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Coevolution of neocortical size, group size and language in humans

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Abstract: Group size covaries with relative neocortical volume in nonhuman primates. This regression equation predicts a group size for modern humans very similar to that for hunter-gatherer and traditional horticulturalist societies. Similar group sizes are found in other contemporary and historical societies. Nonhuman primates maintain group cohesion through social grooming; among the Old World monkeys and apes, social grooming time is linearly related to group size. Maintaining stability of human-sized groups by grooming alone would make intolerable time demands. It is therefore suggested (1) that the evolution of large groups in the human lineage depended on developing a more efficient method for time-sharing the processes of social bonding and (2) that language uniquely fulfills this requirement. Data on the size of conversational and other small interacting groups of humans accord with the predicted relative efficiency of conversation compared to grooming as a bonding process. In human conversations about 60% of time is spent gossiping about relationships and personal experiences. Language may accordingly have evolved to allow individuals to learn about the behavioural characteristics of other group members more rapidly than was feasible by direct observation alone.

Keywords: group size; humans; language; Machiavellian Intelligence; neocortical size

1. Introduction

Primates are, above all, social animals. This has inevitably led to the suggestion that such intense sociality is functionally related to their exceptional cognitive abilities, as reflected in their unusually large brains (Byrne & Whiten 1988; Humphrey 1976; Jolly 1969; Kummer 1982). This claim is supported by the finding that mean group size is directly related to relative neocortical volume in nonhuman primates (Dunbar 1992a; Sawaguchi & Kudo 1990). These analyses suggest that although the size of the group in which animals live in a given habitat is a function of habitat-specific, ecologically determined costs and benefits (see, e.g., Dunbar 1988; 1992b), there is a species-specific upper limit to group size that is set by purely cognitive constraints: animals cannot maintain the cohesion and integrity of groups larger than a size fixed by the information-processing capacity of their neocortex.

The group size identified by this relationship appears to depend on the maximum number of individuals with whom an animal can maintain social relationships by personal contact. Not all these individuals need live in the same physical group: chimpanzees (among a number of other species) have a fission-fusion form of social system in which the community (the group in the sense defined above) is divided at any one time into a number of temporary foraging parties whose composition changes repeatedly (see, e.g., Wrangham 1986). Nor does it follow that a species' social system consists exclusively of one type of group: it is now clear that most primate species live in complex multitiered social systems in which different layers are functional responses to different environmental problems (e.g., the gelada and hamadryas baboons, see Dunbar 1988; 1989a). Rather, the neocortical constraint seems to be on the number of relationships an animal can keep track of in a complex, continuously changing social world: the function subserved by that level of grouping will depend on the individual species' ecological and social context.

It is important to appreciate that the causal relationship between group size and neocortical size depends on the explanatory perspective (or level) adopted. In evolutionary terms, the size of a species' neocortex is set by the range of group size required by the habitat(s) in which it typically lives. However, seen in proximate terms from an individual animal's point of view, current neocortical size sets a limit on the number of relationships it can maintain through time and hence on the maximum size of its group. This means that although the evolution of neocortical size is driven by the ecological factors that select for group size, we can use the relationship in reverse to predict group sizes for living species (Dunbar 1992a).

It is generally accepted that the cohesion of primate groups is maintained through time by social grooming (see Dunbar 1988). Social grooming is used both to establish and to service those friendships and coalitions that give primate groups their unique structure. As might be anticipated, the amount of time devoted to social grooming correlates well with group size, notably among the catarrhine primates (Old World monkeys and apes; Dunbar 1991).

It appears, however, that the relationship between group size and time devoted to grooming is a consequence of the intensity with which a small number of key "friendships" (the primary network) is serviced rather than the total number of individuals in the group (Dunbar

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1991; Kudo et al., submitted). These primary networks function as coalitions whose main purpose is to buffer their members against harassment by the other members of the group. The larger the group, the more harassment and stress an individual faces (see, e.g., Dunbar 1988) and the more important these coalitions. A coalition's effectiveness (in the sense of its members' willingness to come to each other's aid) seems to be directly related to the amount of time its members spend grooming each other (see Seyfarth & Cheney 1984; Dunbar 1984). Hence, the larger the group, the more time individuals devote to grooming with the members of their coalitional clique.

