

*Review*

# The human socio-cognitive niche and its evolutionary origins

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Hominin evolution took a remarkable pathway, as the foraging strategy extended to large mammalian prey already hunted by a guild of specialist carnivores. How was this possible for a moderately sized ape lacking the formidable anatomical adaptations of these competing ‘professional hunters’? The long-standing answer that this was achieved through the elaboration of a new ‘cognitive niche’ reliant on intelligence and technology is compelling, yet insufficient. Here we present evidence from a diversity of sources supporting the hypothesis that a fuller answer lies in the evolution of a new *socio-cognitive niche*, the principal components of which include forms of cooperation, egalitarianism, mindreading (also known as ‘theory of mind’), language and cultural transmission, that go far beyond the most comparable phenomena in other primates. This cognitive and behavioural complex allows a human hunter–gatherer band to function as a unique and highly competitive predatory organism. Each of these core components of the socio-cognitive niche is distinctive to humans, but primate research has increasingly identified related capacities that permit inferences about significant ancestral cognitive foundations to the five pillars of the human social cognitive niche listed earlier. The principal focus of the present study was to review and integrate this range of recent comparative discoveries.

**Keywords:** cognitive niche; egalitarianism; cooperation; theory of mind; language; culture

## 1. INTRODUCTION

The evolution of the genus *Homo* through the past 2.5 Myr or so has seen a tripling in encephalization, eventuating in unprecedented cognitive achievements. The evolutionary explanation for such costly developments must lie not in what they have achieved in present or recent times, but what their evolving forms achieved for our ancestors that made them sufficiently competitive within the regimes of natural selection they faced. What were the distinctive forms of behaviour they were able to generate?

A fundamental arena for answering this question concerns the mode of foraging. Foraging is only one element among many others, such as reproductive behaviour, that together constitute a species’ overall adaptive behavioural strategy, but successful foraging provides the essential foundation for the rest, and occupies the greater part of any primate’s daily activity budget. Has the evolution of humans’ distinctive encephalization and cognition been associated with an equally distinctive mode of foraging?

Fortunately, we can draw upon a confluence of two quite different sources of evidence to answer this question. One is archaeology, which has progressively fleshed out the scope of hominins’ evolving modes of

foraging, notably concerning the rise of hunting and the exploitation of prey much larger than other primates hunt [1]. The other, complementary source of evidence includes the study of living peoples subsisting in the tropics by this style of hunting, typically in conjunction with the gathering, exchange and sharing of plant foods. Because this way of life is fast disappearing, we are fortunate that over the past century, numerous detailed ethnographies have been compiled, which when systematically collated allow us to identify core behavioural principles shared by hunter–gatherer bands [2–4].

These two sources of evidence complement each other. Archaeology offers direct evidence of past behaviour, but in an inherently patchy way because while some elements, such as weapons, are well preserved, others, such as gathering behaviour, are not. Hunter–gatherer ethnographies, by contrast, provide rich details about the behavioural and cognitive patterns of this mode of foraging, but unlike the archaeological evidence, their relevance diminishes the further back into the past we cast our inferences, particularly concerning more ancient ancestors with smaller brains and less sophisticated technologies [4].

The archaeological record tells us that hunting and gathering, as indexed by evidence of wild animal and plant consumption, gave way to domesticated animals and crops only about 10 000–12 000 years ago, in the Middle East [1]. Evidence of the *origins* of hunting and gathering is more fragmentary, but progressively

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earlier traces have been identified. Long-standing evidence includes stone tools, particularly microwear caused by butchery, and complementary evidence of cut marks on bones, for which there is good convergent evidence dating to approximately 1.8 Mya [5]. More controversial is the recent identification of such evidence as long ago as 3.4 Mya [6], antedating the genus *Homo* and the appearance of roughly knapped stone tools around 2.6 Mya [7].

This accumulated evidence of early Pleistocene butchery is now extensive, but does not in itself demonstrate hunting. Some authors have suggested that it might instead reflect scavenging on carcasses of prey killed by carnivores such as lions and hyenas. However, evidence that non-human predatory primates scavenge little (perhaps because of toxicity of old kills, or the dangers of a large-carnivore feeding site) [1,8] argues against this. More direct evidence for active hunting 400 000 years ago came with the discovery of artefacts identified as hunting spears [9] because of their remarkable properties. At around 2 m long, these were fashioned to have the shape and weight distribution of a javelin, suggesting that they were made to be thrown, unlike a stout stabbing spear. Their sophistication suggests that they were pre-dated by a long period of cumulative progress towards this achievement, pushing back the inference of major technology-aided hunting to yet earlier times. Coupling this with the evidence for butchery of large mammals such as rhinos and elephants places the origins of these distinctively hominin forms of hunting, beyond anything seen in other primates, to between 0.5 to 2 Mya [1,8]. Even the more recent of these dates indicates substantial involvement in a mode of foraging incorporating big-game hunting that spanned a long and evolutionarily significant period of time, up until the very recent transition to agriculture.

The other source of evidence derived from recent anthropological studies complements this perspective in showing that all tropical peoples who live by foraging on wild foodstuffs incorporate significant proportions of both plant and animal prey, including large animals where available. While the archaeological record remains relatively mute on early hominins' gathering activities, coupling the consistent picture documented across diverse recent foraging peoples with the evidence for ancient hunting suggests that hominin evolution through the Pleistocene rested upon the rise of some forms of a 'hunting and gathering' way of life that was revolutionary from a comparative primate perspective (analysed in more depth in [8,10]). What, then, are the implications for the new grades of cognition that accompanied the equally unprecedented encephalization that also occurred through this period?

## 2. THE COGNITIVE NICHE

According to Tooby & DeVore [11, p. 209], 'the core of our zoological distinctiveness' lies in a capacity for 'conceptually abstracting from a situation a model of what manipulations are necessary to achieve proximate goals that correlate with fitness'. They referred to this as an ancestral 'cognitive niche'.

In evolutionary biology, the concept of the niche has become indispensable. It refers to a species' complex of specializations that define its mode of adaptation as differentiated from other species, including its close competitors [1]. The resultant 'niche separation' is a fundamental phenomenon in evolution and as relevant for discussing the concept of a 'cognitive niche' as any other. Note that the 'niche' concept encompasses both the environmental features exploited and the complementary adaptations that make this possible (see also Barrett *et al.* [12]). Thus, the niche of lions includes the availability and properties of the large mammals hunted, but also lions' distinctive style of hunting and the teeth, claws and psychology that facilitate this. The concept of human foragers' 'cognitive niche' fits this perspective, with the specialist elements such as speed of pursuit, teeth and claws compensated for by superior intelligence. Of course, the lions' niche also incorporates cognition (memory, decision-making, etc.), so the concept of the hominin 'cognitive niche' really signals a new sophistication in cognitive powers, reflected in massive encephalization [8] and dissected further later.

Manifestations of the evolving hominin cognitive niche include hunting weapons and other artefacts, some well preserved in the archaeological record. Others described in ethnologies extend to advanced planning of weapon-making, trap construction and hunting sorties, extensive tracking of prey and later analysis of what took place during the hunt and why [13]. These well illustrate the 'conceptual abstraction' that Tooby & DeVore referred to. The contrast with the hunting style of other major competitors is graphically illustrated by the example of tracking [14], in which the significance of marks made in the earth by prey is read with great sophistication to draw inferences about such factors as prey type, number, age, disability and, after an attack, the prognosis for a wounded prey's demise.

