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Mind the Gap; or Why Humans Are Not Just Great Apes

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Introduction

EVOLUTION HAS HAD a poor press in the social sciences and the humanities over the past century, though it has not always been so: the nineteenth century witnessed considerable interest among the nascent social sciences in the ideas propounded by the new evolutionists within biology. This is neither the time nor place to delve into the history of why evolutionary ideas subsequently came to be so vehemently eschewed by social scientists. Instead, my aim here is simply to underline the claim that an evolutionary perspective is not, as seems often to be supposed, a competing paradigm for conventional explanations in the social sciences. Rather, an evolutionary perspective should function, as it does in biology, as a framework theory that allows all the disparate subdisciplines to be integrated in a way that they can talk to each other on a level playing field. Biology has benefited enormously from an evolutionary perspective over the past half-century in particular, since an evolutionary framework has allowed ethologists and ecologists to integrate their work with physiologists and molecular geneticists (even though the former still grumble about the latter's molecularisation of biology). I argue that Psychology—a notoriously fractionated discipline at the best of times—could benefit

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in the same way, since an evolutionary approach would allow neuroscientists to talk to social and developmental psychologists in a way that, hitherto, they have conspicuously failed to be able to do.

I do not wish to defend this proposal in detail here. It simply stands as a framework for my lecture. Instead, I will try to demonstrate the value of an evolutionary framework by example. My aim in this lecture is to sketch out an argument as to why humans are so different from other apes and monkeys, despite the fact that we share so much of our evolutionary history with them. My point is that, in doing so, I will have to draw on many different subdisciplines of Psychology (as well as other disciplines like anthropology) whose integration into this story is only possible because evolutionary theory provides us with an overarching framework within which to combine them.

We share a long evolutionary history with the great apes, in particular: the human lineage (including all the many fossil species that have existed over the last six million years or so since our lineage parted company with that of the chimpanzees) is firmly embedded within the African Great Ape family and shares with them many aspects of their biology, genetics, psychology and behaviour. More trivially, we also share a very high percentage of our DNA with chimpanzees (though *quite* what this means is open to question). Yet, it is surely obvious to everyone that we are not 'just great apes'. In several conspicuous ways, we are very different. That difference does not really seem to concern the kinds of anatomical or cognitive differences—our bipedalism and tool-making abilities—that anthropologists have tended to emphasise in the past. Rather, I want to argue that the real difference lies in a much more intangible set of competences—the ability to live in the virtual world of the mind. In a word, this is the world of culture. I will focus on two aspects of human behaviour that are, in many respects, archetypal of human culture: story-telling and religion. Both require us to be able to imagine worlds that do not physically exist. I shall argue that, apes' much-vaunted capacities for cultural learning notwithstanding, no other living species is even on the same page as humans in this respect—because all other animal species lack the neuronal computational power required to make it possible. The key to understanding why this is so lies in the reasons why our brains have evolved.

The evolution of the social brain

The social brain hypothesis was first mooted in the late 1980s by Byrne and Whiten (1988) as an explanation for the fact that primates have much larger brains for body size than any other taxonomic group (a point first noted by Jerison 1973). Most of this increase in brain size is the result of an enlarged neocortex (Finlay and Darlington 1995; Finlay *et al.* 2001), and especially an enlarged frontal lobe (though some other subcortical areas such as the cerebellum are also differentially enlarged in humans: McLeod *et al.* 2003). Primates rely on sociality as a tool for solving the everyday ecological problems of survival and successful reproduction rather than solving these problems by individual trial and error. So the proposal was that primates' more complex social lives imposed significantly greater cognitive demands on them than was the case for other non-primate species.

Since this suggestion was originally proposed, considerable evidence has been adduced in its support (for recent summaries, see Whiten and Byrne 1997; Emery *et al.* 2007; Dunbar and Schultz 2007*a*, 2007*b*). One of the core findings was a quantitative relationship between social group size and relative neocortex size in primates (Fig. 1). On a double-log plot, mean species group size is linearly related to relative neocortex size (indexed as the ratio of neocortex volume to the volume of the rest of the brain). This has been interpreted as implying that some aspect of cognition imposes a constraint on the number of relationships that an individual can maintain as a coherent social network.

Although the essence of the social brain hypothesis is really about social complexity and its cognitive demands (and considerable evidence is now available to show that various indices of behavioural complexity correlate with neocortex size: see Dunbar and Shultz 2007*a*), it is this quantitative relationship with group size that has mainly attracted attention. Indeed, it seems that the social brain hypothesis is often seen as being synonymous with this one core finding. However, it is important not to lose sight of the fact that this group size effect is really only an emergent property of the underlying relationship which focuses on the cognitive demands of behavioural complexity.

This has recently been given added emphasis by new findings that have emerged from attempts to test the social brain hypothesis on non-primate species. Shultz and Dunbar (Shultz and Dunbar 2007; Dunbar and Shultz 2007*b*) have shown that, across a wide range of bird and mammal species (specifically carnivores, ungulates and bats), the social brain