The mean size of the primary network, however, is related to the mean group size for the species. This suggests that groups are built up by welding together sets of smaller primary networks (see also Cheney 1992), and that the total size of the group is ultimately limited not by the number of networks that can be welded together but by the size of the networks themselves.

In this target article I inquire into the implications of these two sets of results for modern humans (*Homo sapiens sapiens*). If we extrapolate from the nonhuman primate regression, what group size would we predict for anatomically modern humans, given our current neocortical size? I then ask whether there are any observed human group sizes that correspond to this predicted value. Since the relationships that maintain group cohesion among nonhuman primates are serviced by social grooming, I use the regression equation for primates to determine how much time humans would have to spend grooming each other if they were to maintain group cohesion in this way for groups of the size predicted from neocortical size. Finally, I ask what implications this might have had for the evolution of language.

2. Methods

A number of different measures have been used in comparative analyses to provide unbiased estimates of relative differences in brain size. These have included the Extra Cortical Neurons Index (the ratio of the observed number of cortical neurons over and above those required for somatic maintenance, as estimated from body size, brain size, and neural density; Jerison 1973), the cerebral Progression Index (the ratio of observed brain or neocortical volume to that predicted for a basal insectivore of the same body size; Stephan 1972), the Encephalisation Quotient (EQ: the residual of brain volume, or neocortical volume, regressed against body weight; Clutton-Brock & Harvey 1980; Jerison 1973; Sawaguchi & Kudo 1990), and the Neocortex Ratio (neocortical volume divided by the volume of the rest of the brain or the volume of the hindbrain; Dunbar 1992a). [See also Falk: "Brain Evolution in *Homo*" *BBS* 13(2) 1990; and Glezer: "Implications of the 'Initial Brain' Concept for Brain Evolution in Cetacea" *BBS* 11(1) 1988.]

In examining the relationship between neocortical size and group size in nonhuman primates, I found all these measures reasonable predictors of group size. The Neocortex Ratio (measured against the rest of the brain excluding the neocortex) gives much the best fit, however, accounting for 76% of the variance in mean group size among 36 genera of prosimian and anthropoid primates (using data on neocortical volume provided by Stephan et al. 1981; see Dunbar 1992a).

This analysis was based on the mean group size observed for a given genus rather than the maximum group size. The main justification for using mean group size in these analyses lies in the nature of primate social groups. In contrast to the relatively simple aggregations typical of many birds and herbivores, primate groups are highly structured, with individual animals embedded in a complex set of social and kinship networks (see Dunbar 1988; 1989a). Whereas bird flocks can shed individuals through trickle migration as soon as they exceed their optimal size, primate groups cannot: they have to wait until the group is large enough to permit it to split into two or more daughter groups of the minimum size necessary to ensure the safety and survival of their members. This means that primate groups tend to oscillate in size over quite a wide range around the optimal value. At the point of fission (by definition, their maximum observed size), groups tend to be unstable and close to social disintegration; this is of course why they undergo fission at that point. Hence, maximum group size is likely to represent the point of complete social collapse rather than the maximum group size that the animals can maintain as a cohesive social unit. Consequently, mean group size is likely to be a better estimate of the limiting group size for a species than the maximum ever observed in any population (for further discussion, see Dunbar 1992a).

3. Results

3.1. Group size in modern humans. The best-fit reduced major axis regression equation between neocortex ratio and mean group size for the sample of 36 primate genera shown in Figure 1 was found to be:

$$\log(N) = 0.093 + 3.389 \log (C_R) \qquad (1)$$

($r^2 = 0.764$, $t_{34} = 10.35$, $p < 0.001$), where N is the mean group size and C_R is the ratio of neocortical volume to the volume of the rest of the brain (i.e., total brain volume minus neocortex; Dunbar 1992a). Use of both major axis and least-squares regression, as well as alternative indices of relative neocortical size, all yield equations that are of about this same magnitude.