Developing the cognitive niche has allowed human foragers to repeatedly mount what Tooby & DeVore described as 'evolutionary surprise attacks' on prey, escalating the arms race between predator and prey such that the latter cannot keep up, through biologically evolving counter-adaptations, with the more rapidly developing, intelligent new forms of assault based on weapons, traps, ambush styles and suites of other clever technological and behavioural innovations. The logic of this cognitive niche hypothesis seems compelling even in such abridged accounts (see, [8,10,11,15] for fuller analyses). The concept may even seem self-evident: what other than a 'cognitive' niche will explain the unprecedented tripling in brain size in a mere 2 million years?

Nevertheless we argue that Tooby & DeVore's hypothesis has more limited explanatory power than a broader version that incorporates key social elements delineating a 'socio-cognitive niche'. Later we address five of these major elements in turn—cooperation, egalitarianism, mindreading (theory of mind), language and culture. More detailed explanations of these domains are available elsewhere [8,10], and the upcoming §3 representing only a précis, updated with key, newer information. An

independent and complementary analysis exploring social dimensions of the cognitive niche, particularly concerning language, has recently been provided independently by Pinker [15].<sup>1</sup>

Section 3 provides the foundation for a much fuller account in §4 of the substantial comparative data recently accumulated that illuminate the evolutionary origins of this human socio-cognitive complex. Section 4 offers the principal ‘new thinking’ that is the theme of this Issue, through its diversity, substance and recency. Section 3 represents new thinking but on a longer time-scale, insofar as it emphasizes a cooperative core in the human socio-cognitive niche that contrasts with late twentieth century preoccupations that included competitive topics in evolutionary psychology, such as cheater detection and homicide (e.g. see overview in [18]), a focus in human and non-human primate studies on Machiavellian intelligence and tactical deception [19]) and a yet broader emphasis on selfishness in evolutionary biology. The latter has been superseded by a richer understanding of multiple-level selection and the fitness benefits to be gained by positive contributions to group-level goods [20].

### 3. THE HUMAN SOCIO-COGNITIVE NICHE

To identify consistent correlates of the hunting–gathering way of life, Erdal & Whiten [2,3] systematically surveyed ethnologies of as many as 24 different foraging societies across four continents. Any one of these societies might offer a poor model of ancestral forms, but patterns observed repeatedly across the variety of localities involved should identify core adaptations to this mode of life. Generalizations summarized in what follows are based upon this principle.<sup>2</sup> Marlowe [4] and Hamilton *et al.* [21] provide further data through surveying 478 and 339 forager societies, respectively, although in less depth. These latter studies converge in indicating that the social context for the topics discussed below is small, relatively stable bands with a median size of only about 30 people [4].

#### (a) *Cooperation*

All ethnologies record marked division of labour between hunters and gatherers, with men typically focused upon hunting and occasional supplementary gathering, and women typically gathering. Parties of each will take different daily foraging routes but, crucially, bring back most of the resources to a central camp to be shared among the band. This sophisticated form of cooperation is unique among apes, and depends on socio-cognitive abilities that can coordinate such crucial components as cycles of band fission and fusion and the holding of food items in anticipation of their being later shared. The band thus acts as a highly competitive ‘group-level predator’ insofar as by contrast with other apes, (i) dietary intake is the result of resources shared among the whole band; and (ii) the division of labour allows a great diversity of animal and plant resources to be accessed by the component foraging parties from multiple directions around the current camp base (which is typically moved nomadically several times a year: [4]).

Further sophisticated levels of cooperation underlie each of the subcomponents of hunting and gathering. For example, San bushman hunting often incorporates extensive group discussion of hunt plans and the significance of tracks encountered, sign language as hunters close in on prey, coordinated searching, and analysis of the outcome of physical attacks on prey (e.g. [14]). Less is recorded about gathering, about which we know less, particularly from a cognitive perspective, than we do for several other primates. However, accounts indicate that gathering is typically a collective activity (e.g. among Hadza, gathering parties average five women: [4]) and relies on information pooling and joint decision-making about foraging pathways and goals. Such information pooling extends to what has been learned during the different parties’ foraging activities being shared between hunters and gatherers around camp fires; so the next day’s plans are formulated using information accumulated across foraging zones (e.g. gatherers tell the next day’s hunters about suitable prey encountered). Other forms of cooperation extend to childcare, with youngsters being left under supervision in the camp while their parents forage.

#### (b) *Egalitarianism*

Erdal & Whiten [2,3] recorded that in all but one of the 24 hunter–gatherer ethnographies consulted, the sharing of food, particularly meat, is described as being generalized across the band as a whole, with food being distributed according to need rather than based on criteria such as hunting prowess or kinship relations. Combined with the division of labour noted earlier, this means that all members of the band consume items that are largely obtained through the efforts of the band as a whole.

Egalitarianism is also seen in everyday political arrangements, with ethnographers repeatedly remarking on the absence of designated leaders and the occurrence instead of negotiation and group-level decision-making. Intermittent aggrandizing attempts by individuals are met with a range of concerted counter-dominant reactions<sup>3</sup> by others, ranging from ridicule to violence and ostracism, that level power relations in the band [3,22].

That human hunter–gatherers also tend to be (broadly) monogamous means that, compared with that of the other great apes, their reproductive success tends to be more equal across the group, rather than dominated by an alpha male or by others of high rank.

These behavioural manifestations together reveal a common thread of hunter–gatherer egalitarianism [2,3]. Egalitarianism and cooperation appear to be mutually reinforcing adaptations (figure 1), insofar as the deep levels of cooperative effort outlined earlier are amply rewarded by the multiple forms of egalitarian sharing.

#### (c) *Mindreading (theory of mind)*

Unlike cooperation and egalitarianism, the attribution to self and others of states of mind has been explicitly studied little in hunter–gatherers. However, an early study by Avis & Harris [23] of Baka hunter–gatherer

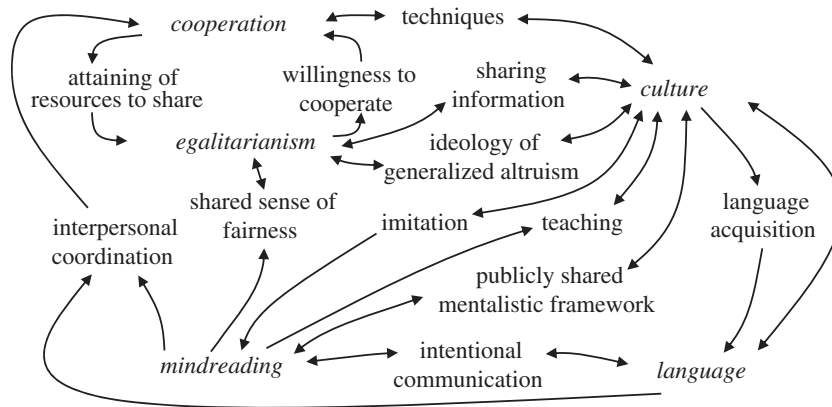


Figure 1. Principal classes of social cognition (in *italic*) in hunter-gatherer bands and inferred reinforcing relationships between them. For explanation and discussion, see text, especially §5.

children showed that 5-year-olds would take into account others' false beliefs just as do children in urban and other communities [24]. The attribution of false beliefs is recognized as a watershed stage in which the child grasps that others may hold mental representations of the world fundamentally different from their own, and it develops through a series of steps that incorporate the attribution of states that include emotions, seeing and knowing [25]. Moreover, some later achievements such as higher order attributions (thinking about what another person may be thinking about one's own ideas, for example) rest on the recursion of the first-order achievements in place by age five. Thus, although research has demonstrated later-developing forms of mental attribution that show interesting cultural variations [26], we have grounds to believe that hunter-gatherers are mentalists, attributing to each other such states as seeing, desiring and believing.

