natural history and material technology. As Peter Richerson, Robert Boyd and their students have pointed out, life as a forager depends on the control of rich, detailed information, especially in the unforgiving environments in which behaviourally modern humans have flourished [12,49]. The information resources on which these lifeways depend were built gradually and passed on reliably. Ecological and technological adaptability depends on a culture's capacity to retain an informational bedrock about locally appropriate technology, local resources and dangers; to improve on that base (especially, but not only if conditions change); and to preserve those improvements for the succeeding generation. That ability, in turn, depends both on individual cognitive capacities for teaching and for social learning, and also on an adapted learning environment. As the apprentice model suggests, high fidelity, high bandwidth social learning depends on both individual adaptations and adapted environments.

Individual cognitive capacity has coevolved with learning environments. That coevolution has deep roots; its origins long-predate our species. Behavioural modernity, I shall argue, represents a threshold in the bandwidth and fidelity of the cross-generation flow of expertise. At that threshold, human groups can both reliably preserve large information stores, and can recognize and retain incremental improvements in those information stores. The new flexibility of *sapiens* groups comes from this enhanced capacity to innovate. These changes in the social organization of learning may well have interacted with genetic change. It has become increasingly clear that there has been significant, selected, change in the human gene pool in the life of our species, though the specific phenotypic effects of these gene changes are as yet rarely known [50–52]. So, gene change may have played some role in the establishment of behavioural modernity. But if so, it was through gradual coevolutionary interaction, and not a sudden genetic trigger just prior to the African Diaspora.

On this view, behavioural modernity itself is the collective capacity to retain and upgrade rich systems of information and technique. The specific component signatures of modernity (symbol use, composite tool making, ecological breadth and the like) are just fallible indicators of this basic cognitive-cum-cultural capacity. None have special significance in themselves.

4. ACCUMULATING COGNITIVE CAPITAL

I suggested above that behavioural modernity is a threshold effect; we see the signal of modernity when a stabilized system of interaction makes the accumulation of cognitive capital reliable. For there is an important distinction between the conditions that allow information to be *preserved* reliably, and those that allow it to be *expanded* reliably. This distinction allows us to make sense of the hominin record. That record seems to show three phases: a long phase of mere preservation, a not yet stable shift to expansion and a final phase in which innovations and additions to the communal stock of information are much more reliably transmitted to the next generation; of course, each phase fades into the next rather than terminating crisply. Thus, hominin history began with a very long phase of technological conservatism. Technology did change, but very slowly. Simple chopping tools and flakes emerge approximately 2.6 Ma in Africa and make a first appearance in Europe some time later. Eventually, at about 1.6 Ma, this technology is supplemented with the classic Acheulian handaxe (and perhaps also with worked bone tools [53]). These handaxes are bi-facially flaked, and often have a somewhat standardized 'tear drop' shape. Middle Stone Age points begin to appear about 280 kyr BP, and this change may signal the arrival of hafted rather than hand-held tools. These points require not just attachment to a shaft; the points themselves require a two-step manufacturing process. From about 200 000 years ago, technological and ecological traditions become less conservative. There are innovations in this period that anticipate later technological revolutions, but these innovations often seem to fade out. The accumulation of innovation is not yet stable. The final phase, of course, is the signature period of behavioural modernity: innovation, regional variation and expansion into all but the most forbidding habitats and inaccessible regions.

One striking element of this pattern is that the pace of innovation is initially very slow. But a second is that (especially over the last 300 000 years or so), change in technological competence is not unidirectional. Technological and ecological innovations appear (and establish over sufficient space and time to leave a trace), but then disappear again. In their reviews, Conard and co-workers emphasize these early appearances of technologies that become signatures of later periods [17,26]. Thus, for example, microliths are regular-shaped, point-like artefacts that are often taken to be a signature technology of behavioural modernity, both because they can be made in regionally distinctive, but still regular, ways and because they are thought to have been mounted on spears or arrows. Hence, they show the capacity to make multi-part artefacts. Yet, Hiscock and O'Connor point out that microliths are found in significant numbers early in one region of the African Middle Stone Age (perhaps 300–250 kyr BP) and again late in the

Middle Stone Age (as part of the Howieson's Port industry; perhaps 70 kyr BP). So microliths are found before the establishment of paradigm, behaviourally modern cultures but patchily in space and time.

So, perhaps sometime between 300 and 200 kyr BP, hominin culture became cumulative in two senses. The volume of culturally mediated learning increases: a larger range of hominin action owes its character to intergenerational social learning. Thus, the range of materials expands (including ochre, bone, antler, ivory). There was an increase in the variety of tools used, in part because technology took on new functions. It was used to make material symbols, to make other artefacts (awls and needles were used to make clothes), in shelter construction and the organization of domestic space [54], and in making clothing [55]. Hominins expanded the range of resources they exploited [56]. Moreover, at some point in hominin evolution, children came to learn the norms and customs of their community, not just the local techniques for making a living. Human behaviour became more diverse and less stereotyped, in ways that were guided by information flows from the preceding generation. The bandwidth of cultural learning expands. But culture transmission gradually becomes cumulative in a second sense as well, permitting the stepwise improvement of specific technologies. For example, fire almost certainly was domesticated in stages, beginning with the maintenance and exploitation of natural fire; probably followed by the development of techniques for making fire portable. These important breakthroughs were followed by ignition technologies and improvements in the control and use of established fire, in hearths and the like [27,57]. Stepwise improvement requires high-fidelity transmission. In the hominin record, the expansion of bandwidth seems to be roughly correlated with increasing fidelity (assuming that more complex technologies depend on higher fidelity), and behaviourally modern cultures depend on both high fidelity and expanded bandwidth. Behavioural modernity probably depends both on an increase in the rate of innovation, as individual humans come to deliberately intervene on the world in ways guided by their increasing understanding, and by improved preservation and amplification of successful innovation (see [58] for a nuanced discussion of the interplay between deliberate innovation and population level processes of preservation). So we need an explanation of both aspects of cultural accumulation.

