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The origins of causal cognition in early hominins

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Abstract Studies of primate cognition have conclusively shown that humans and apes share a range of basic cognitive abilities. As a corollary, these same studies have also focussed attention on what makes humans unique, and on when and how specifically human cognitive skills evolved. There is widespread agreement that a major distinguishing feature of the human mind is its capacity for causal reasoning. This paper argues that causal cognition originated with the use made of indirect natural signs by early hominins forced to adapt to variable late Miocene and early Pliocene environments; that early hominins evolved an innate tendency to search for such signs and infer their causes; that causal inference required the existence of incipient working memory; and that causal relationships were stored through being integrated into spatial maps to create increasingly complex causal models of the world.

Keywords Hominin evolution · Causal cognition · Natural signs · Cognitive maps · Working memory · Overimitation · Belief

What distinguishes the cognitive capacities of human beings from apes has been of enduring interest ever since Charles Darwin concluded that “the difference in mind between man and the higher animals, great as it is, is one of degree and not of kind” (Darwin 1871, p. 128). Anthropologists, primatologists, palaeontologists, cognitive psychologists and philosophers have all contributed to the debate. Scholars have identified a number of behavioural and/or cognitive innovations as *the* crucial advance that set human beings apart from our nearest relatives. These include cooperative hunting of large animals (Hill 1982), sociality stimulated by group gathering (Zihlman and Tanner 1978), tool manufacture (Ambrose 2001),

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development of improved motor skills for throwing (Calvin 2004), 'theory of mind' (Povinelli and Preuss 1995), shared intentionality (Tomasello et al. 2005), intergenerational teaching (Csibra and Gergely 2011), cumulative cultural innovation (Balter 2008), and cognitive recursion as demonstrated in narration and language (Corballis 2011). What is notable about this list, however, is that all these advances occurred within the genus *Homo*. None therefore relates to the earlier period of divergence between the panin and hominin lines.

Research by primatologists over the last half century into the behaviour of great apes in the wild, primarily chimpanzees, has amassed convincing evidence that these apes possess a range of cognitive capabilities and skills previously believed to be uniquely human (Whiten 2005, 2011). These include solving problems by deducing instrumental relationships between observed objects (as when a twig is used to extract ants), repeated tool use (of stone hammers and anvils to crack nuts), social communication, and cooperation in group activities, including hunting (Rekers et al. 2011). Chimpanzees have also been observed to practise deception and appear to discern the intentions of conspecifics, though whether these are sufficient to substantiate claims that apes possess a 'theory of mind' that entails representing mental states seems less likely (Suddendorf and Whiten 2003). What these research findings mean for our understanding of the relationship between the evolutionary trajectories of humans and apes is an ongoing matter of debate (Shettleworth 2012), but they do suggest that human uniqueness is unlikely to be due to any single cognitive or behavioural advance.

One response to this research has been to suggest that human uniqueness depends on possession of a combination of cognitive capacities (cumulative cultural learning, reflexive social cognition, symbol use, language) (Premack 2007). Another has been to elaborate what is arguably the most widely accepted theory of human development, usually referred to as the 'social brain' hypothesis (Dunbar 1998), or the social or cultural intelligence hypothesis (Reader and Laland 2002; Herrmann et al. 2007). This theory explains increased intelligence and its physical correlate, larger brain size, as adaptive responses to increasingly complex social environments as group size expanded. Its most sophisticated version combines social complexity with foraging mode and niche construction (Sterelny 2007). Development is driven by a unique set of self-sustaining feedback processes that evolved only in the genus *Homo* (Heyes 2012; Sterelny 2012).

For the most part, the debate about human uniqueness compares ancestral hominins with living chimpanzees and bonobos despite their separation in time. Our last common ancestor (LCA) is now believed to have lived at least seven million years ago (Mya) (Steiper and Young 2006; Langergraber et al. 2012). Over the years considerable evidence has been unearthed for evolution within the hominin clade. By contrast, evidence for the evolution of chimpanzees over the same period is very scarce. The genus *Homo* first appeared on the African savannah 2.5 million years ago in the form of *Homo habilis*, and the earlier australopithecines push that date back to beyond 4 Mya. By that time, however, the hominin line had been separated from our LCA by some 3 million years. Relatively little attention has been given to how hominins diverged from panins during this early period.

During these first 3 million years of divergent evolution, the gap between hominins and panins must still have been relatively small. We don't know how panins evolved over this period, but responses to environmental pressures in the hominin line included changes in dentition to accommodate omnivory, and in anatomy as quadripedal knuckle running evolved to bipedalism, requiring changes to limbs, pelvis and the carriage of the skull. We can only guess what behavioural changes accompanied these anatomical developments, but they must have been contingent on cognitive function, as the brains of these early hominins continued to perform their dual task of coordinating sensory data and activating appropriate motor responses. It is entirely likely, therefore, that some new cognitive ability evolved to enable these small ape-like hominins to adapt to their new and demanding environment. But what could that have been?

Obviously we can have no direct evidence of any cognitive advance, but we do have two sources of indirect evidence. One that I shall discuss later comes from studies of the mental development of infants; the other from studies of how the climate and environment were changing, which gives us a good idea of the kind of challenges faced by our earliest ancestors. From these changing conditions we can deduce what kind of behaviours would have increased inclusive fitness, and what cognitive capacities would be required to initiate those behaviours. Such a hypothetical reconstruction would be strengthened if cognitive advances could be shown to provide an essential foundation for subsequent developments.