This means that the minds in a hunter-gatherer band interpenetrate each other in all these respects, facilitating the closely integrated cooperation and egalitarian sharing and decision-making described earlier, which allow the band to act as a unified, sophisticated predatory 'organism'. The mutually interpenetrating mindreading provides a central information processing system unattained by other species. There is thus a profound connection between the evolution of mindreading and the features described earlier, in the ways they interact to facilitate the unique form that the human hunting-gathering adaptation has taken (figure 1).

#### (d) *Language*

Language facilitates many of the key behavioural and socio-cognitive pillars of human hunting and gathering outlined earlier and later. For example, it is the principal medium of the joint planning and coordination of the different hunting and gathering forays that later converge; the equitable distribution of resources and the identification of infringements of this; and dialogue about one's own and others' states of mind. The latter phenomena are also part of a two-way relationship, insofar as the intentional use of language to inform others in relevant ways presupposes certain levels of mindreading, and more complex levels of mindreading

permit more elaborate, intersubjective language use. Pinker [15] discusses further ramifications of this language 'pillar' of the complex.

#### (e) *Cumulative culture*

Although foraging peoples are typically nomadic and thus able to carry all their worldly goods on their person, hunter-gatherer culture is enormously richer than the repertoires of traditions seen in other species, largely because the process is cumulative [27,28]. That is true of language and numerous other components essential to the human hunting-gathering way of life. For example, the array of traps, weapons and other foraging tools is often elaborate and far beyond what any person could invent in their lifetime.

A long childhood is devoted to acquiring this extensive cultural heritage [29] and may well represent a human adaptation serving this function. On an evolutionary time-scale, the signs of cumulative culture became discernable in the early Stone Age and progressively escalated [30]. The crucial cognitive advances that have allowed human cumulative culture to become so elaborate have been investigated in comparative studies that have variously suggested the difference lies in children's superior copying (imitative) abilities [31,32], apes' relative conservatism in social learning [33,34] or humans' capacity for pedagogy [16,35] and innovation [36]. These are not mutually exclusive, and there is evidence that hunter-gatherer cultures are transmitted by a rich mixture of observational learning, teaching and story-telling [29].

#### (f) *An interconnected, adaptive complex*

Although it can be difficult to cite direct and comprehensive supporting empirical evidence, reasoning suggests that the different aspects of social cognition and behaviour outlined earlier together form an adaptive complex capable of supporting the unique phenomena that constitute a human hunting-gathering ways of life. Whiten [8,10] labelled this complex 'deep social mind' to emphasize the core features of mental interpenetration and adjustment of individual to group-level goals. Each of the sets of phenomena outlined earlier contributes to unprecedentedly 'deep' social minds in different and inter-linked ways:

mindreading involves deep mental interpenetration between individuals; massive, cumulative cultural transmission means that minds are deeply structured by these processes; language allows deep connections between what interacting people 'have in mind'; and extensive cooperation and egalitarianism mean that the holistic functioning of the social group is paramount for the fitness of its members.

An adaptive complex is constituted through positive feedbacks between all these elements (see also Sterelny [16]), key aspects of which are indicated in figure 1 and addressed further in §5.

#### 4. ANTHROPOID EVOLUTIONARY ORIGINS OF THE ELEMENTS OF 'DEEP SOCIAL MIND'

Each of the human socio-cognitive elements reviewed above contrasts markedly with what is seen in other apes. However, recent research has increasingly revealed linkages too. On this basis, we can infer characteristics of our common ancestors that would have provided significant evolutionary foundations for the human developments discussed here. Much exciting new evidence and consequent new thinking has emerged recently in relation to each of the five phenomena outlined above. The bulk of this work focuses on chimpanzees and this is reflected in what follows.

##### (a) *Cooperation*

Wild chimpanzees do not exhibit the elaborate division-of-labour-based cooperation seen in human hunter-gatherer bands, but they do cooperate, in three principal contexts. One context of obvious relevance to the scenarios of hominin evolution outlined earlier is hunting and this is indeed cooperative when chimpanzees are pursuing their most common large prey, monkeys [37]. Chimpanzees have been observed to signal their intent to hunt through vocalizations, gaze and movements, such that a hunting party is formed; groups are more successful than individuals; and the males most involved in a hunt are more likely to gain portions of meat in the later sharing [37]. In the Taï forest, one of the locations at which hunting is most frequent, Boesch & Boesch [38] offered evidence of a degree of role division, with certain individuals driving forward the prey and others moving into ambush positions, which the authors have distinguished as not merely coordinated, but collaborative hunting.

The latter interpretations are controversial, however, because in observations of such socially complex events unfolding in the treetops, it is difficult to be sure that actions are not explicable through individual opportunism. Complementary experimental analyses with captive chimpanzees have thus been important in more precisely identifying cognitive strategies. Experiments have shown that chimpanzees would collaborate when it was necessary for them to act together to obtain food (pulling a rope to heave a plank bearing food sufficiently close, when pulling one end simply unthreads the rope and gains no food), and would spontaneously remove a peg holding a door closed to release a potential collaborator; moreover, they were discriminating in choosing whichever

of two potential partners had been most helpful before [39].

A second context for cooperation is raiding parties conducted against neighbouring chimpanzee communities [40]. In these, chimpanzees communicate the intent to go on a border patrol, such that a party of males acts in a coordinated fashion, with a goal clearly different from that of hunting monkeys.

The third context for cooperation is internal to the community: the formation of alliances and coalitions. How mid-ranking individuals distribute their support in conflicts can profoundly influence the operative social hierarchy, such as which individual is able to occupy the top rank [41,42]. Thus, chimpanzees cooperate to dominate others who would individually be capable of dominating them.

All these forms of cooperation—cooperating to hunt other species, to raid neighbouring conspecifics and to gain power within one's own community—are shared at some level with our own species, such that it is likely they existed in our shared ape ancestry. Implications of this are discussed further in §5 in relation to these and other aspects of social behaviour and cognition.

##### (b) *Egalitarianism*

The egalitarianism of human hunter-gatherers contrasts strongly with the behaviour of other apes. Thus, while human bands share food right across the community according to need, chimpanzees compete vigorously over large items such as a monkey kill; while the power-structure of hunter-gatherer bands is quite flat, chimpanzees are strongly hierarchical; and while hunter-gatherers are typically monogamous, other apes are not: in chimpanzees, the male in the alpha position commands most of the matings with relatively promiscuous females during his tenure [43].

Despite these contrasts, behaviour has been recorded in chimpanzees that if present in a common ancestor would have provided important foundations on which selection could operate to shape a more egalitarian strategy where this became more beneficial. While sharing is rare, it does occur, and is most likely in the context of carnivory [37,38]. It also occurs in relation to a few large plant food items. In the Taï forest, where hunting is so common, the frequency of sharing is particularly high and it includes a proportion of active sharing episodes in which pieces of meat are directly handed to individuals begging for it [39]. Such data support the hypothesis that a rise in the importance of large-prey hunting in hominin evolution would have selected for more widespread sharing. The sharing that does occur in chimpanzees reflects social ties, with sharing being more common between males who are allies, males and females who have preferred sexual relationships, and mothers and their offspring.