Cross-generational information flow does not in itself require specific adaptations for cultural learning. In their *Animal Traditions*, Avital & Jablonka [14] show that traditions can begin with a lucky accident, with an innovation that is profitable enough to result in adults changing their behaviour to take advantage of their luck. In those species in which the young stay with their parent(s), this lifeway reorganization will have a side effect: the young will come to explore an environment much richer in opportunities to repeat the accident. The improbable in the first generation becomes likely in the second. Traditions in using Oldowan technology might well establish in this way. If making sharp flakes and cores gave the early users of that technology access to (say) carcasses and marrow, the juveniles accompanying those adults would have many chances to acquire stone-working skills through undirected exploration and play. There is archaeological evidence that making and using Oldowan tools was a frequent, regular activity rather than an occasional one. For some sites, cores show signs of heavy, repeated use [59, p. 2]. Crucial information can flow reliably from one generation to the next, even without distinctive adaptations for social learning. Almost certainly, though, early hominins inherited cognitive capacities from their last common ancestor with the chimpanzee clade, capacities that primed them for the uptake of simple stone technologies. Studies of the living great ape species indicate that the earliest hominins were equipped with some of the motor-technical capacities that make stone tool making possible and that they were persistent and effective trial and error learners. Moreover, these studies also suggest that these early hominins had some capacity for cross-generation social learning, through some mix of emulation, coarse-grained imitation and stimulus enhancement [59–61]. So, while there can be information transmission across the generations without adaptation for social learning, almost certainly juvenile hominins noticed adults making and using tools, and responded adaptively to that experience.

So the earliest hominins were able to retain a core of technological and foraging skills. But the conditions that allow accumulation are much more onerous than those that merely allow preservation of a few key skills, and early hominin technologies probably did not depend on high-fidelity social learning. Consider, for example, the signature technology of the erectus-grade hominins, the Acheulian handaxe. Acheulian tool-making probably did not depend on the cross-generational transmission of high-fidelity information about the tool itself. As McNabb and co-workers note in their detailed case study of one specific site, there is little evidence of standardization of group norms governing hand axe design. There is plenty of variability in both shape and degree of symmetry. Indeed, many handaxes show little symmetry [62]. The overall record is complex, for some sites seem to show more constrained variation [63]. Moreover, there is some evidence of local clustering in handaxe shape, giving rise to regional patterns in variation. But even on sophisticated multi-dimensional analysis, these local groupings are not strongly marked: there is roughly a 70 per cent chance of assigning a handaxe to its source of origin, but 60 different variables needed to be measured to assign artefacts to regions with that accuracy [64]. Social learning affects process as well as product, so high-fidelity social learning may have been important to the transmission of manufacturing techniques, for it was necessary to know how to produce large blanks from source material, which could then be shaped into a large cutting tool. But there is no reason to suppose that high-fidelity social learning controlled the shape of the tool itself. The most plausible picture is that the general idea of a large cutting tool plus some techniques for tool-making were transmitted socially, with the help of some capacities for social learning and an organized learning environment [62].

Thus, cultural transmission has had an increasing footprint in the hominin record, a trend culminating in behaviourally modern cultures. I suggest that this trend is due to three interacting factors. One, uncontroversially, is the evolution of minds increasingly well-adapted for culturally learning and, ultimately, teaching (see, for example, [65] for a summary of human communicative adaptations). But while these adaptations are probably necessary for the stability of behaviourally modern cultures, they are not sufficient. As Tehrani & Riede [66] remark, the manual skills required for many traditional craft skills are extraordinarily intricate, and they would be very difficult to master by, for example, imitation learning, even by agents well adapted for such learning. Yet, often such skills are transmitted so reliably that characteristic products reappear recognizably for many generations. Apel [67], for example, details intricately made Neolithic stone daggers from Scandinavia made to a design that was transmitted for at least 24 generations. Tehrani & Riede are right to doubt that such intricate patterns could be transmitted by unsupported imitation, arguing that such cases show the historical depth of active pedagogy. I agree, but teaching often has its effects through structuring the learning environment rather than by direct instruction. So behaviourally modern culture depends on the construction of adapted learning environments; the young come to explore and act in a world that supports and directs learning. This, I shall argue, culminates in something like apprentice learning. A third factor is the changing demography of hominin populations; as we shall see, small population sizes make it harder to maintain and expand informational resources. Moreover, there is likely to be positive feedback between local population size and the volume of cultural learning: innovation increases carrying capacity, allowing growth, which supports specialization and buffers crucial skills against accidental loss [68].

Apprentice learning is a good model of the ways learning environments are organized to make possible the transmission of a high volume of information with high fidelity. These learning environments can evolve gradually, beginning with juvenile interest in parental activities, and parental tolerance of their inquisitive exploration. From that platform, there can evolve both increasingly sophisticated individual adaptations for social learning, and increasing adult support of learning. This form of learning is sufficiently powerful to explain the observed phenomena—the maintenance of complex, demanding skills in populations without literacy or formal educational institutions. A skilled cabinet maker (for example) has absorbed an enormous amount of information and skill from his/her teachers. An apprentice obviously brings to the learning environment a complex set of individual cognitive adaptations: physical skills, theory of mind, joint attention, conditional reasoning, observation learning. Most apprentices acquiring complex skills benefit from explicit advice and instruction (though there seems to be enormous cultural variation in the extent of explicit teaching), and a good deal of information comes from the observation of expertise in action. Often, those learning share information too, about both failure and success. But most learning is hybrid: apprentices mostly learn through socially structured trial-and-error learning. They are surrounded by tools, by partial and complete products and the occasional failure, and by raw materials in various stages of processing. They learn on the job, but they are assigned jobs by those who understand how much or little they can do. So their trial-and-error learning often involves structured trials. Skilled craftsmen assign tasks that they judge to be within, or close to, their current capacity. Those tasks build foundations for more complex skills. The overall result is that apprentice learning systems combine high fidelity with large bandwidth.