There is one cognitive competence that underlies all later human achievements, from tool making to theory of mind to sociocultural niche construction, and that is causal reasoning. In no other species does causal reasoning play the all-embracing role it does in human cognition and behaviour. Humans alone, from infancy, actively seek to construct and test causal relationships and incorporate them into a consistent, cumulative model of how the world works (Gopnik 2000). This causal model not only governs the selection of behaviour, but also informs our sense of ourselves as causative agents. Indeed all the social and cultural activities that make us human entail forming and acting upon causal inferences. No ape demonstrates a remotely equivalent ability. The causal reasoning capacity of chimpanzees is not much greater than that of rats or corvids (McGrew 2013). Prima facie, therefore, it seems possible that a crucial factor in the early divergence between humans and apes was the evolution of causal cognition in the hominin line.

I am hardly alone in suggesting that the evolution of causal thinking was the key development that set humans off on their unique evolutionary trajectory. Lewis Wolpert (2003, 2007) has argued as much, and in a paper published in 2002, Povinelli and Bering maintained that the crucial breakthrough in human cognitive evolution was ‘a new representational system’ that enabled humans to ‘reinterpret’ the observable world by reference to ‘unobservable causes’, both physical and mental. Apes, these authors claimed, do not share our causal understanding of the world because they cannot form and manipulate mental representations[1] (Povinelli and Bering 2002; Penn et al. 2008).

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[1] Perceptual images can be described as representations, but I reserve the term for their cognitive counterparts because they are not automatic responses bound, as perceptual images are, to external stimuli. Moreover cognitive representations are very often composite, constructed in and influenced by the organising structure of memory, which is not the case for direct experience of sensory imagery.

If the evolution of causal cognition laid the necessary foundation for the later development of the range of cognitive skills we associate with being human, when did it evolve and why? In this paper I propose that the evolution of causal cognition was the crucial advance that differentiated ancestral hominin populations from contemporary populations of forest apes. I argue that causal cognition evolved in early hominins in response to the demands of a changing and increasingly variable environment; and that it rested on three cognitive foundations: an innate tendency, driven by curiosity, to notice and categorise natural signs and to connect them causally to covariant categories recalled from memory; an ability to represent perceived signs and remembered categories simultaneously in what I shall call incipient working memory, and to infer a causal connection between them; and a capacity to incorporate causal relationships into cognitive maps, as a way to facilitate rapid access during subconscious selection of behaviour.

The last common ancestor

Dozens of species of apes proliferated during the Miocene in Africa, but we have no idea which gave rise to the LCA of humans and modern apes. This has not curtailed speculation about what kind of creature this LCA might have been. McGrew (2010) has confidently concluded that it must have possessed a range of capabilities and characteristics related to diet, foraging, protection and technology. Diet would have included fruits, leaves, grains, insects and small reptiles. It may have also included underground tubers and bulbs, but whether small mammals were hunted is doubtful. Scavenging was a possibility, but remains another open question. Foraging would have covered a wide area, requiring good spatial memory for the location of food sources and water. While the LCA was semi-terrestrial, trees remained essential, both for protection from predators and for constructing safe sleeping platforms.

The material culture of the LCA was sufficiently evolved, according to McGrew, to include a sizable tool repertoire for use in food acquisition and processing. Much of this technology would have been organic, in the form of twigs and sticks, and so perishable. Lithic tools such as anvils and strikers for cracking nuts would have been undifferentiated but for size, but would often have been reused. McGrew even speculates that the LCA may have made composite tools by joining twigs, or used tools to make tools, by deliberately breaking a stone on an anvil to produce a more useful-sized striker.

This is a pretty impressive list, which leaves our LCA looking remarkably like a composite of all that modern chimpanzees can do. This is not surprising in that McGrew explicitly assumes that "anything that a chimpanzee can do today, the LCA could have done 6–7 Myr ago" (2010, p. 3268); and for that he draws on the full range of recent observations of the behaviour of chimpanzees in the wild. Since some capabilities are confined to particular chimpanzee populations, McGrew concedes that different LCA populations probably exhibited different sets of skills and behaviours.

The problem with making the 'parsimonious assumption' (Whiten 2011) that the behavioural and cognitive abilities exhibited by modern chimpanzees were also present in the population of Miocene apes that constituted our LCA is that it implies that chimps have been treading water for about the last 7 million years, over a period during which cognitive evolution in the hominin clade was nothing short of astonishing. The argument is that apes share an essentially similar set of basic cognitive skills to humans because we share a common ancestry. It is also possible, however, that some parallel evolution occurred—which is to say that chimpanzees have evolved some cognitive abilities similar to those of humans because, to the extent that they have become semi-terrestrial, they have faced comparable environmental challenges. In support of this possibility we can note that several animal species, including rats, corvids, and cetaceans, have also evolved intelligent behaviours, including tool use, that apparently depend on broadly similar cognitive mechanisms (van Horik and Emery 2011). A third possibility, for which there is some support (Lovejoy 2009; White et al. 2009), is that humans and apes have followed divergent, highly specialised, evolutionary trajectories—which necessarily constrains the value of comparisons for identifying and accounting for unique features of human cognition.