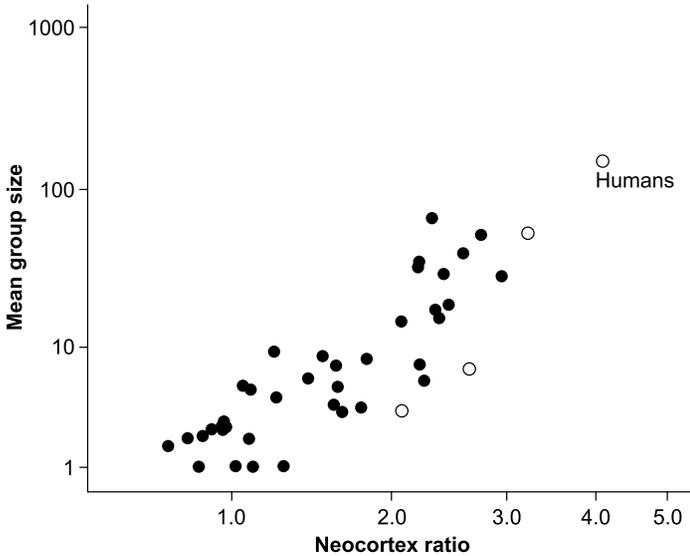


Figure 1. Mean social group size for different species of primates (prosimians, monkeys and apes) plotted against relative neocortex size (indexed as neocortex ratio, the ratio of neocortex volume divided by the volume of the rest of the brain). Ape species are distinguished as open symbols (lower left to top right: gibbons, gorillas, chimpanzees and modern humans). The point labelled for humans is that predicted by the ape regression equation. Redrawn from Dunbar (2008).

hypothesis takes a qualitative rather than a quantitative form. In all these taxonomic groups, it is pairbonded (i.e. reproductively monogamous) species that have disproportionately large brains. Anthropoid primates contrast strikingly with this pattern in that they, and they alone, exhibit a quantitative relationship between group size and brain size.

These results suggest that it is the cognitive demands of pairbonding that underpin the social brain (thereby leading to the initial enlargement of brain size in several animal families), and that anthropoid primates (and maybe one or two other numerically small groups such as elephants and the horse family) have extended the use of these pairbond-like relationships to other non-reproductive group members—thereby creating the quantitative relationship that we observe in their case (Shultz and Dunbar 2007). In effect, they have developed what we might well refer to as ‘friendships’ (Silk 2002; Smuts 1985), relationships that have all the characteristics of pairbonds but without the sexual connotation—although perhaps this may explain why friendships can so easily acquire sexual overtones in humans. In anthropoid primates, friendships function

as alliances—reciprocal coalitions whose members reliably come to each other's aid (see for example, Dunbar 1980, 1989). These serve the important function of buffering individuals against the costs of group-living—competition during foraging, and the persistent forms of low-level harassment consequent on living in close proximity to others that results in infertility in females in both captivity and the wild (Abbott *et al.* 1986; Dunbar 1980).

Because pairbonding is often associated with bi-parental care, it is not intuitively obvious whether the cognitive load is imposed by the demands of pairbonding as such or by those of bi-parental care. Birds allow us to sort this out because some species have one without the other: this dissociation demonstrates unequivocally that it is species with pairbonds, irrespective of whether or not they have bi-parental care, that have large brains. Birds also emphasise a second point: it is species that have *lifelong* pairbonds that have unusually large brains, not those that have annual pairbonds (i.e. those that find new partners each year), indicating that it is something about the costs of long term relationships that is cognitively demanding.

This raises two important issues. One is why pairbonds (and pairbond-like relationships) are so costly in cognitive terms. The other is the more difficult question of just what pairbonds actually are. It is well understood that pairbonds (and especially lifelong pairbonds) incur significant risks for their members: a poor choice of partner will have a massive effect on an individual's fitness because of the opportunity costs of having to start all over again with the business of mate-finding. Such circumstances can arise either because a mate is less fertile than other members of the population or because it is less reliable (either in terms of providing care for the young or in terms of infidelity, or both). The fact that poor judgement could have catastrophic consequences for the individual's fitness—literally by reducing its lifetime reproductive output to zero in the worst case—will inevitably impose intense selection for the ability to make fine judgements about the suitability of prospective mates. However, the need to maintain a high level of behavioural coordination and synchrony must also impose significant demands on cognition. This is particularly obvious in those cases where the pair has to share rearing duties, as in many bird species where one member of the pair has to stay on the nest while the other feeds. If the pair do not coordinate their behaviour effectively, the individual left sitting on the eggs may eventually be forced to choose between starving and abandoning the eggs. In effect, pairbonds are cooperative alliances for joint reproduction and the pair

members have to be willing to recognise and accommodate the partner's interests. In effect, they have to be able to second-guess the partner's needs and factor these into the scheduling of their own requirements. It seems likely that it is this specific need that may have provided the trigger for the evolution of those social cognitive skills associated with theory of mind in humans.

This does, however, raise a serious question: just what is a pairbond? We tend to recognise pairbonds by virtue of the fact that joint reproduction is a key component. But in reality, that is not the animals' experience of it any more than it is ours. Pairbonded species of birds have pairbonds in order to be able to engage in bi-parental care, thereby generating significant reproductive benefits. Bi-parental care is the ultimate goal, but to achieve this they must find an effective solution to the proximate goal of creating and maintaining a functional pairbond. Their perception of what is involved (and hence the underpinning cognitive mechanisms) is the rather intangible unknown. Indeed, we have difficulty trying to specify exactly what is involved even in our own case: we know a relationship when we see or experience one, but we do not have any adequate metric by which we can define it operationally. Relationships of this kind are something we *feel* rather than cognise directly.

This much is perhaps obvious from the social psychology literature on friendships: here, several decades of research have identified two key dimensions to relationships—being close and feeling close (Sternberg 1997; Berscheid *et al.* 1989). The first of these is easy to specify, because it simply has to do with time spent together (in effect, spatial proximity) or the frequency of interaction. The second is more difficult, because it has something to do with our inner emotional experiences and we have great difficulty verbalising these. We intuit them as a form of 'hot' cognition, but they are not as accessible to conscious verbal description as 'cold' cognition. And for that reason, we face a double dilemma in the case of animals, since we lack any means of describing the inner experiences in other species. The time may now have come to grapple directly with the thorny issue of animals' mental experiences: we may not be able to push it quietly under the behaviourist carpet any longer if we want to make any progress in understanding the nature of relationships in humans or other animals.