Moreover, the apprentice learning model is ethnographically and archaeologically plausible. In foraging societies, extensive explicit instruction does not seem to play a prominent role in the acquisition of hunting skills. But children are provided with informational resources. For example, they are provided with miniature hunting weapons [69]; they are sometimes taught how to make the tracks they must follow (see [70, pp. 166–176] for series of photos of aboriginals making pseudo-tracks). They learn games that rehearse key physical skills. They accompany adults on hunts, and these are sometimes reorganized to make this possible [16]. And while there may not be much explicit instruction, they are exposed to an enormous amount of hunting lore [71,72]. They have access to the expertise of those with the relevant skills; they have the time and opportunity to practice, and that practice is guided. Indeed, there are some cultures in which hunting skill is passed on though something like explicit apprenticeship [73]. In these cases high-fidelity, high-bandwidth social learning depends both on an organized and adapted learning environment and on specific cognitive adaptations. Likewise, there is significant anthropological documentation of the acquisition of craft skills in apprentice-style situations. Apprentice transmission of weaving traditions are documented from a range of cultures, though these are often family-based, mother–daughter lineages [66, pp. 321–322]. Lave [74] discusses two examples in some detail: apprentice tailors in Liberia and the study of Islamic law in nineteenth century Cairo. These examples are important because they document the flexibility of apprentice learning and teaching: it supports the acquisition of much more than manual skill. Liberian apprentice tailors learn about the social and economic organization of a tailor's life, not just how to make trousers. Islamic law is not a manual skill, but it is not just a textual skill either. The student learns about the social and institutional organization of Islamic courts, not just about the texts, from being immersed in those institutions.

It is obviously more difficult to reconstruct the social organization of teaching and learning in extinct cultures. Tehrani & Riede [66] suggest that a detailed analysis of the life history of artefacts can identify artefact traditions: continuity in form over time that is not owing to the constraints imposed by raw materials and function. Likewise, Bamforth & Finlay [75] develop criteria for identifying highly skilled stone work, and also less-skilled work that is likely to be the result of

novice practice. In favourable cases, these methods will expose high-fidelity, high-volume social learning in former social worlds. They document the importance of social learning. But by themselves they do not reveal the social organization or cognitive preconditions of such learning. However, there are occasional archaeological symptoms of an apprentice-like organization of craftsmanship. For there are artefacts that appear to have been produced collaboratively, with an expert guiding or helping the less expert. Inexpertly made stone tools sometimes show signs of expert repair or improvement. More systematically, Patricia Crown [76] has demonstrated collaboration between the expert and inexpert in pottery making, both ethnographically and archaeologically, with expert potters often controlling the most difficult parts of the construction process, leaving the less expert (often children) to complete the routine parts. For example, experts lay down the basic design that children then paint in.

Moreover, the size and organization of the local community is also extremely important to its capacity to retain and to accumulate information. As Haim Ofek [27] has noted, a larger market size allows more specialization and more division of labour, both of which impact positively on a group's informational resources. A small group will not be able to afford a specialist firekeeper or bow maker; a medium-sized or large group, perhaps, can. They will have enough customers to support specialization. Specialists typically have higher skill levels, and hence set a higher bar for the next generation. Moreover, a more diverse group with a varied skill set is more likely to innovate than a small, more homogeneous group. Those who specialize in a craft are the most likely to find an improvement in it, and innovation through cross-fertilization is more likely as the overall skill base becomes more diverse and extensive. Specialists may also be more accurate in filtering unsuccessful innovation, and as Enquist & Ghirlanda [77] show, filtering is essential if culture is to become cumulative.

Second, redundancy plays a critical role in buffering the group's informational resources. Larger groups store information in more heads than smaller ones. Information can easily drift out of a small group, through unlucky accidents to those with rare skills (see [78], though in response see [79,80]). In addition, redundancy may play a second role in compensating for low-fidelity cultural learning. Modern humans are clearly individually adapted for social learning [81–83]. But Richerson and colleagues doubt that these adaptations suffice for high fidelity, and argue that the social environment compensates for low fidelity through redundancy. Naive agents have many opportunities to acquire specific skills and critical information, and they develop models to show that redundancy—for example, a naive agent using many models rather than a single model—can compensate for low fidelity one-on-one learning. Thus, so long as there is sufficient redundancy, with members of a population connected in the right ways, a population can preserve its informational resources in transmission to the next generation through low-fidelity channels [12,84–86].

However, while demographic factors are important in the establishment of behaviourally modern cultures, demographic expansion alone does not explain the acceleration of innovation. Redundancy allows low-fidelity transmission to preserve informational resources, allowing already established and widespread skills to be copied via multiple trials to the next generation. But such mechanisms will not allow small, incremental improvements to existing techniques to be preserved, copied to the next generation and spread to be the foundation for further improvement. This claim is somewhat controversial. Henrich has developed redundancy-based models with accumulation despite low fidelity [78], models which have recently been extended [87]. But the conception of skill on which Henrich's model depends is not psychologically plausible. He models the information structure underlying a capacity or skill as a continuous quality. The product of a skill may often be a quantity of some kind: hunting success; the robustness of a pot; the power of a bow. Indeed, we often use those products to measure a skill: in an archery competition, for example, we use a product of the skill—the number of arrows on target—as its measure. But the systems of information and capacity on which those products depend are not continuous quantities. To see this, consider the challenges involved in learning such a skill. The skills of an artisan are hard to master, but that is not because there must be some measurement error while trying to match a quantity. Rather, it is because the informational basis of skill is only partially manifest in any particular act. A specific, somewhat stereotyped motor skill might be modelled, to a first approximation, as a quantity. But a skilled artisan can respond effectively to a range of different circumstances, demands and materials. That is part of skill. A kayak-maker does not manifest all his skills in making any one kayak. An expert flint knapper responds appropriately to variation in raw materials and in functional demands. Stone tool making is not stereotyped in the way, say, a tennis serve (Henrich's example) might well be.