We should be cautious about assuming that parallel evolution has not occurred between panins and hominins (Wood and Harrison 2011). The climatic and environmental changes taking place in central and east Africa during the late Miocene continued to reduce the habitats of forest-dwelling apes through the Pliocene and into the Pleistocene (Jacobs 2004). Some populations of chimpanzees may thus have later been forced to adapt in ways similar to early hominin populations. Differences between extant ape species in tool use and technology more generally, and between different populations of wild chimpanzees, depends among other things on how terrestrial they have become (Meulman et al. 2012). So while some characteristics of chimpanzees may have been present in our LCA, others could have evolved subsequently as some populations adopted a partly terrestrial lifestyle.

Instead of simply transferring characteristics from chimpanzees to our LCA and assuming this was the set of capabilities exhibited by the earliest hominins, we can attempt to model the likely adaptive response of the latter to changing climate and environment. We know that the climate was both cooling and becoming more arid, and that the forest was contracting and giving way to woodland ecosystems, and eventually to grasslands. More significantly, in parts of east Africa these ecosystems were broken up due to the rifting caused by earlier tectonic movement, thus creating a spatially and temporally variable mosaic habitat for wandering family groups of early hominins (Elton 2008).

Miocene apes were forest dwellers, dependent on forest resources for their sustenance. As the ecosystem gradually cooled and dried, and forest at the margins thinned to woodland, some populations of our LCA would have retreated with the forest and remained primarily arboreal. Others, the earliest hominins, perhaps under competitive pressure from forest-dwelling populations, ventured into more open woodlands. In those parts of this woodland ecosystem that formed a mosaic, each variant offered its own challenges and opportunities. For a wide-ranging, semi-terrestrial primate negotiating such an environment, the most useful adaptation would have been behavioural flexibility backed by an enquiring intelligence capable of finding and exploiting new sources of food, and of learning new ways to avoid predation.

Natural signs and causal cognition

The earliest hominins were not well equipped for a semi-terrestrial lifestyle. Like modern apes, late Miocene hominins lacked a sufficiently acute sense of smell to locate edible insects or well camouflaged small animals, as dogs can do. They could not 'sniff the wind' to identify predators; nor was their hearing especially acute. Sharp binocular vision honed by life in the forest was the primary sense they brought to their new environment. Continued dependence on vision was not inevitable: the earliest hominins could conceivably have refined another organ of perception (hearing or smell, say) to provide the information every organism requires in order to locate food, avoid predators, and find potential mates. But they did not: the information they had to rely on was provided primarily by what they could see, including natural signs.

Now many kinds of higher organisms make use of natural signs in negotiating their environments, most often as cues that trigger instinctive responses. The displays of birds of paradise, or the head-bobbing and colour changes of some lizards, are visible natural signs that act as signals to potential mates. Such signs are direct in that they are perceived as they are produced, and elicit an immediate behavioural reaction, whether from conspecifics (as in sexual signaling) or from other species (as in the deadly dance between predator and prey). But there is another class of natural signs that are indirect, for which the environment acts as a medium. An example would be the odour left by an animal, whether deliberately in marking out territory, or inadvertently by brushing against foliage. Such indirect signs can trigger instinctive behavioural responses, as when a dog picks up a scent trail and excitedly follows it. Note that immediately responding to a category of indirect natural signs may be instinctive, but responses to specific signs can be learned through conditioning and reinforcement. Animals with a repertoire of instinctive behaviours can learn to use them in relation to new categories of indirect signs, as dogs do in learning to sniff out drugs.

The visible indirect natural signs encountered by increasingly terrestrial early hominins would have consisted of traces left in the environment by the passage of some animal, prey or predator, as marks of some kind (scratches on a tree, paw prints in the sand, damaged vegetation). Such visible signs are extremely variable, which made it inherently unlikely that an innate behavioural response would evolve for each kind of sign. The alternative was to learn to connect categories of signs to categories of what made them. This is not as easy as it might appear, for attention must be directed from the animal itself to the tracks it makes, and it is unlikely that a hungry hunting hominin would do this. The immediate reaction to sighting some small prey would be to give chase and catch it. One can imagine situations, however, where attention shifts from an animal to the tracks it makes. Small lizards, for instance, might be seen disappearing down their holes leaving only their tracks to incite curiosity; or an already satiated hunter might idly watch lizards scurrying about, and become aware of an identity between the animal and its tracks. In either case, observation would identify a co-occurrence between an animal and the tracks it makes. The trick, however, was not to connect an animal with its tracks, but to work back from observed tracks to what caused them.

The defining characteristic of visible indirect natural signs is that they have been produced through prior behaviour of some animal that is no longer observable. This is also the case when the behaviour of another animal acts as a sign of the presence of something else. Circling vultures indicate the existence of an unobserved carcass. Associating an indirect natural sign with a specific animal, alive or dead, would be of benefit in reducing expenditure of energy in searching for food, if only by indicating direction. Chasing visible prey is straightforward; locating prey that cannot be seen is more cognitively demanding because the animal is spatially and temporally displaced from the observed sign of its existence. A hunter must have some conception of what a sign indicates for it to trigger appropriate behaviour, and this requires recalling to consciousness a category image of the animal previously identified with the sign. And for a sequence of signs to be followed, a hunter must remain conscious of the recalled representation over a period of time.

Following a sequence of visible indirect natural signs is thus quite different from what a dog does, for a dog following a scent trail is responding to a single sign. The trail may be more or less faint, but the scent does not change along it. The scent alone is sufficient to trigger the same instinctive pursuit behaviour all along the trail: there is no need for the dog to be continuously aware of a representation of what it is chasing (though for all we know it may possess one). As the earliest hominins lacked a sufficiently acute sense of smell to follow a scent trail, however, visible natural signs were all they had to go on. The problem was that indirect natural signs could be highly variable. They could only be used as a source of information, therefore, if variant signs could be linked to a single category image whose recall to working memory, and not the signs themselves, was what activated a ‘follow these signs’ response—which is what happens when a causal connection is inferred and acted upon.