Related to the altruistic category of sharing is helping behaviour, which occurs in many forms among hunter-gatherer daily life, from mundane incidents such as helping lift a heavy object to long-term care for the sick or aged. Preschool children will spontaneously help an individual whose goal is blocked

by obstructions or who has dropped something out of reach [44]. Young chimpanzees were shown to spontaneously help others when faced with the latter situation, although not the former [44]. This again reflects a form of social cognition, recognizing when others need help, that could logically provide a crucial foundation for other forms of helping, cooperating and informing [45].

In addition, the coalitions that shape social relationships in chimpanzees represent an elementary form of counter-dominance, in which the status of high-ranking individuals is significantly influenced by the behaviour of others acting in concert against (or for) them. Erdal & Whiten [2] suggested that although the aspects of cooperation and egalitarianism shared by chimpanzees and humans are relatively minimal, if present in our common ancestors, they would logically have provided important seeds for the evolution of the remarkable forms they take in hunter-gatherer bands. As foraging strategies became more dependent on hunting large prey, cooperation and sharing can be expected to have become more common. As brain size and social intelligence evolved, potentially high-ranking individuals would be expected to have become more successful in maintaining the coalitions necessary to maintain high status, but others would have become more skilled at managing coalitions to keep them in check. Each of these processes would provide a selection pressure on the other, leading to an arms race between the Machiavellian social skills of those striving for the highest rank and of those working together to reduce the alpha's dominance, eventually spiralling to a ceiling at which a fully egalitarian, leveled society exists because it is simply not cost-effective to attempt to dominate others [2]. We are not proposing this as an inevitable outcome of iterated bouts of Machiavellian conflict, but rather one that would pertain in specific conditions, of which the most important would likely include small, relatively stable band sizes, enhanced brain size and social intelligence, and benefits to be reaped from sharing resources gained through cooperation.

### (c) *Mindreading (theory of mind)*

It was a decade after Premack & Woodruff [46] first asked 'Does the chimpanzee have a theory of mind?', before substantial empirical work on the question was undertaken [47]. The new research took two principal forms. One was based upon the analysis of direct observations of spontaneous behaviour, notably deception and counterdeception, which Whiten & Byrne [48] interpreted as providing suggestive evidence of apes taking into account others' goals, and what they could or could not see. Initial experimental results appeared consistent with the latter ability, with chimpanzees discriminating what a person could or could not see [49].

However, observations alone are not sufficient to establish if it is indeed such states that apes recognize, and substantial critiques identified limitations in the early experiments [50,51], the latter concluding that 'there is no solid evidence that non-human primates understand the intentionality or states of mind of

others' (p. 340). A suite of further experimental studies appeared to indicate that chimpanzees did not even recognize the conditions of seeing versus not seeing, instead managing only such crude distinctions as a person facing away versus towards oneself, when deciding which of them to beg food from [52].

Virtually all of this corpus of experimental studies in the 20 years following Premack & Woodruff's paper were based upon chimpanzees interacting with humans, typically in situations where the human was offering food rewards to the experimental subject. The picture changed markedly once tests included chimpanzees interacting with conspecifics, in competitive contexts. This showed chimpanzees discriminating between which of two food items a more dominant individual could or could not see when the subject had a chance to grasp one such item shortly ahead of a higher ranking competitor [53]. A variation on this approach showed that chimpanzees would remember what a competitor had or had not seen earlier and thus did or did not *know* about [54]. Experimental approaches now extended to the field have shown that alarm calls are used to warn others of danger selectively when there are grounds to infer their ignorance [55]. Such results are consistent with the inferences drawn in the earlier observational studies of 'tactical deception' [48]. This convergence became tighter through further experiments in which a chimpanzee had the opportunity to steal either of two food items from close to a human protagonist, revealing a preference for conditions in which the human would not be able to see—or in other tests, hear—the stealing taking place [56,57].

A fundamental problem in all such research lies in distinguishing the reading of states of mind from the reading of behaviour and contexts. Mindreading is not telepathy: it must be done through perception of critical aspects of others' actions and their context—so where does sophisticated behaviour-reading become mind-reading? Whiten ([58]; see now [59]) suggested a crucial criterion should be that the putative mindreader interprets different observables as meaning the same thing: a particular state of mind, such as 'seeing'; this then acts as an 'intervening variable' represented in the mindreader's brain, that in turn predicts different outcomes, according to context (another individual's not seeing something offers an opportunity for either deceiving them, or informing them, for example). Call *et al.* [60] adopted this framework in showing that in different contexts, chimpanzees would discriminate when another individual's failures to deliver a food reward were intentional, rather than were merely reflecting incompetence.

Summarizing these and other studies, Call & Tomasello ([61]; see also [62]) shifted far from their 1997 conclusion and instead argued that the spate of new studies showed that 'there is solid evidence from several different experimental paradigms that chimpanzees understand the goals and intentions of others, as well as the perception and knowledge of others' (p. 187). They added, however, that 'Nevertheless, despite several seemingly valid attempts, there is currently no evidence that chimpanzees understand false beliefs'. Chimpanzees have failed to discriminate

situations in which an event not witnessed by another individual, such as the movement of an object from one hidden location to another, leaves them with beliefs out of step with reality [63]. Accordingly, Call & Tomasello [61] end their review by stating that ‘Our conclusion for the moment is, thus, that chimpanzees understand others in terms of a perception-goal psychology, as opposed to a full-fledged, human-like belief-desire psychology’ (p. 187).

The new thinking derived from this recent corpus of experiments is that the social cognition we should attribute to our common ancestors on the basis of shared human–ape capacities includes elements (perception-goal psychology) that are simpler than, yet logically were capable of providing a foundation for, the more advanced human forms (belief-desire reasoning, in this case) of mindreading that have evolved.

#### (d) *Language*

For several decades a principal approach to the question of non-human apes’ language-like capacities has focused on the acquisition of sign language. This revealed remarkable abilities to recognize the symbolic significance of a large lexicon of such signs, coupled with a notable lack of symbol combinations and the declarative and information-sharing efforts characteristic of children [64]. More recent and exciting progress has focused on the natural vocalizations and gestures of apes in the wild [65].

##### (i) *Vocal communication*

Vocalizations that refer an audience to particular foci in the world, such as different classes of predator, have long been established in monkeys but studied little in apes. Such vocalizations have come to be called ‘functionally referential’ to recognize that they perform a key function of human language in communicating about external referents, but at a functional as opposed to an intentional level.

Recent studies have revealed a number of significant language-like qualities in chimpanzees’ functionally referential vocalizations. Observational inferences have been followed up by experiments demonstrating that vocalizations signal the quality of different foods located by the caller, even extending to variants labelling particular high-quality food types [66]. These calls are not automatic, but instead are given preferentially in the presence of valuable social partners [67]. There is also both observational and experimental playback evidence for the use of vocalizations that distinguish the social roles of participants (aggressor versus victim), allowing listeners to discriminate the direction of aggression in fights they cannot see [68], and likewise recognize the severity of the attack being made [69].