These models make a convincing case for the importance of demography. Moreover, Powell, Shennan and Thomas's extension of Henrich's work shows that the models are robust, and that the parameter values that predict accumulation map quite plausibly onto estimates of human populations just prior to the establishment of behavioural modernity. But these extensions retain the oversimplified picture of the relationship between a capacity and its underlying informational basis. So while they show that demography plays a crucial role in the establishment of behavioural modernity, so too does high-fidelity learning. In general, low-fidelity learning plus redundancy is not enough for accumulation. In summary, then, the cultural learning characteristic of the Upper Palaeolithic transition and later periods of human culture—social transmission with both a large bandwidth and sufficient accuracy for a ratchet of improvement—requires individual cognitive adaptations for cultural learning, highly structured learning environments and population structures that both buffer existing resources effectively and which support enough specialization to generate a supply of innovation.

There were no medieval craft guilds in the Upper Palaeolithic, though the adze-making traditions of Neolithic New Guinea are strikingly convergent on that social practice [88]. But if the model developed in this paper is correct, information-rich, expertise-dependent, forager lifestyles depended on a similar combination of an organized learning environment and specific adaptations for social learning. The pulse of cultural and technological innovation that is most dramatically visible in the archaeological record in the Upper Palaeolithic revolution is a signal of such a social world: a social world which makes possible high-fidelity, high-bandwidth transmission across the generations. Individuals in these social worlds were equipped for social learning. But they depended on an adapted environment, as well, and on populations which spread risk and supported specialist expertise. The persistence of these lifeways depended on highly skilled agents sharing their expertise and on the reliable replication of the learning environment in which crucial expertise was acquired. This combination, and only this combination, allowed cognitive capital to be accumulated and behaviourally modern cultures to emerge.

5. TESTING THE MODEL

No-one doubts that the evolution of enhanced social learning was one of the most distinctive features of hominin evolution, and that it was one important factor driving the increasing phenotypic difference between the hominin and the chimpanzee clade. This paper has tried to identify that evolutionary trend more precisely, especially its culmination in behaviourally modern culture. Further, it develops a model of the evolutionary preconditions of behavioural modernity. Individual cognitive adaptations for learning and teaching were doubtless important, but not in themselves sufficient. An adapted learning environment—best understood as apprentice transmission—and a favourable demographic profile were also necessary. But it is one thing to advance a plausible model, another to test it. So how can the model be turned into a testable hypothesis about the origins and establishment of behavioural modernity? Archaeology, ethnography and experimental psychology can be combined to test the model, though only in preliminary ways.

The most obvious test is archaeological: comparing the predictions of the niche construction model of behavioural modernity with alternatives. One alternative is Peter Hiscock and Sue O'Connor's suggestion that the supposed '*sapiens* paradox' is a pseudo-problem created by preservation biases. They suspect that there was no qualitative difference between first *sapiens* cultures and those of 50 kyr BP. Smaller groups use fewer artefacts, and so their immediate archaeological footprint is smaller, even in those places were they were found, and they were found in fewer places. Moreover, the older the site, the more likely it is to be degraded. Even so, if there is no qualitative difference in cultural complexity between the first *sapiens* peoples and those of the later Pleistocene, the apparent gap should steadily close in the face of increasing sampling, and by correcting for sampling biases in comparing records. A (approximate) steady-state model can also be tested against the record of more recent cultures (like those of Ancient Australia) where preservation problems may be less formidable. On the niche construction view, there is a genuine difference between stabilized high-fidelity, high-volume cultures, their ancestors and some successors. So the apparent difference should persist in the face of increased sampling effort and bias correction.

The most prominent alternative to the niche construction model is Richard Klein's genetic-pulse hypothesis. In contrast to Klein's picture, the niche construction model does not predict a unidirectional increase in the capacity to mobilize informational resources, even after the fundamental genetic capacities essential to that mobilization have evolved. For the developmental environment is critical, and subject to multiple routes of disturbance. Nor do we find a unidirectional pattern. So, for example, it has recently been argued that behavioural modernity appears to arrive gradually, with its elements not tightly coupled, in multiple locations, and perhaps incipiently in Neanderthals as well as *sapiens* [17,19,24,26]. Richard Klein continues to resist the idea that there are convincing early examples of modern-like behaviour. Moreover, he argues that population pressure models are the only alternative to his genetic breakthrough hypothesis, and notes that they face serious challenges: (i) population pressure models owe us an account of how the need for innovation generates the capacity to innovate; (ii) population pressure models need to explain why hominin populations expanded *prior* to the acquisition of new skills and capacities; (iii) in the crucial period in Africa (100–50 kyr BP), there is no independent evidence of an increased human population or increased ecological footprint [20,89]. While these are serious problems for population pressure models, the apprentice learning model does not depend on population pressure to explain the onset of behavioural modernity. The crucial factor is the size of, and interactions within, the local group, not the ecological footprint of the metapopulation on the landscape's resources.

Suppose that Klein is right to discount ancient signals of apparently modern behaviour, Hiscock & O'Connor point out that the apparent disappearance, then return, of signs of modernity in the record after 50 kyr BP is an equally serious challenge to the genetic switch model of behavioural modernity. A one-factor genetic-switch model cannot explain the variability in the signs of modernity that postdate the switch. If additional demographic, cultural or genetic factors are added to the genetic switch model to track variability, the genetic switch itself becomes redundant. In short, the genetic switch model seems to predict a qualitative change in cultural complexity somewhere around 60 000–50 000 kyr BP, followed by a new, higher equilibrium. Arguably, the data do not support the sudden upward shift. But perhaps they do not support the idea that there was a higher equilibrium, either. For this reason the Australian archaeological record is an informative lens through which to view the interaction of individual cognition with collective capacity.