The bonds that bind

The social brain hypothesis, then, argues that maintaining and servicing the kinds of intense relationships found in pairbonds (in most birds and mammals) and friendships (among anthropoid primates) involves serious cognitive work, which in turn is reflected in the size of a species' brain. But it is, at the same time, apparent, both from the human social psychology literature on friendships and from the ethological literature on how primates service their relationships, that cognition is only part of the story. There is a deeply emotional component to relationships that derives in both cases from doing things together. This leads us, perhaps inevitably, into the issue of how primates bond their social groups.

For Anthropoid primates, and in particular Old World monkeys and apes, social grooming is the principal mechanism used for social bonding. Grooming is an intense activity in which one individual leafs through the fur of another, removing bits of vegetation, dead skin and other debris. It is very much a one-on-one activity, in which the groomer is often deeply concentrated on its task. Grooming lowers the heart rate in the groomee and reduces the frequency of signs of tension and stress (yawning, scratching, etc.: Goosen, 1981; Castles *et al.* 1999), to the point where the recipient of grooming can become so relaxed it actually falls asleep. Many species devote considerable proportions of their day to social grooming—in the limiting case, as much as one fifth of the waking day. Grooming shares many of the features of massage: it is physically stimulating and mildly painful, and thus triggers the release of endorphins (the brain's own painkillers) (Keverne *et al.* 1989). It is endorphins that are probably responsible for these soporific effects.

However, the real significance of this is that these psychopharmacological effects mediated by grooming seem to play a crucial role in the process of building the trust and reciprocity that form the basis of primate social relationships. We have no real idea how endorphins give rise to bonded relationships, but one possibility is that they simply allow two individuals to feel relaxed enough in each other's company to spend time together. Time is a commodity that we have to invest to create a relationship, and there seems to be a more or less linear relationship between time spent together and the strength of a relationship—at least in terms of functional consequences such as willingness to come to a grooming partner's aid (see Dunbar 1980, 1984, 1989). It may be that endorphins simply provide the proximate reinforcer that makes it worth spending time with someone else, or it may be that these neuroendocrines are themselves

intimately involved in the bonding process. Either way, it seems that their role is critical.

Humans and the social brain

Modern humans have much larger brains (and especially neocortices) than other primates, and we can legitimately ask what the relationship between neocortex size and group size in primates can tell us about human group sizes. As Figure 1 suggests, there are quite distinct grades in this relationship within the primates: apes lie to the right of monkeys, and monkeys lie to the right of prosimians, suggesting that servicing groups of a given size requires proportionately more computational power as you pass from prosimians through monkeys to the apes (Dunbar 1998). Hence, the appropriate regression line from which to predict human group sizes is that for apes. Interpolating the modern human neocortex ratio into the ape equation yields a predicted group size of ~150 (Fig. 1).

A search of the ethnographic literature revealed that this is in fact the typical size of hunter-gatherer communities (Dunbar 1993; Hamilton *et al.* 2007). More remarkably perhaps, this figure of ~150 appears frequently in many aspects of historical and contemporary human organisation (Table 1). It was the mean village size recorded for almost all English counties in the Domesday Book as well as during the eighteenth century, and is the typical size of the company in most modern armies, the number of recipients of a typical Christmas card distribution list in Britain, and the size of the social network in reverse 'small world' experiments, amongst others. Thus, a wide range of contemporary social phenomena seem to yield much the same kinds of grouping patterns, despite marked differences in both scale and organisation. The only substantive difference between social networks in traditional hunter-gatherer and agricultural societies and modern post-industrial societies seems to be that, in traditional societies, everyone in the community has more or less the same network of 150 acquaintances, whereas in modern urban societies our networks are highly fragmented—my 150 consists of a set of subnetworks that barely overlap. You and I may share one small set of friends, say through work, but there is no overlap at all in the remaining subsets—we do not share any relatives, nor do we share hobby circles, church networks, spouses' friends, schoolgate friends (the often temporary friendships built up through one's children's school friends) or sports club friends. Networks in modern societies are fragmented and dispersed

Table 1. Examples of human social groupings that conform to the predicted size of ~150 individuals^a.

Grouping	Typical size	Source
Neolithic villages (Middle East, 6500–5500 BC)	150–200	Oates (1977)
Maniple ('double century') (Roman army: 350–100 BC)	120–130	Montross (1975)
Domesday Book (1085): (average county village size)	150	Hill (1981), Bintliff (1999)
Eighteenth-century English villages (mean of county means)	160	Laslett (1971)
Tribal societies (mean and range of communities; $N=9$)	148 (90–222)	Dunbar (1993)
Hunter-gatherer societies (mean clan size; $N=213$)	165	Hamilton <i>et al.</i> (2007)
Hutterite farming communities (Canada) (mean, $N=51$)	107	Mange and Mange (1980)
'Nebraska' Amish parishes (mean, $N=8$)	113	Hurd (1985)
Church congregations (recommended ideal size)	200	Urban Church Project (1974)
E. Tennessee rural mountain community	197	Bryant (1981)
Social network size (mean, $N=2$ 'small world' experiments)	134	Killworth <i>et al.</i> (1984)
Goretex Inc: factory unit size	150	Gladwell (2000)
Company (mean and range for 10 Second World War armies)	180 (124–223)	MacDonald (1955)
Christmas card distribution lists (mean total recipients: $N=43$)	154	Hill and Dunbar (2003)
Research specialities (sciences and humanities) (mode, $N=13$)	100–200	Becher (1989)

^a Confidence intervals around the predicted mean are 100–200 (Dunbar 1993).