There is now some evidence of modifiability. In comparison with gestures among apes (see below) and human vocalizations, it has long been thought that primate vocalizations show little modifiability in form, although there is learning in respect of the referents [70]. However, studies have demonstrated a tendency for chimpanzee vocalizations to be modified to more closely match those of close companions [71],

and wild chimpanzees have more recently been shown to have more distinct vocalizations in relation to neighbouring communities than to more distant ones, again implying some modifiability, as well as social learning [72]. The structure of wild chimpanzee calls have also been shown to be modified as a function of the audience at hand, concerning functional reference to aggressive interactions, as outlined earlier.

There is increasing, complementary evidence of production of vocalizations being flexible in their deployment according to the audience. For example, females’ giving of copulation calls is varied according to the rank of their mating partners and is further inhibited if high-ranking females are nearby [73]. Females are less likely to give a pant-grunt greeting to others of high rank if the alpha male is nearby. Males produce food-associated rough grunts when a close social partner is in the vicinity. Females produce screams that appear to exaggerate the indicated severity of an attack by another chimpanzee if others likely to help them are available, notably an individual who outranks the aggressor [68].

Finally, there is new evidence on apes’ use of sequential structuring of elements of vocalizations, creating different meanings. Clay & Zuberbühler [74] have shown that bonobos produce five acoustically distinct call types when encountering food, and they mix these types together into longer sequences. Playback experiments showed that the combined sequences, but not the individual elements, conveyed meaning to listening bonobos about the quality of food encountered. The combinatorial sequences were not syntactic, but they carried more information than the five types of calls of which they were composed.

Together, these new findings suggest that vocal behaviour in the *Pan* genus, while lacking the flexible learning and true syntax of human language, is a more subtle and sophisticated communication system than earlier suspected [65]. These findings make it easier than hitherto to entertain an evolutionary vocal continuity in the evolution of human language.

##### (ii) *Gestural communication*

Apes’ gestural repertoires are extensive compared with those of monkeys [75]. Moreover, chimpanzees have been shown to appropriately adjust the silent, audible or contact mode of their gestures to the attentional state of their audience, whom they continually monitor [76]. Where initial gestures fail, apes have been shown to generate alternative gestures or elaborate on those already used [77]. These features have been interpreted as indicating that apes’ gestures are used intentionally and flexibly to a greater degree than is evident in their vocalizations, supporting scenarios involving a gestural rather than a vocal origin for human language [16]. Studies have also reported extensive gestural repertoires in apes. In the first comprehensive study of gestures’ use in wild chimpanzees, Hobaiter & Byrne [75] distinguished 66 different gesture types in the Budongo forest, a value comparable to earlier reports for Gombe (56) and Mahale (61).

However, the gestural hypothesis of language origins does not necessarily need to be a dichotomous alternative to a vocal origin. A newer view is that apes use both gestures and vocalization in combination and there is evidence that they are more successful when they do so. PET scans of the brains of chimpanzees showed heightened metabolic activity in Broca's area (specialized for language in the human case) in individuals who both vocalized and gestured, as opposed to those who gestured only [78].

#### (e) *Culture*

Whiten [79] recently offered a comprehensive comparative review in this journal concerning cultural phenomena in chimpanzees and humans, and their implications for cultural evolution in early hominins. Whiten *et al.* [80] similarly provided a recent comparative analysis of the underlying social learning processes in the two species. Here we thus more briefly highlight the key comparisons relevant to the present evolutionary analysis.

Studies in the wild have identified over 40 different chimpanzee traditions across Africa that span much of chimpanzees' behavioural repertoires, extending to forms of food processing, tool use, grooming, and social and sexual behaviours [81,82]. Moreover, each chimpanzee community studied for a long term has been shown to possess a unique profile of these traditions, such that the behavioural repertoire of each chimpanzee assigns it to a particular geographic location, as do human cultural profiles [82].

Experimental diffusion studies with captive chimpanzees have confirmed a capacity to transmit and sustain such multiple traditions, consistent with the picture of wild chimpanzee cultures outlined earlier [81,82]. In diffusion experiments, alternative techniques have been seeded in single individuals in each of two separate communities, and their subsequent differential spread across the communities monitored [83]. Six of such studies have demonstrated a capacity to sustain several traditions in the same communities, and the spread of these from community to community [34,84]. Such studies have also provided evidence of conformity to local cultural norms [85] and of cultural conservatism [34], echoing the results of field experiments introducing artificial foraging opportunities to communities with different cultural repertoires in place [86].

Although there are of course important differences in social learning processes underlying the cultural capacities of the two species, numerous aspects of social learning are also shared [80]. Both species possess a 'portfolio' of such processes, including forms of both imitative and emulative learning; selectivity in relation to aspects of models' actions, models' status, and physical causality; conformity to population norms; intentional control of copying; and copying intended rather than actual, failed acts [80,87–92]. In sum, the new thinking of the past decade is that despite the yawning gulf in the cultural achievements of chimpanzees and humans, a rich core of cultural cognition is shared and this likely reflects ancestral states from which hominin cultural evolution took off.

## 5. CONCLUDING DISCUSSION

Section 3 outlined five principal pillars of 'deep social mind', and suggested that these together form an inter-related, adaptive socio-cognitive complex that evolved to support humans' unique form of hunting–gathering niche. There are multiple potential interactive lines of linkage between these pillars, indicated in figure 1, and reasoning suggests that most or even all such potential linkages are realized through two-way positive feedback (see also [15,17], and Sterelny [16]), instances of which can be outlined as follows. Several key aspects are indicated in figure 1.

*Mindreading* ↔ *Culture*. Mindreading facilitates cultural transmission through the recognition of knowledge, ignorance, intentions and other mental states of others, underwriting teaching. In turn, culture supports mindreading through a publicly shared mentalistic framework, which also links with language in that it is explicitly expressed through a lexicon including such concepts as 'desires', 'thoughts' and 'beliefs'.

*Language* ↔ *Culture*. Culture supports language through the whole process of language acquisition. In turn, language carries large swathes of cultural transmission, from instruction to story-telling.

*Mindreading* ↔ *Language*. Mindreading has been argued to underwrite the intentionality of human language, in which utterances are delivered with the intent that others will take certain meanings from them. In turn, terminology and talk about what is in or on our minds is embodied in language.

*Cooperation* ↔ *Egalitarianism*. Cooperation and egalitarianism reinforce each other because foragers are more likely to be prepared to cooperate in the quest for resources if they will receive a reasonable share of them. This linkage is so tight that in the following, for economy, we refer to this sub-complex as 'cooperative-egalitarianism'.

*Cooperative-egalitarianism* ↔ *Culture*. Cooperation and egalitarianism support the free sharing of information that supports cultural transmission, the sharing of innovations and thus cultural evolution. In turn, culture provides techniques (such as those of hunting weaponry) that support forms of cooperation, and an explicitly stated ideology of generalized altruism that supports egalitarianism.

*Cooperative-egalitarianism* ↔ *Language*. Language facilitates interpersonal coordination such as planned foraging expeditions, and reciprocal agreements such as marriage.

*Cooperative-egalitarianism* ↔ *Mindreading*. Mindreading facilitates interpersonal coordination, empathy and a shared sense of fairness. In turn, the cooperative and egalitarian ethos of human hunter–gatherers means that there are positive reasons for offering one's states of mind to be read by others, rather than keeping them opaque.