Now at its most basic, to infer a causal relationship requires regular co-occurrence to be established between one category of perceived phenomena (paw prints, scratch marks) and another that was not just prior to it, but spatially adjacent at the time. Such a regularity relationship is the ‘minimally sufficient’ condition necessary to ensure that the effect *could* be produced by the cause (Baumgartner 2008). This broadly Humean understanding of causation requires construction of a neural linkage between two mental representations of phenomena or events, and its meta-representation as causal. Ascribing a cause to an indirect natural sign requires recalling a mental representation of the category inferred as the prior cause by working back from the observed effect on the basis of a reasonable belief that cause and effect co-occur (or co-vary) with reassuring regularity (Holyoak and Cheng 2011).

The ability to infer causal relationships between indirect natural signs and what produced them is something no monkey or ape possesses (Penn and Povinelli 2007). Monkeys and apes do not respond to the tracks of predators: only when they perceive the actual danger do they sound the alarm (Cheney and Seyfarth 1990).

The ability to follow tracks only developed in the hominin line (Calvin and Bickerton 2000). Being able to infer the cause of indirect natural signs would, therefore, have given ancestral hominins that possessed the competency an edge over competing groups because it increased the probability of finding prey—but only if variable signs could be linked to a single category image of the prey in such a way as to activate an appropriate behavioural response.

The ability of early hominins to infer a causal relationship would have required, at the very minimum, the cognitive capacity to entertain two mental representations simultaneously, the visual image of an observed sign and the category image recalled from memory through its prior association with the sign. If a causal relationship was to be established, the second representation could not displace the first from consciousness: both had to be retained in what we can call 'incipient working memory'. It has been suggested that working memory originated at the interface between awareness of sensory data and the activation of behaviour through the 'recruitment' of neural components of both (Postle 2006). This is how I conceive of the development of 'incipient working memory': observation of a sign activated a neural linkage that recalled a correlated representation to consciousness, the effect of which was to activate one motor response rather than another—which is to say it influenced or biased the selection of behaviour. This could occur without the relationship between visual image and recalled representation being consciously meta-represented as causal. That came later with the evolution of extended-capacity working memory able to keep track of up to seven mental representations, and with differentiated functions providing a 'visuo-spatial sketchpad' for the representation of images, a 'phonological loop' through which to process language, and an 'episodic buffer' to moderate the storage of representations in long-term memory, all presided over by a 'central executive' (Baddeley 2012).[2] By contrast, incipient working memory acted as a mental platform whose capacity was probably at first limited to two representations, the causal relationship between them being instinctively instantiated through the bias exerted by representation of the cause on the selection of an appropriate motor response.

The ability to make use of the information provided by visible indirect natural signs, I would argue, was what provided the initial impetus that set hominin cognitive evolution off on a divergent course from that of the forest apes. An ability to infer the causes of any indirect natural signs they observed would have enabled early hominins better to adapt to their challengingly variable environment. Natural selection of this ability built on two crucial competencies: excellent binocular vision, and innate curiosity. The first prerequisite for causal cognition was, as we have seen, the evolution of a mental platform, incipient working memory, able to accommodate both an image of the observed natural sign and a representation drawn from memory of a natural category regularly associated with it. Conscious representation of the recalled category was the mental activity that biased activation of the causally connected behaviour. But there was another cognitive requirement

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[2] Evolution of 'enhanced working memory' may well be what gave *Homo sapiens* the edge over the Neandertals by allowing more stored knowledge to be accessed and held in mind, so enabling complex problems to be considered in innovatory ways (Wynn and Coolidge 2004).

for causal relationships to influence behaviour quickly and effectively, and that was rapid retrieval from memory of the related category. For that to happen, causal connections could not be randomly stored in memory: they had to be structurally organised—and the most parsimonious way of doing this would have been in relation to existing cognitive structure.

Now animals from bees to rats to chimpanzees are able to find their way around home territories by reference, it has been suggested, of some kind of spatial cognitive map. Debate continues among researchers as to whether animals really do construct cognitive maps (Portugali 1996), and if so what role they play in guiding behaviour. It seems indisputable, however, since animals do possess skills of spatial recall and navigation, that they store topographical and other useful knowledge about their territories, and that this is organised in some consistent way. Most of the research since Tolman (1948) coined the term ‘cognitive map’ has been done on rats given the task of locating food, but one study (recounted in Sterelny 2003) demonstrated how well chimps can find food they had previously seen hidden, presumably by mentally mapping sites in relation to each other. Squirrels and jays also rely on spatial memory to find food they have previously cached (Brodin 2010).

It seems likely, therefore, that the earliest hominins would already have had the capacity to construct spatial maps, which could serve as a framework for the storage of connections between observed indirect natural signs and causally related categories. Familiar features of the environment could then trigger recall of causally associated representations—to the possible presence of a predator, say, at some location, even if visible paw prints noted earlier had been erased—a capability with obvious survival benefits that would have been positively selected for. Support for the hypothesis that causal interpretations of natural signs would have been stored in relation to cognitive maps comes from evidence that the human conceptual system actually develops on foundations constituted by spatial image-schemas (Mandler 2010).