With a neocortical volume of 1006.5 cc and a total brain volume of 1251.8 cc (Stephan et al. 1981), the neocortex ratio for humans is $C_R = 4.1$. This is about 30% larger than the maximum value for any other primate species (see Dunbar 1992a). Strictly speaking, of course, extrapolation from regression equations beyond the range of the X-variable values on which they are based is frowned on. We can justify doing so in this case, however, on the grounds that our concern at this stage is exploratory rather than explanatory. We accordingly do so in the knowledge that the confidence limits around any predictions are likely to be wide.

Equation (1) yields a predicted group size for humans of 147.8. Because the equation is log-transformed and we are extrapolating well beyond the range of neocortex ratios on which it is based, the 95% confidence limits around this prediction (from formulae given by Rayner 1985) are moderately wide (100.2–231.1). Equations based on alternative indices of neocortical size (see Dunbar 1992a, Table 2) yield predicted group sizes that range

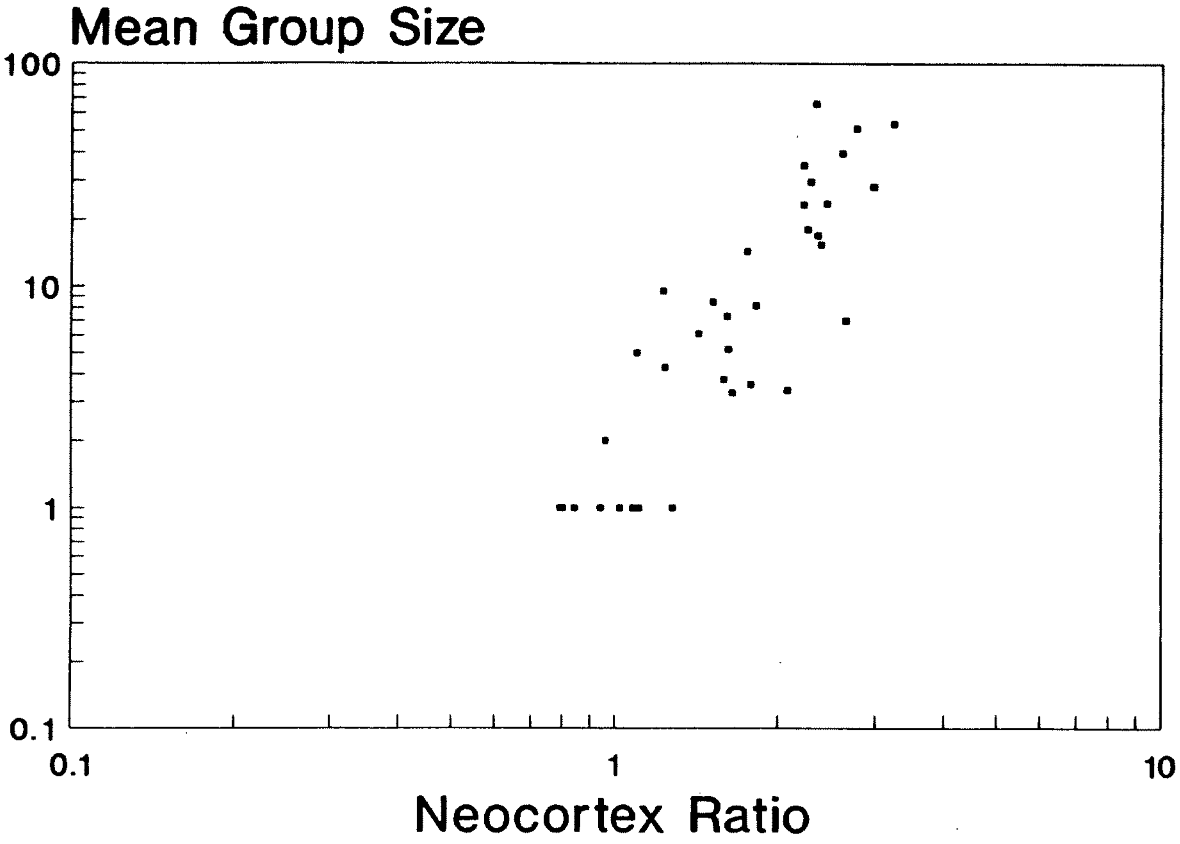

Figure 1. Group size plotted against neocortex ratio for nonhuman primates (redrawn from Dunbar 1992a).

from 107.6 (EQ residual of neocortical volume regressed against body weight) to 189.1 (Jerison's Extra Neocortical Neurons Index) and 248.6 (absolute neocortical volume), all of which are within (or close to) the 95% confidence limits on the neocortex ratio equation.

In trying to test this prediction, we encounter two problems. One is deciding just what counts as the "natural" condition for *H. s. sapiens;* the other is the problem of defining the appropriate level of grouping for human societies living under these conditions.

It is generally accepted that human cultural evolution has proceeded at a much faster pace than our anatomical evolution during the past few millenia. Given that our brain size has its origins in the later stages of human evolution some 250,000 years ago (Aiello & Dean 1990; Martin 1983), we may assume that our current brain size reflects the kinds of groups then prevalent and not those now found among technologically advanced cultures. The closest we can get to this is to examine those modern humans whose way of life is thought to be most similar to that of our late Pleistocene ancestors: the hunter-gatherers (Sahlins 1972; Service 1962).

Given that hunter-gatherers are the only appropriate source of information, we then face the problem of deciding what constitutes the appropriate level of grouping within hunter-gatherer societies. There has, however, been considerable debate within anthropology as to the precise structure of these societies (see Birdsell 1970; Lee 1982; Morris 1982; Service 1962; Williams 1974). Regardless of how this debate is eventually resolved, it is clear that most hunter-gatherers live in complexly structured social universes with several different levels of grouping.