These inferences about positive feedback loops are here outlined at the level of short- to medium-term causality: that is to say, each of these aspects of social cognition appears to operate to support others in the day-to-day life of hunter–gatherers. However, it is a plausible hypothesis that the same positive feedback loops operate developmentally, with children's progress in each associated aspect of social cognition



creating a more positive context for advancement in others; and that the same has been true over longer, evolutionary time-scales with respect to the focus of the present paper, hominin cognitive evolution. The evolutionary hypothesis would be that as these different aspects of social cognition became more advanced, their potential for positive feedback with respect to the others grew, providing the levels of accelerating selection pressure necessary to explain the extraordinary momentum and scale of late hominin encephalization.

Reasons to think that such positive feedback loops have been a rising, and even accelerating phenomenon, rather than being in place from the start of the transition from ancestral apes arise from considering the precursors to the various aspects of deep social mind inferred from great ape studies reviewed in §4. It is much less easy to discern likely correlates among apes of the kinds of positive feedback outlined in figure 1. This may be in part because the different elements are themselves not sufficiently developed: for instance, communication lags far behind the powers of human syntactic speech to facilitate other elements in figure 1 [15]; while chimpanzee political dynamics may carry the seeds of egalitarianism, chimpanzees are far from egalitarian. Another key factor is that the relatively simple forms of such aspects of social cognition as mindreading and culture that we see in apes appear to be deployed predominantly in essentially individualistic and even competitive contexts, rather than in the more broad-based collaborative ones that permeate hunter-gatherer life. The evolutionary scenario that the analysis of this study thus leads us to is one in which each of the principal aspects of social cognition reviewed have evolved in apes because of the specific benefits of each of them, whereas the positive interactions between them outlined in figure 1 were a progressive feature in hominin evolution.

## ENDNOTES

<sup>1</sup>Whiten [8,10] and Pinker [15] represent independent analyses of the concept of the cognitive niche, the latter apparently unaware of the former. However, the two converge on the central inference that the human cognitive niche is essentially a socio-cognitive niche. Pinker also infers ‘a suite of mutually reinforcing selection pressures’ (p. 8995). Sterelny [16,17] also converges with conclusions drawn in these papers in relation to sociality and cognition in hunting-gathering hominins, but does not explicitly discuss the concept of the cognitive niche.

<sup>2</sup>An obvious concern is whether contemporary and recent hunter-gatherers are unrepresentative in having been pushed into marginal habitats. Marlowe [4] has tackled this issue directly in relation to band size and shown this to be unrelated to resources availability.

<sup>3</sup>Boehm refers to a ‘reverse dominance hierarchy’ because an aspiring alpha individual can be ostracized so strongly that this becomes an apt description; however, this is rare and Erdal & Whiten [2] noted that the normal phenomenon is one in which hierarchies are levelled, making ‘counter-dominance’ their preferred term for the phenomenon.

## NOTE ADDED IN PROOF

Boyd *et al.* [93] have recently taken issue with the scope of the ‘cognitive niche’ (see Endnote 1), arguing that it is the emergence of a ‘cultural niche’ that has been crucial in the later phases of human evolution. Their paper accordingly resonates with some central

arguments in the present paper, most particularly the discussion of cumulative culture as one of the principal pillars of a human socio-cognitive niche.

## REFERENCES

- 1 Boyd, R. & Silk, J. 2009 *How humans evolved*, 5th edn. New York, NY: Norton.
- 2 Erdal, D. & Whiten, A. 1994 On human egalitarianism: an evolutionary product of Machiavellian status escalation? *Curr. Anthropol.* **35**, 175–183. (doi:10.1086/204255)
- 3 Erdal, D. & Whiten, A. 1996 Egalitarianism and Machiavellian intelligence in human evolution. In *Modelling the early human mind* (eds P. Mellars & K. Gibson), pp. 139–150. Cambridge, MA: McDonald Institute Monographs.
- 4 Marlowe, F. W. 2005 Hunter-gatherers and human evolution. *Evol. Anthropol.* **14**, 54–67. (doi:10.1002/evan.20046)
- 5 Potts, R. 1996 *Humanity’s descent: the consequences of ecological instability*. New York, NY: Avon Books.
- 6 McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., Bobe, R. & Bearat, H. A. 2010 Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* **466**, 857–860. (doi:10.1038/nature09248)
- 7 Semaw, S. *et al.* 2003 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *J. Hum. Evol.* **45**, 169–177. (doi:10.1016/S0047-2484(03)00093-9)
- 8 Whiten, A. 1999 The evolution of deep social mind in humans. In *The descent of mind* (eds M. Corballis & E. G. Lea), pp. 155–175. Oxford, UK: Oxford University Press.
- 9 Thieme, H. 1997 Lower Paleolithic hunting spears from Germany. *Nature* **385**, 807–810. (doi:10.1038/385807a0)
- 10 Whiten, A. 2006 The place of ‘deep social mind’ in the evolution of human nature. In *Human nature* (ed. M. A. Jeeves), pp. 207–222. Edinburgh, UK: Royal Society of Edinburgh.
- 11 Tooby, J. & DeVore, I. 1987 The reconstruction of hominid behavioral evolution through strategic modelling. In *The evolution of human behavior: primate models* (ed. W. G. Kinzey), pp. 183–227. New York, NY: SUNY Press.
- 12 Barrett, L., Henzi, S. P. & Lusseau, D. 2012 Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Phil. Trans. R. Soc. B* **367**, 2108–2118. (doi:10.1098/rstb.2012.0113)
- 13 Lee, R. B. & DeVore, I. (eds) 1968 *Man the hunter*. Chicago, IL: Aldine de Gruyter.
- 14 Lee, R. B. 1979 *The !Kung San: men, women and work in a foraging society*. Cambridge, UK: Cambridge University Press.
- 15 Pinker, S. 2010 The cognitive niche: coevolution of intelligence, sociality and language. *Proc. Natl Acad. Sci. USA* **107**, 8993–8999. (doi:10.1073/pnas.0914630107)
- 16 Sterelny, K. 2012 Language, gesture, skill: the coevolutionary foundations of language. *Phil. Trans. R. Soc. B* **367**, 2141–2151. (doi:10.1098/rstb.2012.0116)
- 17 Sterelny, K. 2007 Social intelligence, human intelligence and niche construction. *Phil. Trans. R. Soc. B* **362**, 719–730. (doi:10.1098/rstb.2006.2006)
- 18 Laland, K. N. & Brown, G. R. 2011 *Sense and nonsense: evolutionary perspectives on human behaviour*, 2nd edn. Oxford, UK: Oxford University Press.
- 19 Byrne, R. W. & Whiten, A. (eds) 1988 *Machiavellian intelligence: social complexity and the evolution of intellect*