The initial expansion of humans into the Sahul about 45 000 years BP could not have been accidental. These humans had the capacity to plan and cooperate. Moreover, they had technology complex enough to cross significant stretches of ocean [90]. However, before the Last Glacial Maximum, 20 kyr or so ago, the archaeological record resembles that of Middle Stone Age Africa. So for the first 25 000 years of their occupation, the first Australians seem to have had a limited technological toolkit; exploited a narrow resource band; and showed limited signs of symbolic culture. Eventually, the standard symptoms of behavioural modernity do appear. But as in the African case, the archaeological signatures of behavioural modernity do not appear together in space and time. Ochre use and burial of the dead is relatively early, as is the use of freshwater shellfish (perhaps 40 kyr BP). There are beads from about 35 kyr BP. But the first signs of marine shellfish exploitation and bone tools, and cave art with recognizable motifs are all much younger. Moreover, the lithic toolkit stays quite simple until the Holocene (see [91, p. 211, fig. 9]). Only over the last 20 000 years, do we consistently see the usual archaeological signatures of behavioural modernity: broad-range foraging; environmental management; technological innovation; and obvious symbolic culture [36,92,93], though it is possible that this too is a sampling effect [25].

Allen & O'Connell [90] interpret this record as showing that people can be behaviourally modern without showing that they are behaviourally modern. To arrive at all, they must have been technologically and ecologically flexible, but as a consequence of environmental and demographic factors, modernity left no trace for upwards of 25 kyr. O'Connell & Allen do not consider the idea that Australians ceased to be modern after they arrived; nor do Habgood & Franklin. Neglecting this possibility makes sense if we think modernity is coded and canalized in individual genomes, if it is an attribute individuals have largely independently of their cultural environment. But it makes no sense if behavioural modernity is partially dependent on the organization of social life—a social life that would have changed fundamentally as small numbers of people dispersed into an enormous landscape. The communal resources available to very small groups dispersed over enormous and inhospitable distances would be very different to those available to communities based on the fertile islands and shallow seas of southeast Asia. Quite likely, informational resources were buffered less well, and group size was too small to support much specialization, depressing innovation. On the niche construction model but not genetic switch models, behavioural modernity can be lost as well as gained, and losses should be detectable in the record.

In short, we have three different predictions. The Hiscock–O'Connor suggestion (it is no more than that) predicts an approximate steady state, discounted by preservation biases and the effects of group size. There is no qualitative upward trend in cultural complexity before the Holocene. The niche construction model does predict such a trend, but it is potentially fragile, so interruption and reversal is possible. The gene-switch model predicts a sharp upward shift, once the gene has spread through the population, followed by a stable, higher equilibrium.

In principle, ethnographic data can test the model. The model predicts that crucial skills are acquired by socially supported trial-and-error learning: adults with expertise are actively involved in juvenile learning. However, the form of that involvement will vary by culture and by skill, for the core skills of small-scale societies were very varied. They included: stone technology; fire and fire management; woodworking; the use of skins and other materials for clothes and covering; making shelters; folk medicine; tracking and hunting skills; natural history expertise; and (eventually) weaving and pottery. These skills vary in their transparency to reverse engineering; their transparency to observational learning techniques; the ease with which stepwise improvement is possible; the precision needed in production (their error tolerance); the cost of raw materials and hence the cost of experimentation; and the risks of failed trials. So we would expect the mix of explicit instruction, supervised experiment and support by the provision of tools, raw materials and exemplars to vary from case to case. But we do not expect to find ethnographic evidence that core skills are acquired by independent trial-and-error learning. Nor de we expect to find them acquired by instruction alone.

Moreover, the model predicts differences between skills that are transmitted vertically, within families, and those that are transmitted communally, with many-to-many transmission. Communal transmission buffers skill acquisition by spreading risk, and perhaps allows a higher rate of accumulation, if the most skilled members of the community serve as models for the next generation. In practice, ethnographic data is at best suggestive. There are a few admirable case studies [15,88]. But there is simply not enough systematic, broadly based data. For example, Katharine McDonald's admirable survey of forager skill acquisition has almost no information about making hunting equipment, for almost all hunting was done with store-bought equipment. Hunting with dogs and guns changes the skill base needed for hunting too, so it is far from clear that we can project information about near-contemporary foraging people back into the past.

There is some prospect of supplementing ethnographic and archaeological data by experiment. It is still early days for experimental work on fidelity, bandwidth and accumulation in social learning (for a review, see [94]). But there is already suggestive work on the diffusion of technique in humans and great apes. While the results are far from conclusive, they suggest that both emulation and imitation play important roles in social learning and that, at least in some simple cases, imitation may not be necessary for accumulating improvement [59,61]. For example, Christine Caldwell and Ailsa Millen, in experiments using paper plane construction as the target skill, found that reverse-engineering the product was sufficient to learn and sometimes improve designs. Improvement was possible when naive subjects were allowed to examine finished planes, even when they never saw them being made [95]. As they note,

paper planes are a simple technology, with the design often being obvious from the product, so this result may not generalize to many other cases.

The ideal experiments, then, would combine ethnographic and archaeological data identifying those techniques that seem to persist stably, perhaps using the criteria discussed in Tehrani & Riede [66], with an experimental programme. That programme would probe the learning environments necessary and sufficient for those techniques' acquisition. The niche construction model predicts, of course, that without rich and extensive scaffolding, core skills are not transmittable. Unfortunately, very serious logistical problems prevent implementation of this ideal. Informal report suggests that, for example, advanced stone tool working skills take many years of intensive practice to acquire [67]. That is just as the model predicts, but it follows that direct experimental study of complex skill transmission is not tractable. The hope is to decompose complex skills into relatively independent constituents, whose acquisition can be studied in experiments of reasonable duration.

In brief, the model is partially testable against both archaeological and ethnographic evidence, but not in very rigorous ways. Greater rigour is possible, if ethnography and archaeology can be used to identify target skills, and if those target skills can then be decomposed into component capacities whose transmission conditions can be studied experimentally.

REFERENCES

1 Odling-Smee, J., Laland, K. & Feldman, M. 2003 *Niche construction: the neglected process in evolution*. Princeton, NJ: Princeton University Press.

2 Turner, J. S. 2000 *The extended organism: the physiology of animal-built structures*. Cambridge, UK: Harvard University Press.