(often over considerable geographical distances), whereas in traditional societies they typically form a single cohesive community—even though that community itself may be distributed over a wide geographical area (as in many contemporary hunter-gatherers).

This figure of ~150 seems to mark a distinct limit for relationship quality: there seems to be a marked difference in the quality of the relationships we have with those who are inside the chosen circle versus those who are outside. My informal definition for this limit to our social world is that it is everybody whom we know as persons, everyone with whom we have a definable personal relationship. Those inside this circle are individuals towards whom we feel some sense of obligation, whom we trust

would help us out if we so requested, who would reciprocate our sense of personal commitment. We know where these individuals fit into our network of relationships, they know where we fit into theirs, and our knowledge in both cases is based on personal acquaintance. Sometimes, that knowledge can be indirect (friends of friends, or a shared grandparent), but it defines those to whom we owe personal obligations; if we offend them, or spurn them in some way, that offence will come to haunt us through the effect it has on the relationships that link us. In contrast, beyond this circle of 150, people cease to be individuals, at least in so far as our relationships are concerned. Even though we recognise them as individuals (i.e. we can put names to faces), our relationships with them are less personal and more typological. We need rules of thumb to guide our interactions with them rather than being able to rely on personalised knowledge. In such cases, the rule is usually cued by some appropriate badge that signifies the status of an individual and how we should address them, and this often requires that we formally badge them in order to recognise them—uniforms, badges of rank, styles of speech, and so on.

As with all primate social groups, human social networks are highly structured. We do not interact equally with all members of our immediate social world. Rather, it seems that our social world consists of a series of hierarchically inclusive circles of acquaintanceship that are reflected in both the perceived intimacy of the relationship and the frequency of interaction (Hill and Dunbar 2003). These circles of acquaintanceship seem to have a very consistent structure: each annulus includes about twice as many people as the one immediately inside it, so that the cumulative numbers of individuals included in successive circles exhibit a constant scaling ratio of approximately 3 (Zhou *et al.* 2005; see also Hamilton *et al.* 2007). Roughly speaking, they progressively include 5, 15, 50, 150, 500 and 1500 individuals (see Dunbar 1993; Zhou *et al.* 2005), and, for all we know, may extend beyond that in a further series of circles that have the same ratios.

The role for cognition

The fact that brain size correlates with social group size implies that this involves a cognitive limit. However, we know surprisingly little about the kinds of cognition that might be involved in managing social relationships. Although everyone probably agrees that this is some form of ‘social cognition’, quite what that entails remains unclear. The only aspect of this

that we know much about is what has become known as theory of mind (Leslie 1987; Perner 1991). Theory of mind is the ability to reflect on another individual's mind states. As such, it is one level in a potentially endless reflexive series of mind states and beliefs about mind states known as the levels of intentionality (Dennett 1987). We know a great deal about theory of mind (second-order intentionality) because developmental psychologists have explored it in considerable depth. In simple terms, it is the cognitive rubicon that children pass through at about the age of 4–5 years, although some individuals (autistic people) never achieve this even as adults (Baron-Cohen *et al.* 1985). However, the problem with theory of mind is that we know a great deal about its natural history but, as Roth and Leslie (1998) have pointed out, we have almost no idea what it actually involves in cognitive terms.

Nonetheless, even though the exact processes involved may be somewhat opaque, we can perhaps use the notion of intentionality to give us some purchase on the problem of how humans differ from other primates since the orders of intentionality form a natural scale, and thus seem to provide us with an index of social cognitive competence. The claim that intentionality itself is no more than some aspect of executive function (Ozonoff 1995; Mitchell 1997; Barrett *et al.* 2003; Stylianou 2007) would provide a justification for this. My concern here is less with the debates about whether or not theory of mind (or, more generally, intentionality) is modular or the outcome of executive function (although my inclination is towards the latter) than with the simpler claim that the intentionality scale seems to provide us with a metric of social cognitive competence (as indexed by the ability to hold several individuals' mental states in mind at the same time).

This being so, our main interest at this point is what the natural limits of intentional reasoning might be in humans. We have assayed normal adults in a number of separate studies, and it seems that the limits of function for adults are consistently fifth order ('I *believe* that you *suppose* that I *imagine* that you *want* me to *believe* that . . .') (Kinderman *et al.* 1998; Stiller and Dunbar 2007). Around two-thirds of individuals have their limit at or below fifth-order intentionality, and three-quarters have their limit at or below sixth order. There is considerable individual variation around this (Stiller and Dunbar 2007), and we have shown that the higher levels are lost during the active phase of at least two well-known clinical conditions (bipolar disorder: Kerr *et al.* 2003; paranoid schizophrenia: Swarbrick 2000). These competences develop over a period of time between age 5 (when children first acquire theory of mind, or

second-order intentionality) and the early 'teens (when they finally acquire fifth-order adult-level competences; Henzi *et al.* 2007).

Intentionality and the virtual world

The issue of interest here is what can be achieved with different levels of intentionality. If intentional competences allow us to hold several different individuals' mind states in mind at the same time, then it seems likely that they will impose constraints on cultural phenomena that require us to think intentionally. This is perhaps most obvious in the case of imaginative play. Leslie (1987) noted that theory of mind may be crucial for children to be able to engage in fictive (i.e. pretend) play where they have to imagine that the world is other than it really is (i.e. dolls can drink tea, the steering wheel on the back of a chair is a real car). Leslie's point can be extended to drama. Consider the case of the audience watching Shakespeare's *Othello*. They have to believe that Iago intends that Othello imagines that Desdemona is in love with Cassio, an activity involving four levels of intentionality. However, notice that, at this point, the kind of story they are dealing with is not especially demanding (or, for that matter, particularly enthralling). Why should Othello care if Desdemona fantasises about Cassio? The bottom line of everyday life is that very few of us would be anything but mildly bemused by such a trivial phenomenon, and the story would end there as a dull narrative. What gives Shakespeare's play its bite is the fact that Iago is able to persuade Othello that Cassio reciprocates Desdemona's feelings, thereby creating a romantic triangle and raising the stakes high enough for all of us to be gripped by the drama (especially when, with the benefit of spectator-sight, we are aware of Iago's scheming plan). At this point, of course, the audience is having to work at fifth-order intentionality, and is thus at the natural limits for the great majority of the population.