- in monkeys, apes and humans*. Oxford, UK: Oxford University Press.
- 20 Boyd, R. & Richerson, P. 2009 Culture and the evolution of human cooperation. *Phil. Trans. R. Soc. B* **364**, 3281–3288. (doi:10.1098/rstb.2009.0134)
  - 21 Hamilton, M. J., Milne, B. T., Walker, R. S., Burger, O. & Brown, J. H. 2007 The complex structure of hunter-gatherer social networks. *Proc. R. Soc. B* **274**, 2195–2202. (doi:10.1098/rspb.2007.0564)
  - 22 Boehm, C. 1993 Egalitarian behaviour and reverse dominance hierarchy. *Curr. Anthropol.* **34**, 227–254. (doi:10.1086/204166)
  - 23 Avis, J. & Harris, P. L. 1991 Belief-desire reasoning among Baka children: evidence for a universal conception of mind. *Child Dev.* **62**, 460–467. (doi:10.2307/1131123)
  - 24 Shahaecian, A., Peterson, C. C., Slaughter, V. & Wellman, H. M. 2011 Culture and the sequence of steps in theory of mind development. *Dev. Psychol.* **47**, 1239–1247. (doi:10.1037/a0023899)
  - 25 Wellman, H. M., Fang, F. X. & Peterson, C. C. 2011 Sequential progressions in a theory of mind scale: longitudinal perspectives. *Child. Dev.* **82**, 780–792. (doi:10.1111/j.1467-8624.2011.01583.x)
  - 26 Lillard, A. 1998 Ethnopsychologies: cultural variations in theories of mind. *Psychol. Bull.* **123**, 3–32. (doi:10.1037/0033-2909.123.1.3)
  - 27 Tomasello, M. 1999 *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
  - 28 Whiten, A., Hinde, R. A., Stringer, C. B. & Laland, K. N. 2011 Culture evolves. *Phil. Trans. R. Soc. B* **366**, 938–948. (doi:10.1098/rstb.2010.0372)
  - 29 Hewlett, B. S., Fouts, N. H., Boyette, A. H. & Hewlett, B. L. 2011 Social learning among Congo Basin hunter-gatherers. *Phil. Trans. R. Soc. B* **366**, 1168–1178. (doi:10.1098/rstb.2010.0373)
  - 30 Stout, D. 2011 Stone toolmaking and the evolution of human culture and cognition. *Phil. Trans. R. Soc. B* **366**, 1050–1059. (doi:10.1098/rstb.2010.0369)
  - 31 Tennie, C., Call, J. & Tomasello, M. 2009 Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B* **364**, 2405–2415. (doi:10.1098/rstb.2009.0052)
  - 32 Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B. & Laland, K. N. 2012 Identification of the social processes underlying human cumulative culture. *Science* **335**, 1114–1118. (doi:10.1126/science.1213969)
  - 33 Marshall-Pescini, S. & Whiten, A. 2008 Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Anim. Cogn.* **11**, 449–456. (doi:10.1007/s10071-007-0135-y)
  - 34 Hopper, L. M., Lambeth, S. P., Schapiro, S. J. & Brosnan, S. F. 2011 Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Anim. Behav.* **81**, 1195–1202. (doi:10.1016/j.anbehav.2011.03.002)
  - 35 Csibra, G. & Gergely, G. 2011 Natural pedagogy as evolutionary adaptation. *Phil. Trans. R. Soc. B* **366**, 1149–1157. (doi:10.1098/rstb.2010.0319)
  - 36 Whiten, A., Horner, V. & Marshall-Pescini, S. R. J. 2003 Cultural panthropology. *Evol. Anthropol.* **12**, 92–105. (doi:10.1002/evan.10107)
  - 37 Boesch, C. 1994 Cooperative hunting in wild chimpanzees. *Anim. Behav.* **48**, 653–667. (doi:10.1006/anbe.1994.1285)
  - 38 Boesch, C. & Boesch, H. 1989 Hunting behaviour of wild chimpanzees in the Taï National Park. *Am. J. Phys. Anthropol.* **78**, 547–573. (doi:10.1002/ajpa.1330780410)
  - 39 Melis, A. P., Hare, B. & Tomasello, M. 2006 Chimpanzees recruit the best collaborators. *Science* **311**, 1297–1300. (doi:10.1126/science.1123007)
  - 40 Mitani, J. C. & Watts, D. 2005 Correlates of territorial boundary patrol behaviour in wild chimpanzees. *Anim. Behav.* **70**, 1079–1086. (doi:10.1016/j.anbehav.2005.02.012)
  - 41 de Waal, F.B.M. 1982 *Chimpanzee politics*. London, UK: Jonathan Cape.
  - 42 Mitani, J. C. 2010 Cooperation and competition in chimpanzees: current understanding and future challenges. *Evol. Anthropol.* **18**, 215–227. (doi:10.1002/evan.20229)
  - 43 Stumpf, R. M. 2011 Chimpanzees and bonobos: inter and intraspecies diversity. In *Primates in perspective* (eds C. J. Campbell, A. Fuentes, K. C. Mackinnon, M. Panger & S. K. Bearder), 2nd edn, pp. 340–356 Oxford, UK: Oxford University Press.
  - 44 Warneken, F. & Tomasello, M. 2006 Altruistic helping in human infants and young chimpanzees. *Science* **311**, 1301–1303. (doi:10.1126/science.1121448)
  - 45 Warneken, F. & Tomasello, M. 2009 Varieties of altruism in children and chimpanzees. *Trends Cogn. Sci.* **13**, 397–402. (doi:10.1016/j.tics.2009.06.008)
  - 46 Premack, D. & Woodruff, G. 1978 Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* **1**, 515–526. (doi:10.1017/S0140525X00076512)
  - 47 Whiten, A. (ed.) 1991 *Natural theories of mind: evolution, development and simulation of everyday mindreading*. Oxford, UK: Basil Blackwell.
  - 48 Whiten, A. & Byrne, R. W. 1988 Tactical deception in primates. *Behav. Brain Sci.* **11**, 233–273. (doi:10.1017/S0140525X00049682)
  - 49 Povinelli, D. J., Nelson, K. E. & Boysen, S. T. 1990 Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **104**, 203–210. (doi:10.1037/0735-7036.104.3.203)
  - 50 Heyes, C. M. 1998 Theory of mind in nonhuman primates. *Behav. Brain Sci.* **21**, 101–134.
  - 51 Tomasello, M. & Call, J. 1997 *Primate cognition*. Oxford, UK: Oxford University Press.
  - 52 Povinelli, D. J. & Eddy, T. J. 1996 What young chimpanzees know about seeing. *Monogr. Soc. Res. Child Dev.* **61**, 1–152.
  - 53 Bräuer, J., Call, J. & Tomasello, M. 2007 Chimpanzees really know what others can see in a competitive situation. *Anim. Cogn.* **10**, 439–448. (doi:10.1007/s10071-007-0088-1)
  - 54 Hare, B., Call, J. & Tomasello, M. 2001 Do chimpanzees know what conspecifics know? *Anim. Behav.* **61**, 139–151. (doi:10.1006/anbe.2000.1518)
  - 55 Crockford, C., Wittig, R. M., Mundry, R. & Zuberbühler, K. 2012 Wild chimpanzees inform ignorant group members of danger. *Curr. Biol.* **22**, 142–146. (doi:10.1016/j.cub.2011.11.053)
  - 56 Hare, B., Call, J. & Tomasello, M. 2006 Chimpanzees deceive a human competitor by hiding. *Cognition*. **101**, 495–514. (doi:10.1016/j.cognition.2005.01.011)
  - 57 Melis, A. P., Call, J. & Tomasello, M. 2006 Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *J. Comp. Psychol.* **120**, 154–162. (doi:10.1037/0735-7036.120.2.154)
  - 58 Whiten, A. 1996 When does behaviour reading become mindreading? In *Theories of theories of mind* (eds P. Carruthers & P. K. Smith), pp. 277–292. Cambridge, UK: Cambridge University Press.
  - 59 Shettleworth, S. 2010 *Cognition, evolution and behaviour*, 2nd edn. Oxford, UK: Oxford University Press.
  - 60 Call, J., Hare, B. H., Carpenter, M. & Tomasello, M. 2004 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action? *Dev. Sci.* **7**, 488–498. (doi:10.1111/j.1467-7687.2004.00368.x)
  - 61 Call, J. & Tomasello, M. 2008 Does the chimpanzee have a theory of mind? 30 years later. *Trends Cogn. Sci.* **12**, 187–192. (doi:10.1016/j.tics.2008.02.010)