Thus, the !Kung San of southern Africa live in camps whose composition can change from day to day but whose membership is mostly drawn from a distinct set of individuals whose foraging area is based on a number of more or less permanent waterholes; several of these "regional groups" make up a much larger tribal grouping typically based on a common dialect and occupancy of a given geographical area (see Lee 1982). The temporary living groups are drawn together into their larger regional groupings for up to three months each year, when they congregate at traditional dry season camps based on what is often the only permanent waterhole in the region.

Lee (1982) refers to this as a concentration/dispersal social system and suggests that its origins lie in the unpredictable nature of food and water sources in typical Bushman habitats. He also argues that this flexible form of social system is typical of most (if not all) modern hunter-gatherers: rather similar patterns of social organisation have been documented, for example, among the Australian aboriginals (Meggitt 1965a; Strehlow 1947), various Eskimo societies (Damas 1968; Spencer 1959), many of the North American Indian tribes (Drucker 1955; Helm 1968; Leacock 1969; Steward 1938); and among the Congo pygmies (Hewlett 1988; Turnbull 1968).

Given this complexity, any attempt to determine the "true" group size in hunter-gatherers would almost certainly be challenged by anthropologists on innumerable ethnographic grounds. In addition, two other more general objections might be raised. One is that most surviving hunter-gatherers occupy marginal habitats; this may well influence both the size and the structure of their social systems (as is known to be the case with baboons, for example; Dunbar 1992a; in press). The second objection is that most living hunter-gatherer societies have been seriously disrupted, either directly or indirectly, by contact with modern colonial cultures.

In view of these caveats, and so as to avoid the kind of fruitless definitional arguments that have so often beset the literature in this area, I will proceed more cautiously and ask simply whether we find any groups at all that are consistently of the size predicted for modern humans by equation (1). Given the definition of grouping elaborated in the Introduction, the central issue is not whether a particular *form* of grouping occurs in every social system but whether a particular *size* of grouping does.