Though the outline of the evolution of causal cognition given above is hypothetical, some such development is likely to have accompanied the behavioural and anatomical changes that occurred over the first 3 million years of hominin evolution. Incipient working memory and storage of causal connections in relation to cognitive maps evolved in parallel with innate dispositions to notice natural signs and infer their causes—propensities that built on the curiosity exhibited by all primates in the details of their environments. In humans, intuiting causal relationships manifests as a ‘drive to explain’ that generates its own rewards (Gopnik 2000), evidence for which comes from research into early child development (Sobel and Kirkham 2006), reinforced by neuroscience (Gottlieb et al. 2013). So crucial is this drive during the first 2 years of life that some scholars have taken causal understanding to be a ‘developmental primitive’ applied automatically across all cognitive domains (Corrigan and Denton 1996).

Though ontogeny can never be taken to repeat phylogeny in any precise way, infant mental development provides support for the above outline of early hominin cognitive evolution. From birth infants display an instinctive curiosity about the natural world, mediated by their own interaction with it. By 7 months, what appears to be an innate capacity comes into play to construct causal relationships (Newman et al. 2008). This builds on prior development of sensorimotor learning committed to procedural memory of how movement can be transferred from one object (cause) to another (effect) (Mandler 2007). Subsequent stages build on fine-tuning of infant-object interactions. Between the ages of 19 and 22 months infants develop the mental ability to recall a representation of something unseen in relation to something observed (Gelman 2009), opening the way for conscious causal reasoning from observed effect to unobserved cause to develop in children during their third year of life (Gopnik 2000; Gopnik et al. 2004). 'Theory of mind' in the form of an ability to construct causal relationships between inferred mental states and observed behaviour normally develops from the age of four on (Astington and Dack 2008). In other words, causal comprehension progresses from perception of physical interactions, to the construction of causal inferences between observed images and recalled categories, to construal of mental states as causes of social behaviour. Since this sequence parallels the evolutionary stages envisaged to have occurred during early hominin cognitive evolution, it can be taken to provide some support for it.

Evolution of an innate tendency to construct causal relationships did have to overcome one hurdle, however. Though causal inferences reflect empirical observation, it is the activity of the brain that establishes the neural linkages that instantiate them. Causal inferences are mental constructs that go beyond the information provided by observed covariance (Waldmann et al. 2006); and in doing so they can be in error—as when sickness is ascribed to sorcery. As there is no guarantee, therefore, that causal interpretations accurately reflect external reality, causal inferences possess only the epistemological status of hypotheses, or theories (Gopnik and Meltzoff 1997).

Inferred causal relationships can be erroneous for several reasons: because sensory processing can be inaccurate, leading to category mistakes (identifying a rope as a snake); because memory may be mistaken; and because inferences may be biased by prejudice or emotion. A more serious error from a behavioural perspective is to conceive correlation as causation. Since temporal sequence is necessary to establish a causal inference, the human brain is predisposed to conclude, wrongly, that it is also sufficient. *Post hoc ergo propter hoc* is a logical fallacy: it also reflects a psychological tendency to construct causal inferences on the basis of insufficient evidence. A causal connection can be inferred from just a single observation. Unavoidably, therefore, cognition is a 'probabilistic activity' (Sperber and Hirschfeld 2004). So since causal relationships constructed by early hominins held only with a certain degree of probability, acting upon them entailed risk. Indistinct marks might indicate the presence of a predator, or not. The psychological response to inherent uncertainty would have manifested as anxiety.

Getting causal connections wrong could have exacted a high price for small hominins hunting alone, and it is difficult to see how natural selection could have produced such a capacity in a solitary species. So how did such an error-prone cognitive process evolve? For an individual, there are two ways of strengthening a hypothetical causal inference: through repeated observation; and through instrumental testing, by acting upon it. While the former depends on experience that a tyro hunter would not possess, the latter amounts to conducting a trial in order to monitor feedback, which would do nothing in a potentially dangerous situation to reduce anxiety. In a social species, however, two additional means of confirmation become available: the endorsement of expert others; and coherence within a structure of previously confirmed shared beliefs (Fugelsang and Dunbar 2005). Taking account of the responses of other group members draws on their experience to provide the repeated observation required to confirm individual causal inferences, thereby reducing anxiety. Shared beliefs develop through collective activities, as over time the inferences on which they rest are integrated into memory. Coherence thus also reflects the experiences of the group. In early hominins coherence would have been achieved subconsciously, through the easing of anxiety.

Only because early hominins were social animals living in small groups did the potential exist for causal relationships inferred by an individual to be tested by reference to the experience of other group members. An inference could be indicated by some anticipatory movement and/or display of emotion. Group agreement could, for example, have been indicated by stamping excitedly and disagreement by backing away, which would have been enough to encourage collective action or prevent a rash response. The sort of situation we can envisage might have occurred when a member of a small foraging group noticed some indistinct marks that could have been made by predator or prey. If causal inference was to the former, the safe course of action would have been to make for the nearest tree: if to the latter, to seek out the prey. Either inference was hypothetical, though the consequences of error were very different. If an inference to a nearby predator was wrong, all that would have been lost was a meal. But if the inference that possible prey made the marks was incorrect, following them could be fatal. In the latter case, if more experienced group members inferred a predator as cause and indicated their concern, not only would their behavior have averted danger, it would also have occasioned social learning. Note, however, that positive or negative reactions were immediate responses to the behavior of a group member: they were not designed to teach. Active pedagogy came later. My point is that group confirmation or disconfirmation of causal inferences created the conditions for causal cognition to evolve through natural selection, which I take to be the most significant advance in intelligence achieved by early hominins.[3]