But, in putting this story together, Shakespeare himself has to go one level higher than his audience, to sixth order: he has to *intend* that the audience *believes* . . . I suggest that this might explain why the capacity to enjoy good literature is a widespread human universal, but the ability to *compose* good literature is not—storytelling demands social cognitive competences that are beyond the normal range for the great majority of the population. Thus it is that, when we sit down to write those novels we have so long aspired to write, our natural limits at fifth-order intentionality constrain most of us into writing dull narratives.

We can use the same framework for exploring the cognitive demands of religion, because this too requires us to work with an imagined world—a world that we cannot see or feel directly because it exists only in our heads. The transcendental experiences that we have during religious events are undoubtedly very real, but they are not the stuff of real physical experiences created by the world impinging on our senses. They belong, rather, to an inner virtual world of the imagination.

A task analysis of the mentalising demands of religious beliefs suggests that it is perfectly possible to have religion with any order of intentionality; however, the *form* of religion depends on the levels of intentionality at which you can work (Table 2). Crucially, there appears to be a critical difference between the forms of religion possible at fourth- and fifth-order intentionality. At fourth order, you can have what I refer to as social religion: I can enjoin you to believe what I believe to be true about some deity’s interests in us, but you do not have to agree with that claim even though you may accept that I am convinced by the truth of what I believe: there is no compulsion on you to believe. I can only make you agree with me by using a police force (of either a secular or a heavenly kind). But, in that case, your level of personal and intellectual commitment to the project is likely to be very limited. However, fifth order seems to represent a crucial rubicon: at fifth order, it seems that, when I accept that you believe this claim to be true, I *ipso facto* also commit myself to the veracity of your claim. We now have what I term ‘communal religion’—a set of beliefs that bind us into a single community whose members share the same world view. At this point, we have a very powerful mechanism enforcing the communal will, for making us all sign up to

Table 2. Forms of religious belief made possible by different levels of intentionality.

Intentionality Level	Possible statements of belief	Form of Religion
First	<i>I believe</i> that god [. . . exists]	none
Second	<i>I believe</i> that god is <i>willing</i> [. . . to intervene if you disobey his laws]	supernatural fact
Third	<i>I intend</i> that you <i>believe</i> that god is <i>willing</i> [. . . to intervene . . .]	personal religion
Fourth	<i>I intend</i> that you <i>believe</i> that I <i>want</i> god to be <i>willing</i> [. . . to intervene . . .]	social religion
Fifth	<i>I intend</i> that you <i>believe</i> that god <i>understands</i> that I <i>want</i> him to be <i>willing</i> [. . . to intervene . . .]	communal religion

the communal project (whatever that may happen to be). We do not need a police force to make us behave in a religious way: we are all deeply and personally committed to it and adhere to these beliefs of our own free will.

What makes us so different?

I return to my opening question: why are humans not just great apes? I have suggested that the answer lies in our capacity to live in a virtual mental world. We can engage in activities that are well beyond the competences of even the great apes. Indeed, they are so far beyond the competences of other species that there is no chance that the proverbial chimpanzee sitting at a typewriter will ever produce the works of Shakespeare within any reasonable length of time (and I speak on the scale of millennia here). The one remaining question is why we humans should have needed such extraordinary cognitive abilities.

From an evolutionary point of view, this is especially puzzling because brain tissue is exceptionally expensive. Aiello and Wheeler (1995) pointed out some time ago that brain tissue is among the most expensive matter in the body to maintain, and that this provides a very steep gradient up which natural selection has to drive brain evolution if it is to increase brain size (their 'expensive tissue hypothesis'). There is some tentative comparative evidence (Dunbar 2003*a*, 2003*b*) given some additional support by recent as yet unpublished human neuroimaging studies—that intentional competences are correlated with some aspects of brain volume. If so, then it follows that the selection pressure for the capacity to manage the higher orders of intentionality incurs a very significant energetic cost to the individuals concerned. The advantages to be gained from investing in such capacities must thus be considerable. What might these be?

Primate societies are implicit social contracts. Like all social contracts, their stability and functionality depends on the members trading off short and long term benefits. As with pairbonds, a group will only remain stable as a coalition providing members are willing to compromise on some of their short term benefits in order to gain in the long run through group-level effects. These group level effects come in the form of increased survival, and hence higher reproductive rates, mainly as a result of reduced predation rates (Dunbar 1988; Shultz *et al.* 2004) though there

may also be more direct benefits in terms of the survival of individual offspring (Silk *et al.* 2003; Silk 2007).

However, all social contracts of this kind face the same problem: freeriders. There is always a significant benefit to be gained by individuals who take the benefits of sociality but do not pay all the costs (Enquist and Leimar 1993; Nettle and Dunbar 1997; Dunbar 1999). Since the intrusiveness of freeriders is proportional to the size of the population, the large communities that characterise humans face a significantly greater challenge in this respect than those of our primate cousins. As a result, more sophisticated mechanisms are needed to ensure that freeriders do not overwhelm the community. While there is a number of cognitive mechanisms for managing freeriders (Dunbar 1999), the absence of grooming on a large scale means that we inevitably lack the endorphin-based mechanisms that lie at the root of primate sociality. This is a serious issue, because it creates a 'bonding gap' of quite significant proportions (Dunbar, *in press*) that could seriously destabilise the fragile basis on which group-level collaboration depends. Something was needed to fill that gap.