3 Lewontin, R. C. 2000 *The triple helix*. Cambridge, MA: Harvard University Press.

4 Gilbert, S. 2001 Ecological developmental biology: developmental biology meets the real world. *Dev. Biol.* **233**, 1–12. (doi:10.1006/dbio.2001.0210)

5 Gilbert, S. F. 2002 From epigenisis to epigenetics: the genome in its ecological context. *Ann. NY Acad. Sci.* **981**, 202–218. (doi:10.1111/j.1749-6632.2002.tb04919.x)

6 Ridley, M. 2000 *Mendel's demon: gene justice and the complexity of life*. London, UK: Weidenfeld and Nicholson.

7 Bonner, J. T. 1998 Origins of multicellularity. *Integr. Biol.* **1**, 27–36. (doi:10.1002/(SICI)1520-6602(1998)1:1<27::AID-INBI4>3.0.CO;2-6)

8 Sterelny, K. 2009 Novelty, plasticity and niche construction: the influence of phenotypic variation on evolution. In *Mapping the future of biology: evolving concepts and theories* (eds A. Barberousse, M. Morange & T. Pradeu). Dordrecht, The Netherlands: Springer.

9 Jablonka, E. & Lamb, M. 2005 *Evolution in four dimensions*. Cambridge, MA: MIT Press.

10 Laland, K. & Brown, G. 2002 *Sense and nonsense: evolutionary perspectives on human behaviour*. Oxford, UK: Oxford University Press.

11 Mesoudi, A., Whiten, A. & Laland, K. N. 2006 Towards a unified science of cultural evolution. *Behav. Brain Sci.* **29**, 329–347. (doi:10.1017/S0140525X06009083)

12 Richerson, P. J. & Boyd, R. 2005 *Not by genes alone: how culture transformed human evolution*. Chicago, IL: University of Chicago Press.

13 Shennan, S. 2002 *Genes, memes and human history: Darwinian archaeology and cultural evolution*. London, UK: Thames and Hudson.

14 Avital, E. & Jablonka, E. 2000 *Animal traditions: behavioural inheritance in evolution*. Cambridge, UK: Cambridge University Press.

15 Bock, J. 2005 What makes a competent adult forager. In *Hunter–gatherer childhoods: evolutionary, developmental and cultural perspectives* (eds B. S. Hewlett & M. E. Lamb), pp. 109–128. New York, NY: Aldine.

16 MacDonald, K. 2007 Cross-cultural comparison of learning in human hunting: implications for life history evolution. *Hum. Nat.* **18**, 386–402. (doi:10.1007/s12110-007-9019-8)

17 Conard, N. 2007 Cultural evolution in Africa and Eurasia during the Middle and Late Pleistocene. In *Handbook of paleoanthropology* (eds W. Henke & I. Tattersall), pp. 2001–2037. Berlin, Germany: Springer.

18 Finlayson, C. 2005 Biogeography and evolution of the genus Homo. *Trends Ecol. Evol.* **20**, 457–463. (doi:10.1016/j.tree.2005.05.019)

19 Finlayson, C. & Carrión, J. 2007 Rapid ecological turnover and its impact on Neanderthal and other human populations. *Trends Ecol. Evol.* **22**, 213–222. (doi:10.1016/j.tree.2007.02.001)

20 Klein, R. 2008 Out of Africa and the evolution of human behavior. *Evol. Anthropol.* **17**, 267–281. (doi:10.1002/evan.20181)

21 Tattersall, I. 2009 Human origins: out of Africa. *Proc. Natl Acad. Sci. USA* **106**, 16 018–16 021. (doi:10.1073/pnas.0903207106)

22 Klein, R. & Edgar, B. 2002 *The dawn of human culture*. New York, NY: Wiley.

23 McBrearty, S. 2007 Down with the revolution. In *Rethinking the human revolution: new behavioural and biological perspectives on the origin and dispersal of modern humans* (eds P. Mellars, K. Boyle, O. Bar-Yosef & C. Stringer), pp. 133–151. Cambridge, UK: McDonald Institute Archaeological Publications.

24 McBrearty, S. & Brooks, A. 2000 The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J. Hum. Evol.* **39**, 453–563. (doi:10.1006/jhev.2000.0435)

25 Hiscock, P. 2008 *Archaeology of ancient Australia*. London, UK: Routledge.

26 Hiscock, P. & O'Conner, S. 2006 An Australian perspective on modern behaviour and artefact assemblages. *Before Farming* **2**, 4.

27 Ofek, H. 2001 *Second nature: economic origins of human evolution*. Cambridge, UK: Cambridge University Press.

28 Stiner, M. C. 2001 Thirty years on: the 'broad spectrum revolution' and paleolithic demography. *Proc. Natl Acad. Sci. USA* **98**, 6993–6996. (doi:10.1073/pnas.121176198)

29 Zilhão, J. *et al.* 2010 Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proc. Natl Acad. Sci. USA* **107**, 1023–1028. (doi:10.1073/pnas.0914088107)

30 McBrearty, S. & Stringer, C. 2007 The coast in colour. *Nature* **449**, 793–794. (doi:10.1038/449793a)

31 Conard, N. 2006 An overview of the patterns of behavioural change in Africa and Eurasia during the Middle and Late Pleistocene. In *From tools to symbols from early hominids to humans* (eds F. d'Errico & L. Blackwell), pp. 294–332. Johannesburg, South Africa: Wits University Press.

32 d'Errico, F., Henshilwood, C., Vanhaeren, M. & van Niekerk, K. 2005 *Nassarius kraussianus* shell beads from Blombos Cave: evidence for symbolic behaviour in the Middle Stone Age. *J. Hum. Evol.* **48**, 3–24. (doi:10.1016/j.jhevol.2004.09.002)

33 Marean, C. *et al.* 2007 Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* **449**, 905–908. (doi:10.1038/nature06204)

34 Zilhão, J. 2007 The emergence of ornaments and art: an archaeological perspective on the origins of 'behavioral modernity'. *J. Archaeol. Res.* **15**, 1–54. (doi:10.1007/s10814-006-9008-1)

35 Kuhn, S. & Stiner, M. C. 2007 Palaeolithic ornaments: implications for cognition, demography and identity. *Diogenes* **54**, 40–48. (doi:10.1177/0392192107076870)

36 Brumm, A. & Moore, M. 2005 Symbolic revolutions and the Australian archaeological record. *Camb. Archaeol. J.* **15**, 157–175. (doi:10.1017/S0959774305000089)

37 Kuhn, S., Stiner, M. C., Reese, D. S. & Güleç, E. 2001 Ornaments of the earliest Upper Paleolithic: new insights from the levant. *Proc. Natl Acad. Sci. USA* **98**, 7641–7646. (doi:10.1073/pnas.121590798)

38 Kuhn, S. & Stiner, M. C. 2007 Body ornamentation as information technology: towards an understanding of the significance of early beads. In *Rethinking the human revolution* (eds P. Mellars, K. Boyle, O. Bar-Yosef & C. Stringer), pp. 45–54. Cambridge, UK: McDonald Institute for Archaeological Research.