Two other mental phenomena whose origins have long been debated may have evolved in relation to causal cognition, namely overimitation and belief. Overimitation refers to a hardwired behavioural bias in young children, but not found in apes, exactly to copy even unnecessary actions of adults in order to produce an observed causal effect. In other words, children automatically encode all the actions they observe in the unconscious belief that they are causally meaningful. This has the negative effect of complicating and potentially distorting the structure of causal belief, but the positive effect of fast-tracking social learning, by providing a means of incorporating specific causal relationships into behavioural repertoires (Lyons et al. 2007). Evolution of overimitation would have been of advantage to early hominins because it would have enabled causal relationships to be established

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[3] Support for the significance of sociality for the evolution of intelligence comes also from studies of other social primates (Kamil 2004).

through imitation, rather than through possibly erroneous individual inference. The downside, however, of basing behaviour on imitated causal inference lay in the possibility that the copied behaviour was designed to deceive, or that the inference was wrong. These sources of uncertainty could be overcome, however, if copied behaviour was accompanied by a feeling of conviction. Belief provides just such a psychological sense, so it may well have evolved as a third interlocking element in conjunction with causal inference and overimitation. The combination of the three would have enabled some populations of early hominins to gain advantage over others in responding to their challenging environment.

A final point to note is that the variability of indirect natural signs in a mosaic environment prevented a small repertoire of communicative gestures becoming hardwired, as in monkeys (Seyfarth et al. 1980). Instead gestures became formalised through imitation and transmission, eventually developing into a mimed vocabulary of signals with associated sounds (Bickerton 1990). This progressively more discriminating and sophisticated mode of communication provided a more effective means of considering and confirming increasingly tenuous causal interpretations of social behavior in terms of mental states and motivations. The need for causal confirmation is thus likely to have been a significant driver in the evolution of language.

The above scenario is speculative, but possible. The development of causal comprehension in infants lends some support. It remains to test the hypothesis through tying it down more closely to what we know about the conditions under which the earliest hominins evolved.

The case for evolution of causal cognition in early hominins

Just where and when the small groups of Miocene apes lived that made up the last common ancestral population of both panins and hominins can only be a matter of speculation—and given the geographical spread of the fragmentary remains of the earliest hominins so far excavated (*Sahelanthropus* in Chad, *Orrorin* in Kenya, and *Ardipithecus kadabba* in Ethiopia, all dating back some 6 million years), we are unlikely ever to know. What we do know is that the earliest hominin populations could no longer depend on the resources of a forest environment, and that they had to adapt to a drying woodland ecosystem in which food was harder to find, more dispersed, and less abundant.

With *Ardipithecus ramidus*, however, we are on somewhat firmer ground. This species lived around 4.4 million years ago in the Afar Rift region of Ethiopia in an environment described in a combined international study as “woodland with small patches of forest” (White et al. 2009). The same study also concluded that *A. ramidus* was both arboreal and primitively bipedal, that it was more widely omnivorous than chimpanzees, and that its brain was much the same size.

From anatomical evidence we may conclude that *A. ramidus* had already adapted to semi-terrestrial living, and so could exploit new opportunities provided by a mosaic environment, as forest gave way to patchy woodland (Elton 2008). To subsist in this drying and increasingly variable woodland ecosystem would have required *A. ramidus* to seek out new terrestrial food resources. But this was a dangerous environment. *A. ramidus* could walk semi-upright, but must have been a clumsy runner. Even for good escape climbers, spending more time on the ground would inevitably have exposed them to increased danger from predators. These early hominins were not hunters, but the hunted (Hart and Sussman 2005). Predation would have exerted selection pressure (Zuberbühler and Jenny 2002), which would have favoured use of every possible source of information about where danger lay or food could be found, including indirect natural signs.

The more uniform and unchanging an environment is, the more likely behavioural responses will become hardwired. In a highly variable mosaic environment exhibiting increasing seasonal variation, however, behavioural flexibility was a more valuable adaptive response (Elton 2008). Such environments were cognitively demanding, in that the locations and seasonal availability of an extended range of new food sources had to be accurately remembered. Early hominins were therefore obliged to keep track of many more features of their environments than did the mainly forest-dwelling contemporary ancestors of chimpanzees.

The features monitored by early hominins like *A. ramidus* included not only food sources and predators, but also their own kind. *A. ramidus* was a social species that foraged widely in small family groups. For their own protection, they had to keep an eye out for each other. So any innate tendency to notice and interpret natural signs would have been reinforced by both the biophysical and sociocultural environments that *A. ramidus* inhabited. The relationships between variable indirect natural signs and their causes were too numerous to be hardwired to specific responsive behaviours, so had to be learned. And to be of value in triggering appropriate behaviour they had also to be readily accessible. Such storage, I have suggested, was most likely organised in relation to existing spatial cognitive maps, because this would have been the most parsimonious solution.[4]

So committed to memory, causal connections did not at first require any substantial increase in cranial capacity, for all that was necessary was for observation of an indirect natural sign to evoke a category representation of predator or prey. Making such connections depended on no more than reinforcement learning. The next step was to construe connections reflecting covariance as causal relationships, which could be done through acting upon them and monitoring the effect (Schulz et al. 2007). In this way a model began to be constructed of how categories of objects and events were causally connected. Only when causal reasoning was extended from naïve physics and biology to composite tool manufacture, increased social interaction and cumulative cultural learning was greater brain capacity required. But that came later.