In fact, the pattern of brain size evolution suggests that this really only became a serious issue in the later stages of human evolution following the appearance of archaic humans (*Homo heidelbergensis* and allies) around half a million years ago (Dunbar, *in press*). At this point, brain size took off with a rapid rate of increase, implying a corresponding increase in the size of communities that had to be bonded. Nonetheless, our capacity to create the large communities that were presumably needed to ensure survival (and the reasons why we needed such large communities remain unclear) must have depended on solving the bonding issue satisfactorily. While social conformity and 'good behaviour' can always be imposed by punitive action on backsliders (Orstrom *et al.* 1994; Clutton-Brock and Parker 1995; Fehr *et al.* 2002), there are limits to which such action can really enforce social cooperation. Since there are always benefits to be gained from freeriding and there is a significant chance that any one freerider will escape detection and/or punishment, the temptation to freeride will mean that some proportion of individuals will always do so, no matter how effective punishment is in reducing the absolute frequency (for an identical problem in relation to poaching and conservation, see Cowlshaw and Dunbar 2000). Social cooperation is far more effective when individuals act willingly because they all voluntarily sign up to the communal project (Orstrom *et al.* 1994). Mechanisms that create a sense

of communality are, thus, more likely to result in the required levels of altruism than the use of social control.

As has long been appreciated in the social sciences, both religion and story-telling play an important role in social bonding in all human cultures (Durkheim 2001). Religion does so through the capacity of rituals to trigger the release of endorphins, since many of these are of just the kind of mildly stressful activities that are especially good at releasing endorphins. Religion, of course, also has the advantage of having an intellectual dimension, and here the cognitive demands become important in creating the kind of dual-process bonding mechanism that we find in primate social grooming. To the extent that the intellectual component of religion is a form of story-telling, story-telling itself enters the frame as an important mechanism for community bonding. However, story-telling goes beyond mere religious explanations for the way the world is and should be; it offers its own kind of opportunity to develop a form of entertainment that can be just as powerful a bonding mechanism in its own right.

One could argue that both of these are mere epi-phenomena—non-adaptive by-products of the fact that we have big brains. Exactly this claim has, of course, been made for music (Pinker's (1998) 'music as evolutionary cheesecake' argument). However, such a claim rests uncomfortably with the time, money and effort that, irrespective of culture, humans invest in all three of these phenomena. In fact, all human societies value story-telling for itself as a form of entertainment, and many of these stories are intimately involved in creating a sense of community: origin stories, tribal histories, and moral tales are among the commonest of campfire 'tellings', and all contribute directly to providing a sense of community. Indeed, the very performance itself often contributes directly, not least through laughter (another powerful releaser of endorphins: Dunbar 2004). By way of confirmation, van Vugt *et al.* (submitted) have recently demonstrated experimentally that laughing together causes strangers (but not existing friends) to be significantly more generous towards each other in public goods games. It is important to note that religion and story-telling both acquire their community-enhancing properties through language: without language, it would not be possible to tell a 'big enough story' to create the bonding effects or to persuade people to take part in religious rituals on a regular basis. It seems that regular participation in these community-bonding exercises is essential, almost as though it was a form of inoculation requiring boosters at set intervals to maintain a consistent level of performance.

But aside from the trivially obvious answer of language, what is it that limits these ‘activities of the mind’ to humans alone? One answer has to be that only humans can cope with the fifth-order intentionality that is necessary to allow these phenomena to produce the effects they do. The best that any non-human species can do seems to be second-order intentionality—and even that is probably true only of great apes (O’Connell and Dunbar 2003), since the consensus is that all other animal species can aspire only to first order. If mentalising skills really are an emergent property of executive function competences (Barrett *et al.* 2003) and these in turn are a function of the computational power (and hence size) of the brain (Dunbar 2003a), then the simple explanation for this striking difference between ourselves and all other species lies in the size of our brain (and, perhaps more specifically, the frontal lobes, since these are generally considered to be the *locus operandi* for those capacities that we conventionally refer to as executive functions). In effect, the differences between us and all other animals come down to the fact that the size of our brain allows us to do something that is simply not possible with a smaller brain. While brain organisation and aspects of neural efficiency (see for example Burki and Kaessmann 2004) must, of course, play a role, there are good arguments for thinking that it is simply the size of the computer that may be important (see for example Duncan 2001). No matter what the differences in structure and organisation may be, we do have a size issue to explain away and our over-large brains cannot be there merely by accident or as a trivial by-product of something else. In sum, the difference between us and our nearest cousins is not simply a matter of having greater intelligence (however we want to measure that) but what that greater intelligence allows us to do (namely, live in a virtual world), and why we need that emergent capacity at all (i.e. to enable us to bond much larger communities than would otherwise be possible for a monkey or an ape).

References

- Abbott, D. H., Keverne, E. B., Moore, G. F. and Yodyingvad, U. (1986), ‘Social suppression of reproduction in subordinate talapoin monkeys’, *Miopithecus talapoin*, in J. Else and P. C. Lee (eds.), *Primate Ontogeny* (Cambridge), pp. 329–41.
- Aiello, L. C. and Wheeler, P. T. (1995), ‘The expensive tissue hypothesis: the brain and the digestive system in human evolution’, *Current Anthropology*, 36: 199–221.