39 Renfrew, C. 2007 *Prehistory: the making of the human mind*. New York, NY: Modern Library.

40 Hauser, M. 2009 The possibility of impossible cultures. *Nature* **460**, 190–196. (doi:10.1038/460190a)

41 Bickerton, D. 2002 From protolanguage to language. In *The speciation of modern Homo sapiens* (ed. T. J. Crow), pp. 101–120. Oxford, UK: Oxford University Press.

42 Lieberman, P. 1998 *Eve spoke: human language and human evolution*. New York, NY: WW Norton & Company.

43 Mithen, S. 2005 *The singing Neanderthals: the origins of music, language, mind and body.* London, UK: Weidenfeld & Nicholson.

44 Mithen, S. 1996 *The prehistory of the mind*. London, UK: Phoenix Books.

45 Dehaene, S. 1997 *The number sense: how the mind creates mathematics*. Oxford, UK: Oxford University Press.

46 Everett, D. L. 2005 Cultural constraints on grammar and cognition in Piraha: another look at the design features of human language. *Curr. Anthropol.* **46**, 621–646. (doi:10.1086/431525)

47 Frank, M. C., Everett, D. L., Fedorenko, E. & Gibson, E. 2008 Number as a cognitive technology: evidence from Pirahã language and cognition. *Cognition* **108**, 819–824. (doi:10.1016/j.cognition.2008.04.007)

48 Clark, A. 2008 *Supersizing the mind: embodiment, action, and cognitive extension*. Oxford, UK: Oxford University Press.

49 Henrich, J. & McElreath, R. 2003 The evolution of cultural evolution. *Evol. Anthropol.* **12**, 123–135. (doi:10.1002/evan.10110)

50 Laland, K., Odling-Smee, J. & Myles, S. 2010 How culture shaped the human genome: bringing genetics and the human sciences together. *Nat. Rev. Genet.* **11**, 137–148. (doi:10.1038/nrg2734)

51 Nielsen, R., Hellmann, I., Hubisz, M., Bustamante, C. & Clark, A. G. 2007 Recent and ongoing selection in the human genome. *Nat. Rev. Genet.* **8**, 857–868. (doi:10.1038/nrg2187)

52 Varki, A., Geschwind, D. H. & Eichler, E. E. 2008 Explaining human uniqueness: genome interactions with environment, behaviour and culture. *Nat. Rev. Genet.* **9**, 749–763. (doi:10.1038/nrg2428)

53 Backwell, L. & d'Errico, F. 2008 Early hominid bone tools from Drimolen, South Africa. *J. Archaeol. Sci.* **35**, 2880–2894. (doi:10.1016/j.jas.2008.05.017)

54 Wadley, L. 2001 What is cultural modernity? A general view and a South African perspective from Rose Cottage Cave. *Camb. Archaeol. J.* **11**, 201–221. (doi:10.1017/S0959774301000117)

55 Gilligan, I. 2007 Neanderthal extinction and modern human behaviour: the role of climate change and clothing. *World Archaeol.* **39**, 499–514. (doi:10.1080/00438240701680492)

56 O'Connell, J. F. 2006 How did modern humans displace Neanderthals? Insights from hunter–gatherer ethnography and archaeology. In *When Neanderthals and modern humans met* (ed. N. Conard), pp. 43–64. Tübingen, Germany: Kerns Verlag.

57 Brown, K., Marean, C., Herries, A., Jacobs, Z., Tribolo, C., Braun, D., Roberts, D. L., Meyer, M. C. & Bernatchez, J. 2009 Fire as an engineering tool of early modern humans. *Science* **325**, 859–862. (doi:10.1126/science.1175028)

58 Lansing, J. S. & Fox, K. M. 2011 Niche construction on Bali: the gods of the countryside. *Phil. Trans. R. Soc. B* **366**, 927–934. (doi:10.1098/rstb.2010.0308)

59 Whiten, A., Schick, K. & Toth, N. 2009 The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. *J. Hum. Evol.* **30**, 1–16. (doi:10.1016/j.evolhumbehav.2008.08.006)

60 Laland, K. & Galef, B. (eds) 2009 *The question of animal culture*. Cambridge, MA: Harvard University Press.

61 Whiten, A., McGuigan, N., Marshall-Pescini, S. & Hopper, L. M. 2009 Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Phil. Trans. R. Soc. B* **364**, 2417–2428. (doi:10.1098/rstb.2009.0069)

62 McNabb, J., Binyon, F. & Hazelwood, L. 2004 The large cutting tools from the South African Acheulian and the question of social traditions. *Curr. Anthropol.* **45**, 653–677. (doi:10.1086/423973)

63 McNabb, J. 2005 Reply. *Curr. Anthropol.* **46**, 460–463.

64 Lycett, S. & Gowlett, J. 2008 On questions surrounding the Acheulian 'Tradition'. *World Archaeol.* **40**, 295–315. (doi:10.1080/00438240802260970)

65 Gintis, H. 2011 Gene–culture coevolution and the nature of human sociality. *Phil. Trans. R. Soc. B* **366**, 878–888. (doi:10.1098/rstb.2010.0310)