The ability to extract the information available in indirect natural signs would have been particularly valuable when used to follow a sequence of signs to locate prey. Such a sequence could consist of anything from a line of easily-followed similar marks in wet sand to an ill-defined succession of variable and intermittent traces. Recognising a sequence of indirect natural signs as a trail would have

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[4] Note that the structural differentiation of memory into semantic and episodic components was a later development dependent on the evolution of language.

marked a significant cognitive advance for early hominins over forest apes. To do so required connecting up a sequence of signs by ascribing them to a single cause. Following a trail would have permitted early hominins to locate prey or become aware of predators—an ability no population of contemporary apes possessed. I am not suggesting that early hominins were tracking game over long distances: that was a later Pleistocene development. The tracks I am referring to were the kind a small reptile leaves that gives away its hiding place. Inferring what caused such traces would have provided real fitness benefits for a small, environmentally pressured hominin. But for that to happen, the signs making up the sequence had to be mentally connected to a single recalled representation of the animal believed to have made them.

Around 4 million years ago forest remnants in the Afar region had mostly given way to woodland, and *Ardipithecus ramidus* had been replaced by *Australopithecus anamensis*—though how the two were phylogenetically related remains to be established (White et al. 2006). Elsewhere habitats were more mixed, with woodland thinned out to bushland and grassland, interspersed with isolated wetlands and pockets of forest in places (Behrensmeyer and Reed 2013). This varied and changing mosaic environment was not produced by any significant global change in climate, but rather was due to localised conditions that included both tectonic and volcanic activity that broke up the landscape and drainage, creating escarpments and isolated wetlands, while beyond the few riverine valleys gradual drying thinned out vegetation to produce more open country (Reynolds et al. 2011).

Australopithecus evolved, therefore, in an environment that was becoming increasingly variable—a trend that continued during later hominin evolution (Behrensmeyer 2006). This environment offered both opportunities and dangers, as flora and fauna differed from place to place over a foraging range that of necessity was extensive. Australopithecines adapted by becoming fully bipedal, and by exploiting a range of new food resources, including hunting small mammals; they were already omnivorous, but meat-eating increased. In just this sort of environment improved tracking skills would have yielded dividends, as small game—and predators too—moved into open savannah between patchy woodland and marshy areas.

Under these conditions, australopithecines are likely to have extended their use of indirect natural signs in two ways: to follow tracks further (and keep contact with each other while doing so) (Shaw-Williams 2014), and to recognize and respond to a greater range of different signs. Tracking prey entailed patiently connecting signs over longer distances, during which trackers needed to keep in mind the representation of the animal they believed they were following. This placed greater demands on working memory. The extension of natural signs to other indicators, such as the sudden flight of birds or changing weather conditions, would have come easily if australopithecines already possessed an innate propensity to infer causal relationships. Together the cognitive demands of persistent tracking and identification of new signs would have exerted selective pressure to increase capacity of both working memory as a platform for the selection of behaviour, and cognitive structure to accommodate a more complex model of the world.

The cranial capacity of australopithecines showed some increase over the ardipithecines, but encephalisation became marked only with the evolution of *Homo*. Small increases in brain/body ratio among the australopithecines could have reflected pressures to increase memory capacity exerted by construction of more complex mental maps to include more causal relationships. Increased selective pressures for greater cognitive capacity is likely to have come at first, however, from expanding the spatially organised model of the world to include recognition of causal relationships as second-order meta-representations (Solomon et al. 1999). The causal interpretation of indirect natural signs would have facilitated the hunting of larger game, while causal reasoning was essential both for tool manufacture (Wolpert 2003; Vaesen 2012)[5] and to interpret social behaviour (van Horik and Emery 2011).

To make a tool, even of the primitive Oldowan kind produced by the late gracile australopithecine *A. garhi* and early *H. habilis*, entails associating the sequence of strikes required for manufacture with an image or category representation of its eventual form—which suggests that the capacity to follow a sequence of natural signs could have served as a model for the transition from the use of available natural tools (from stones to sticks and twigs) to the sequences of actions required for tool*making*. Both tracking, with its requirement to relate a sequence of natural signs to a mental representation of prey being tracked, and toolmaking, in which a sequence of actions relate to end use, are likely to have exerted selective pressure for greater capacity working memory and more proficient means of storing causal connections so as to apply them more effectively in the selection of behaviour. While the former exerted pressure for greater cranial capacity, the latter required improved working memory to act as a mental platform where the image of the goal to be achieved (prey or tool) could serve to select appropriate motor activity (Stout 2011).

In summary, the cognitive evolutionary process I am suggesting goes like this. The advance achieved by the earliest hominins over contemporary populations of forest apes was to incorporate motor activity generated by inferring the causes of visible indirect natural signs into their behavioural repertoires. The capacity to so this rested on three cognitive abilities: to recall a category image through its covariance association with a current observation; to represent both simultaneously in consciousness by means of the platform provided by incipient working memory; and to store such relationships in an easily accessible way, which I have suggested was through incorporation of causal connections into cognitive maps. Limited capacity working memory appears to characterise ape cognition, and was likely present in the LCA of hominins and panins; but not the capacity either to infer causal relationships and act upon them, or to integrate causal inferences into cognitive structure (Read 2008).