- 62 Call, J. & Santos, L. R. 2012 Understanding other minds. In *The evolution of primate societies* (eds J. Mitani, J. Call, P. Kappeler, R. Palombit & J. Silk), Chicago, IL: Chicago University Press.
- 63 Kaminski, J., Call, J. & Tomasello, M. 2008 Chimpanzees know what others know but not what they believe. *Cognition* **109**, 224–234. (doi:10.1016/j.cognition.2008.08.010)
- 64 Savage-Rumbaugh, E. S. 1986 *Ape language: from conditioned response to symbol*. New York, NY: Columbia University Press.
- 65 Fedurek, P. & Slocombe, K. E. 2011 Primate vocal communication: a useful tool for understanding human speech and language evolution? *Hum. Biol.* **83**, 153–173. (doi:10.3378/027.083.0202)
- 66 Slocombe, K. E. & Zuberbühler, K. 2006 Food-associated calls in chimpanzees: responses to food types or food preferences? *Anim. Behav.* **72**, 989–999. (doi:10.1016/j.anbehav.2006.01.030)
- 67 Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P. & Zuberbühler, K. 2010 Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behav. Ecol. Sociobiol.* **64**, 1959–1966. (doi:10.1007/s00265-010-1006-0)
- 68 Slocombe, K. E., Kaller, T., Call, J. & Zuberbühler, K. 2010 Chimpanzees extract social information from agonistic screams. *PLoS ONE* **5**, 11473. (doi:10.1371/journal.pone.0011473)
- 69 Slocombe, K. E., Townsend, S. W. & Zuberbühler, K. 2009 Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: evidence from a playback study. *Anim. Cogn.* **12**, 441–449. (doi:10.1007/s10071-008-0204-x)
- 70 Cheney, D. L. & Seyfarth, R. M. 1990 *How monkeys see the world: inside the mind of another species*. Chicago, IL: University of Chicago Press.
- 71 Mitani, J. C. & Gros-Louis, J. 1998 Chorusing and call convergence in chimpanzees: tests of three hypotheses. *Behaviour* **135**, 1041–1064. (doi:10.1163/156853998792913483)
- 72 Crockford, C., Herbinger, I., Vigilant, L. & Boesch, C. 2004 Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology* **10**, 221–243. (doi:10.1111/j.1439-0310.2004.00968.x)
- 73 Townsend, S. & Zuberbühler, K. 2009 Audience effects in chimpanzee copulation calls. *Commun. Integr. Biol.* **2**, 282–284. (doi:10.4161/cib.2.3.6796)
- 74 Clay, Z. & Zuberbühler, K. 2009 Food-associated calling sequences in bonobos. *Anim. Behav.* **77**, 1387–1396. (doi:10.1016/j.anbehav.2009.02.016)
- 75 Hobaiter, C. & Byrne, R. W. 2011 The gestural repertoire of the wild chimpanzee. *Anim. Cogn.* **14**, 745–767. (doi:10.1007/s10071-011-0409-2)
- 76 Liebal, K., Call, J. & Tomasello, M. 2004 The use of gesture sequences in chimpanzees. *Am. J. Primatol.* **64**, 377–396. (doi:10.1002/ajp.20087)
- 77 Cartmill, E. A. & Byrne, R. W. 2007 Orangutans modify their gestural signalling according to their audience's comprehension. *Curr. Biol.* **17**, 1345–1348. (doi:10.1016/j.cub.2007.06.069)
- 78 Tagliatalata, J. P., Russell, J. L., Schaefer, J. A. & Hopkins, W. D. 2011 Chimpanzee vocal signalling points to a multimodal origin of human language. *PLoS ONE* **6**, e18852. (doi:10.1371/journal.pone.0018852)
- 79 Whiten, A. 2011 The scope of culture in chimpanzees, humans and ancestral apes. *Phil. Trans. R. Soc. B* **366**, 997–1007. (doi:10.1098/rstb.2010.0334)
- 80 Whiten, A., McGuigan, H., Hopper, L. M. & Marshall-Pescini, S. 2009 Imitation, over-imitation, emulation and the scope of culture for child and chimpanzee. *Phil. Trans. R. Soc. B* **364**, 2417–2428. (doi:10.1098/rstb.2009.0069)
- 81 Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999 Cultures in chimpanzees. *Nature* **399**, 682–685. (doi:10.1038/21415)
- 82 Whiten, A. 2005 The second inheritance system of chimpanzees and humans. *Nature* **437**, 52–55. (doi:10.1038/nature04023)
- 83 Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J. & de Waal, F. B. M. 2007 Transmission of multiple traditions within and between chimpanzee groups. *Curr. Biol.* **17**, 1038–1043. (doi:10.1016/j.cub.2007.05.031)
- 84 Whiten, A. & Mesoudi, A. 2008 Establishing an experimental science of culture: animal social diffusion experiments. *Phil. Trans. R. Soc. B* **363**, 3477–3488. (doi:10.1098/rstb.2008.0134)
- 85 Whiten, A., Horner, V. & de Waal, F. B. M. 2005 Conformity to cultural norms of tool use in chimpanzees. *Nature* **437**, 737–740. (doi:10.1038/nature04047)
- 86 Gruber, T., Muller, M. N., Strimling, P., Wrangham, R. & Zuberbühler, K. 2009 Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Curr. Biol.* **19**, 1846–1852. (doi:10.1016/j.cub.2009.08.062)
- 87 Whiten, A., Horner, V., Litchfield, C. A. & Marshall-Pescini, S. 2004 How do apes ape? *Learn. Behav.* **32**, 36–52. (doi:10.3758/BF03196005)
- 88 Tomasello, M. & Carpenter, M. 2005 The emergence of social cognition in three young chimpanzees. *Monogr. Soc. Res. Child Dev.* **70**, 1–132.
- 89 Horner, V. K. & Whiten, A. 2005 Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children. *Anim. Cogn.* **8**, 164–181. (doi:10.1007/s10071-004-0239-6)
- 90 Buttelmann, D., Carpenter, M., Call, J. & Tomasello, M. 2007 Enculturated chimpanzees imitate rationally. *Dev. Sci.* **10**, 31–38. (doi:10.1111/j.1467-7687.2007.00630.x)
- 91 Price, E. E., Lambeth, S. P., Schapiro, S. J. & Whiten, A. 2009 A potent effect of observational learning on chimpanzee tool construction. *Proc. R. Soc. B* **276**, 3377–3383. (doi:10.1098/rspb.2009.0640)
- 92 Tennie, C., Call, J. & Tomasello, M. 2010 Evidence for emulation in chimpanzees in social settings using the floating peanut task. *PLoS ONE* **5**, e10544. (doi:10.1371/journal.pone.0010544)
- 93 Boyd, R., Richerson, P. J. & Henrich, J. 2011 The cultural niche: why social learning is essential for human adaptation. *Proc. Natl Acad. Sci. USA* **108**, 10 918–10 925.