66 Tehrani, J. & Riede, F. 2008 Towards an archaeology of pedagogy: learning, teaching and the generation of material culture traditions. *World Archaeol.* **40**, 316–331. (doi:10.1080/00438240802261267)

67 Apel, J. 2008 Knowledge, know-how and raw material—the production of Late Neolithic flint daggers in Scandinavia. *J. Archaeol. Methods Theory* **15**, 91–111. (doi:10.1007/s10816-007-9044-2)

68 Ghirlanda, S. & Enquist, M. 2007 Cumulative culture and explosive demographic transitions. *Quality Quantity* **41**, 591–600. (doi:10.1007/s11135-007-9070-x)

69 Haagen, C. 1994 *Bush toys: aboriginal children at play.* Canberra, Australia: Aboriginal Studies Press.

70 Morrison, R. 1981 *A field guide to the tracks and traces of Australian animals*. Adelaide, Australia: Rigby.

71 Marlowe, F. 2007 Hunting and gathering: the human sexual division of foraging labor. *Cross-Cult. Res.* **41**, 170–194. (doi:10.1177/1069397106297529)

72 Marlowe, F. W. 2005 Hunter–gatherers and human evolution. *Evol. Anthropol.* **14**, 54–67. (doi:10.1002/evan.20046)

73 Bahn, P. 2007 Hunting for clues in the Palaeolithic. *Antiquity* **81**, 1086–1088.

74 Lave, J. 1996 Teaching, as learning, in practice. *Mind, Cult. Activity* **3**, 149–164. (doi:10.1207/s15327884mca0303_2)

75 Bamforth, D. & Finlay, N. 2008 Introduction: archaeological approaches to lithic production skill and craft

learning. *J. Archaeol. Methods Theory* **15**, 1–27. (doi:10.1007/s10816-007-9043-3)
76 Crown, P. 2007 Life histories of pots and potters: situating the individual in archaeology. *Am. Antiquity* **72**, 677–690. (doi:10.2307/25470440)
77 Enquist, M. & Ghirlanda, S. 2007 Evolution of social learning does not explain the origin of human cumulative culture. *J. Theor. Biol.* **246**, 129–135. (doi:10.1016/j.jtbi.2006.12.022)
78 Henrich, J. 2004 Demography and cultural evolution: why adaptive cultural processes produced maladaptive losses in Tasmania. *Am. Antiquity* **69**, 197–221. (doi:10.2307/4128416)
79 Henrich, J. 2006 Understanding cultural evolutionary models: a reply to Read's critique. *Am. Antiquity* **71**, 771–778. (doi:10.2307/40035890)
80 Read, D. 2006 Tasmanian knowledge and skill: maladaptive imitation or adequate technology. *Am. Antiquity* **71**, 164–184. (doi:10.2307/40035327)
81 Csibra, G. & Gergely, G. 2005 Social learning and social cognition: the case for pedagogy. In *Processes of change in brain and cognitive development* (eds M. H. Johnson & Y. Munakata). Oxford, UK: Oxford University Press.
82 Gergely, G., Egyed, K. & Kiraly, I. 2007 On pedagogy. *Dev. Sci.* **10**, 139–146. (doi:10.1111/j.1467-7687.2007.00576.x)
83 Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. 2005 Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* **28**, 675–691. (doi:10.1017/S0140525X05000129)
84 Gil-White, F. 2005 Common misunderstandings of memes (and genes): the promise and the limits of the genetic analogy to cultural transmission processes. In *Perspectives on imitation: from mirror neurons to memes* (eds S. Hurley & N. Chater). Cambridge, UK: MIT Press.
85 Henrich, J. & Boyd, R. 2002 On modelling cognition and culture: why cultural evolution does not require replication of representations. *J. Cogn. Cult.* **2**, 87–112.
86 Henrich, J., Boyd, R. & Richerson, P. 2008 Five misunderstandings about cultural evolution. *Hum. Nat.* **19**, 119–137. (doi:10.1007/s12110-008-9037-1)
87 Powell, A., Shennan, S. & Thomas, M. 2009 Late Pleistocene demography and the appearance of modern human behavior. *Science* **324**, 298–1301. (doi:10.1126/science.1170165)
88 Stout, D. 2002 Skill and cognition in stone tool production: an ethnographic case study from Irian Jaya. *Curr. Anthropol.* **43**, 693–722. (doi:10.1086/342638)
89 Klein, R. 2009 Darwin and the recent African origin of modern humans. *Proc. Natl Acad. Sci. USA* **106**, 16 007–16 009. (doi:10.1073/pnas.0908719106)
90 Allen, J. & O'Connell, J. F. 2008 Getting from Sunda to Sahul. In *Islands of inquiry: colonisation, seafaring and the archaeology of maritime landscapes* (eds G. Clark, F. Leach & S. O'Connor), pp. 31–46. Canberra, Australia: ANU E-Press.
91 Habgood, P. & Franklin, N. 2008 The revolution that didn't arrive: a review of Pleistocene Sahul. *J. Hum. Evol.* **55**, 187–222. (doi:10.1016/j.jhevol.2007.11.006)
92 Keen, I. 2006 Constraints on the development of enduring inequalities in Late Holocene Australia. *Curr. Anthropol.* **47**, 7–38. (doi:10.1086/497672)
93 O'Connell, J. F. & Allen, J. 2007 Pre-LGM Sahul (Pleistocene Australia-New Guinea) and the archaeology of early modern humans. In *Rethinking the human revolution* (eds P. Mellars, K. Boyle, O. Bar-Yosef & C. Stringer), pp. 395–410. Cambridge, UK: McDonald Institute for Archaeological Research.
94 Mesoudi, A. & Whiten, A. 2008 The multiple roles of cultural transmission experiments in understanding human cultural evolution. *Phil. Trans. R. Soc. B* **363**, 3489–3501. (doi:10.1098/rstb.2008.0129)
95 Caldwell, C. & Millen, A. 2009 Social learning mechanisms and cumulative cultural evolution: is imitation necessary? *Psychol. Sci.* **20**, 1478–1483. (doi:10.1111/j.1467-9280.2009.02469.x)