Meta-representation of the relationship between a perceptual image and a recalled representation as *causal* required an increase in the capacity of working memory to consciousness of three items: observed effect, inferred cause, and the

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[5] For which both fine muscular coordination (the effector subsystem) and a 'spatial-praxic' subsystem to permit visual-spatial mental manipulation would have been necessary (Welshon 2010).

relationship between them, an advance probably associated with the early australopithecines. Once this capacity had evolved, it opened the way for causal reasoning to be extended beyond the interpretation of natural signs. Fully conscious working memory of the kind required to support reflective thought took hundreds of thousands more years to evolve (Coolidge and Wynn 2009), but limited working memory would have been sufficient to permit the general principle derived from the causal interpretation of natural signs to be applied to other behaviours, notably tool manufacture and use (Vaesen 2012). The capacity of working memory expanded further in *Homo* to enable representation of alternative scenarios and conscious intervention in the selection of behaviour.

Throughout the transition from Ardipithecus to the australopithecines to early *Homo*, selection favoured phenotypic plasticity in response to environmental complexity and variability (Grove 2011). That is, the direction of evolution continued to be towards finer calibration of behaviour in response to variable conditions. Behaviour associated with the causal interpretation of indirect natural signs progressed from locating the hiding places of small prey to extended tracking of large wounded animals over long distances, known as ‘persistence hunting’ (Liebenberg 2008). And the crude splitting of Oldowan tools eventually led to production of finely honed Acheulian implements. Perhaps most significant, however, were changes in social behaviour brought about by the extension of causal understanding to the attribution of motivations and intentions to explain and respond to the behaviour of conspecifics (Sperber et al. 1995), the competence known as ‘theory of mind’ (Humphrey 1993; Garfield et al. 2001; Humphrey 2002; Gärdenfors 2003). As the interpretation of social behaviour, from body language to deliberate signalling, was even more conjectural than the ascription of causes to indirect natural signs, social verification became more necessary to minimise uncertainty and anxiety. The human proclivity for gossip (Dunbar 1996) is likely to have developed as much in response to the need for verification of hypothetical interpretations of social behaviour in terms of mental states as to the reinforcement it gave to intra-group bonding.

In conclusion: the significance of causal reasoning

The development of causal reasoning, I have argued, was the earliest significant advance in the evolution of human cognition. It laid the basis for the set of cognitive competencies that are essentially human—‘theory of mind’, technological innovation, social cooperation, and political organisation, all built on the foundation of elementary causal inference. In addition, relating cause to effect required recognition of temporal order: instantiated in cognitive structure causal reasoning led directly to consciousness of time.

The neural instantiation of temporal sequence inherent in causal relationships laid the basis for anticipatory cognition (Osvath and Gärdenfors 2005), early evidence of which can be seen in the transportation of food (meat from a kill, gathered plant foods), and the manufacture of stone tools from material transported over a distance to ‘accumulation sites’ (Potts 1991). In subsequent cognitive evolution, the temporal dimension of mind was projected forward through the instrumental relationship of present cause to future effect. This, plus expansion of the capacity of working memory as a platform for the juxtaposition of representations, provided the essential ingredients for our remarkable capacity for 'mental time travel' (Suddendorf and Corballis 2007).

Meta-representing observed covariance as causal introduced hierarchical organisation as a 'general organizing principle' for information processing in human cognition (Tsien 2007). Mapping causal inferences and the relationships between them resulted in an integrated mental structure that was not only hierarchical but also recursive,[6] to accommodate sub-sequences. The benefits attached to constructing such an integrated model of the world (in the form of a 'causal map') (Gopnik et al. 2004) exerted selective pressure for greater memory capacity and larger brains.

The capacity of working memory increased to meet the need to connect causal sequences essential for strategic planning, whether to make tools, or hunt, or win a mate. Increased capacity allowed mental representations to be variously connected, and inferences to be combined in novel ways to create alternative imagined futures, so providing variation for the selection of innovatory behaviour (Suddendorf et al. 2009).

Finally, the extension of causal inference to interpret social signals in terms of mental states and motivation led to the assembly of more complex models of causal beliefs integrating the biophysical and sociocultural environments, which required a correspondingly expanded role for executive processes in the selection of behaviour. So indeed it can be claimed that inferring, structurally organising, and applying causal inferences was what 'made us human' (Wolpert 2007).

In summary, my argument in this paper has been that the ability to identify and infer the causes of visible indirect natural signs, a source of information not utilized by any other primate, was the earliest cognitive development that differentiated early hominins from contemporary populations of forest apes. The LCA of humans and chimpanzees bequeathed to both lines only a crude form of causal understanding. In the variable environment encountered by early hominins, the causal interpretation of indirect natural signs brought real fitness benefits. As a result, building on innate curiosity, a tendency evolved to notice such signs and infer their causes. The ability to do this required that the observed sign and the remembered category image of the putative cause be represented simultaneously in incipient working memory. Interpreting the relationship between them as causal and integrating causal relationships into cognitive maps of their environment enabled early hominins to select behaviours best adapted to the mosaic conditions that confronted them. Inferences of the causes of natural signs facilitated pursuit of prey and heightened awareness of predators. This foundational advance in causal cognition occurred, I maintain, over the 3–4 million years that separated the LCA between humans and chimpanzees from the australopithecines. On this foundation, causal reasoning was thereafter extended to whole new domains, from tool

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[6] Empirical studies indicate that the brain/mind imposes a hierarchical/recursive structure even when processing descriptions of everyday events (Mesoudi and Whiten 2004).

manufacture and ‘theory of mind’ to large-scale social cooperation and niche construction.

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