- Baron-Cohen, S., Leslie, A. M. and Frith, U. (1985), 'Does the autistic child have a theory of mind?', *Cognition*, 21: 37–46.
- Barrett, L., Henzi, S. P. and Dunbar, R. I. M. (2003), 'Primate cognition: from "what now?" to "what if?"', *Trends in Cognitive Sciences*, 7: 494–7.
- Becher, T. (1989), *Academic Tribes and Territories* (Milton Keynes).
- Berscheid, E., Snyder, M. and Omoto, A. M. (1989), 'The relationship closeness inventory: assessing the closeness of interpersonal relationships', *Journal of Personality and Social Psychology*, 57: 792–807.
- Bintliff, J. (1999), 'Settlement and territory', in G. Barker (ed.), *Companion Encyclopedia of Archaeology* (London), pp. 505–45.
- Burki, F., Kaessmann, H. (2004), 'Birth and adaptive evolution of a hominoid gene that supports high neurotransmitter flux', *Nature Genetics*, 36: 1061–3.
- Bryant, F. C. (1981), *We're All Kin: a Cultural Study of a Mountain Neighbourhood* (Knoxville, TN).
- Byrne, R. and Whiten, A. (eds.) (1988), *Machiavellian Intelligence* (Oxford).
- Castles, D., Whiten, A. and Aureli, F. (1999), 'Social anxiety, relationships and self-directed behaviour among wild female olive baboons', *Animal Behaviour*, 58: 1207–15.
- Clutton-Brock, T. H. and Parler, G. A. (1995), 'Punishment in animal societies', *Nature*, 373: 209–16.
- Cowlshaw, G. and Dunbar, R. I. M. (2000), *Primate Conservation Biology* (Chicago).
- Dennett, D. (1987), *The Intentional Stance* (Cambridge, MA).
- Dunbar, R. I. M. (1980), 'Determinants and evolutionary consequences of dominance among female gelada baboons', *Behavioural Ecology and Sociobiology*, 7: 253–65.
- Dunbar, R. I. M. (1984), *Reproductive Decisions: an Economic Analysis of Gelada Baboon Social Strategies* (Princeton, NJ).
- Dunbar, R. I. M. (1988), *Primate Social Systems* (London).
- Dunbar, R. I. M. (1989), 'Reproductive strategies of female gelada baboons', in A. Rasa, C. Vogel and E. Voland (eds.), *Sociobiology of Sexual and Reproductive Strategies* (London), pp. 74–92.
- Dunbar, R. I. M. (1993), 'Coevolution of neocortex size, group size and language in humans', *Behavioral and Brain Sciences*, 16: 681–735.
- Dunbar, R. I. M. (1998), 'The social brain hypothesis', *Evolutionary Anthropology*, 6: 178–90.
- Dunbar, R. I. M. (1999), 'Culture, honesty and the freerider problem', in R. I. M. Dunbar, C. Knight and C. Power (eds.), *The Evolution of Culture* (Edinburgh), pp. 194–213.
- Dunbar, R. I. M. (2003a), 'Why are apes so smart?', in P. Kappeler and M. Pereira (eds.), *Primate Life Histories and Socioecology* (Chicago, IL), pp. 285–98.
- Dunbar, R. I. M. (2003b), 'The social brain: mind, language and society in evolutionary perspective', *Annual Review of Anthropology*, 32: 163–81.
- Dunbar, R. I. M. (2004), 'Language, music and laughter in evolutionary perspective', in D. K. Oller and U. Griebel (eds.), *Evolution of Communication Systems: A Comparative Approach* (Cambridge, MA), pp. 257–74.
- Dunbar, R. I. M. (2008), 'Cognitive constraints on the structure and dynamics of social networks', *Group Dynamics*, 12: 7–16.

- Dunbar, R. I. M. (2008), 'Why only humans have language', in R. Botha and C. Knight (eds.), *The Prehistory of Language* (Oxford).
- Dunbar, R. I. M. (in press), 'Mind the bonding gap: constraints on the evolution of hominin societies', in S. Shennan (ed.), *Pattern and Process in Cultural Evolution* (Berkeley, CA).
- Dunbar, R. I. M. and Shultz, S. (2007a), 'Understanding primate brain evolution', *Philosophical Transactions of the Royal Society of London*, 362B: 649–58.
- Dunbar, R. I. M. and Shultz, S. (2007b), 'Evolution in the social brain', *Science*, 317: 1344–7.
- Duncan, J. (2001), 'An adaptive coding model of neural function in prefrontal cortex', *Nature Neuroscience*, 2: 820–9.
- Durkheim, E. (2001 [1900]), *Elementary Forms of Religious Life* (Oxford).
- Emery, N., Clayton, N. and Frith, C. (2007), *Social Intelligence: From Brain to Culture* (Oxford).
- Enquist, M. and Leimar, O. (1993), 'The evolution of cooperation in mobile organisms', *Animal Behaviour*, 45: 747–57.
- Fehr, E., Fishbacher, U. and Gächter, S. (2002), 'Strong reciprocity, human cooperation and the enforcement of social norms', *Human Nature*, 13: 1–25.
- Finlay, B. L. and Darlington, R. B. (1995), 'Linked regularities in the development and evolution of mammalian brains', *Science*, 268: 1578–84.
- Finlay, B. L., Darlington, R. B. and Nicastro, N. (2001), 'Developmental structure in brain evolution', *Behavioral and Brain Sciences*, 24: 263–308.
- Gladwell, M. (2000), *The Tipping Point* (London).
- Goosen, C. (1981), 'On the function of allogrooming in Old-World monkeys', in A. B. Chiarelli and R. S. Corruccini (eds.), *Primate Behaviour and Sociobiology* (Berlin), pp. 110–20.
- Hamilton, M. J., Milne, B. T., Walker, R. S., Burger, O. and Brown, J. H. (2007), 'The complex structure of hunter-gatherer social networks', *Proceedings of the Royal Society, London*, 271B: 2195–202.
- Henzi, P., de Sousa Pereira, L., Hawker-Bond, D., Stiller, J., Dunbar, R. I. M. and Barrett, L. (2007), 'Look who's talking: developmental trends in the size of conversational cliques', *Evolution and Human Behavior*, 28: 66–74.
- Hill, D. (1981), *An Atlas of Anglo-Saxon England* (Oxford).
- Hill, R. A. and Dunbar, R. I. M. (2003), 'Social network size in humans', *Human Nature*, 14: 53–72.
- Hurd, J. P. (1985), 'Sex differences in mate choice among the "Nebraska" Amish of central Pennsylvania', *Ethology and Sociobiology*, 6: 49–57.
- Jerison, H. J. (1973), *Evolution of the Brain and Intelligence* (London).
- Kerr, N., Dunbar, R. I. M. and Bentall, R. P. (2003), 'Theory of mind deficits in bipolar affective disorder', *Journal of Affective Disorders*, 73: 253–9.
- Keverne, E. B., Martensz, N. and Tuite, B. (1989), 'Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships', *Psychoneuroendocrinology*, 14: 155–61.
- Killworth, P. D., Bernard, H. P. and McCarty, C. (1984), 'Measuring patterns of acquaintanceship', *Current Anthropology*, 25: 385–97.
- Kinderman, P., Dunbar, R. I. M. and Bentall, R. P. (1998), 'Theory-of-mind deficits and causal attributions', *British Journal of Psychology*, 89: 191–204.

- Laslett, P. (1971), *The World we have Lost* (London).
- Leslie, A. M. (1987), 'Pretense and representation—the origins of "theory of mind"', *Psychological Review*, 94: 412–26.
- MacDonald, C. B. (1955), 'Company', *Encyclopedia Britannica*, 14th edn., pp. 143–4.
- McLeod, C. E., Zilles, K., Schleicher, A., Rilling, J. K. and Gibson, K. E. (2003), 'Expansion of the neocerebellum in Hominoidea', *Journal of Human Evolution*, 44: 401–29.
- Mange, A. and Mange, E. (1980), *Genetics: Human Aspects* (New York).
- Mitchell, P. (1997), *Introduction to Theory of Mind* (London).
- Montross, L. (1975), 'Tactics', *Encyclopedia Britannica*, 15th edn.
- Nettle, D. and Dunbar, R. I. M. (1997), 'Social markers and the evolution of reciprocal exchange', *Current Anthropology*, 38: 93–9.
- Oates, J. (1977), 'Mesopotamian social organisation: archaeological and philological evidence', in J. Friedman and M. J. Rowlands (ed.), *The Evolution of Social Systems* (London), pp. 457–85.
- O'Connell, S. and Dunbar, R. I. M. (2003), 'A test for comprehension of false belief in chimpanzees', *Evolution and Cognition*, 9: 131–9.
- Orstrom, E., Gardner, R. and Walker, J. (1994), *Rules, Games and Common-Pool Resources* (Ann Arbor, MI).
- Ozonoff, S. (1995), 'Executive functions in autism', in E. Schopler and G. B. Mesibov (eds.), *Learning and Cognition in Autism* (New York), pp. 199–218.
- Perner, J. (1991), *Understanding the Representational Mind* (Cambridge, MA).
- Pinker, S. (1998), *How the Mind Works* (London).
- Roth, D. and Leslie, A. M. (1998), 'Solving belief problems: toward a task analysis', *Cognition*, 66: 1–31.
- Shultz, S. and Dunbar, R. I. M. (2007), 'The evolution of the social brain: Anthropoid primates contrast with other vertebrates', *Proceedings of the Royal Society, London*, 274B: 2429–36.
- Shultz, S., Noe, R., McGraw, S. and Dunbar, R. I. M. (2004), 'A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition', *Proceedings of the Royal Society, London*, 271B: 725–32.
- Silk, J. B. (2002), 'The 'F'-word in primatology', *Behaviour*, 139: 421–46.
- Silk, J. B. (2007), 'Social components of fitness in primate groups', *Science*, 317: 1347–50.
- Silk, J. B., Alberts, S. C. and Altmann, J. (2003), 'Social bonds of female baboons enhance infant survival', *Science*, 302: 1232–4.
- Smuts, B. B. (1985), *Sex and Friendship in Baboons* (New York).
- Sternberg, R. J. (1997), 'Construct validation of a triangular love scale', *European Journal of Social Psychology*, 27: 313–35.
- Stiller, J. and Dunbar, R. I. M. (2007), 'Perspective-taking and social network size in humans', *Social Networks*, 29: 93–104.
- Stylianou, M. (2007), *Does Executive Function Training Improve Mentalising Ability?* Ph.D. thesis, University of Liverpool.
- Swarbrick, R. (2000), *A Social Cognitive Model of Paranoid Delusions*. Ph.D. thesis, University of Manchester.

- Urban Church Project (1974), *Let My People Grow!* Workpaper No. 1. Unpublished report to the General Synod of the Church of England, London.
- van Vugt, M., Hardy, C., Stow, J. and Dunbar, R. I. M. (submitted), 'Laughter as social lubricant: a biosocial hypothesis about the pro-social functions of laughter and humor'.
- Whiten, A. and Byrne, R. W. (eds.) (1997), *Machiavellian Intelligence II: Extensions and Evaluations* (Cambridge).
- Zhou, W.-X., Sornette, D., Hill, R. A. and Dunbar, R. I. M. (2005), 'Discrete hierarchical organisation of social group sizes', *Proceedings of the Royal Society, London*, 272B: 439–44.