Unfortunately, ethnographers have not often regarded censuses as an important feature of their investigations: although most studies allude to groupings of different kinds and often describe the structural relationships between them in great detail, they seldom provide quantitative data on their sizes. Table 1 summarises all the data I have been able to find in the ethnographic literature for a number of historical and contemporary hunter-gatherer and swidden horticulturalist societies. I have included swidden horticulturalists since these may reasonably be considered to be settled hunter-gatherers insofar as their social organisation is concerned (see Johnson & Earle 1987).

The data in Table 1 suggest that group sizes fall into three quite distinct size classes: small living groups of 30–50 individuals (commonly measured as overnight camps but often referred to as *bands* in some of the hunter-gatherer literature), a large population unit (the tribe, or in some cases the subtribe) that typically numbers be-

Table 1. *Group sizes in modern hunter-gatherer societies*

		Mean size[a]			
Society	Location	Overnight camp	Band/ village	Tribe	Source
Walbiri	Australia	c. 25–30	221.5	886	Meggitt (1965a)
various	New Guinea	—	128.7[b]	?	Ellen (1978)
Tauade[c]	New Guinea	27.3	202.5	1,237.3	Hallpike (1977)
Mae Enga[d]	New Guinea	48	90 (350)	2,290	Meggitt (1965b)
Gebusi	New Guinea	26.5[e]	53–159	450	Knauft (1987)
Kaluli	New Guinea	60.0[f]	109.1	1,200	Schieffelin (1976)
Ruhua Nualu	Indonesia	—	180.0[b]	?	Ellen (1978)
Bihar	India	26.8	90–120	c. 1,625	Williams (1974)
Andamanese	Andaman Is	40–50	?	471	Williams (1974)
G/wi San	S. Africa	21–85	?	2,000	Silberbauer (1972)
!Kung San	Botswana	18.6	152.3	2,693	Lee (1982)
Mbuti	Zaire	—	60–150[b]	?	Harako (1981) Turnbull (1968)
Aka	W. Congo	25–35	60–100	(c. 1,050+)	Hewlett (1988)
Ammassalik	Greenland	31.8	?	413	Service (1962)
Inuit	Canada	?	150.0	483	Irwin (1987)
Central Eskimo	Canada	?	c. 100	600	Damas (1968)
Dogrib	USA	c. 10–60	c. 60–250[f]	?	Helm (1968)
Shoshone	USA	62.7	?	?	Service (1962)
California Indians	USA	c. 50–75	?	?	Steward (1955)
Yanomamo	Venezuela	—	101.9[b]	663[g]	Chagnon (1979)
Ona	Tierra del Fuego	40–120	?	?	Steward (1936)
Mean[h]:		37.7	148.4[i]	1,154.7	
Sample size:		8	9	13	
Coefficient of variation (%):		41.7	29.1	64.4	

[a] Some sources only give a range in group size. "?" indicates that the level of grouping is specifically mentioned by the enthnographer, but no census data are given; "—" indicates that the grouping specifically does not occur.

[b] Settled hunter-gatherers or traditional horticulturalists living in permanent villages.

[c] The values are, respectively, the mean size of clans, tribes, and dialects, as defined by Hallpike (1977), from a total language group of about 8,700; this interpretation is closest to the usage in the target article.

[d] The values are, respectively, the mean size of patrilineages, subclans (clans in parentheses), and phratries, as defined by Meggitt (1965b), from a total tribal group estimated at 60,000 (see comment on note [c], above).

[e] Helm (1968) quotes sizes as numbers of "conjugal pairs"; I have assumed an average of three living children per conjugal pair.

[f] Mean number of residents in a longhouse.

[g] Mean size of "population blocs" of Chagnon (1979) from a total Yanomamo population estimated to be about 15,000.

[h] For societies in which actual census data are given.

[i] The larger value for the Mae Enga would give a mean of 177.3; the median values would be 150.0 and 152.3, respectively.

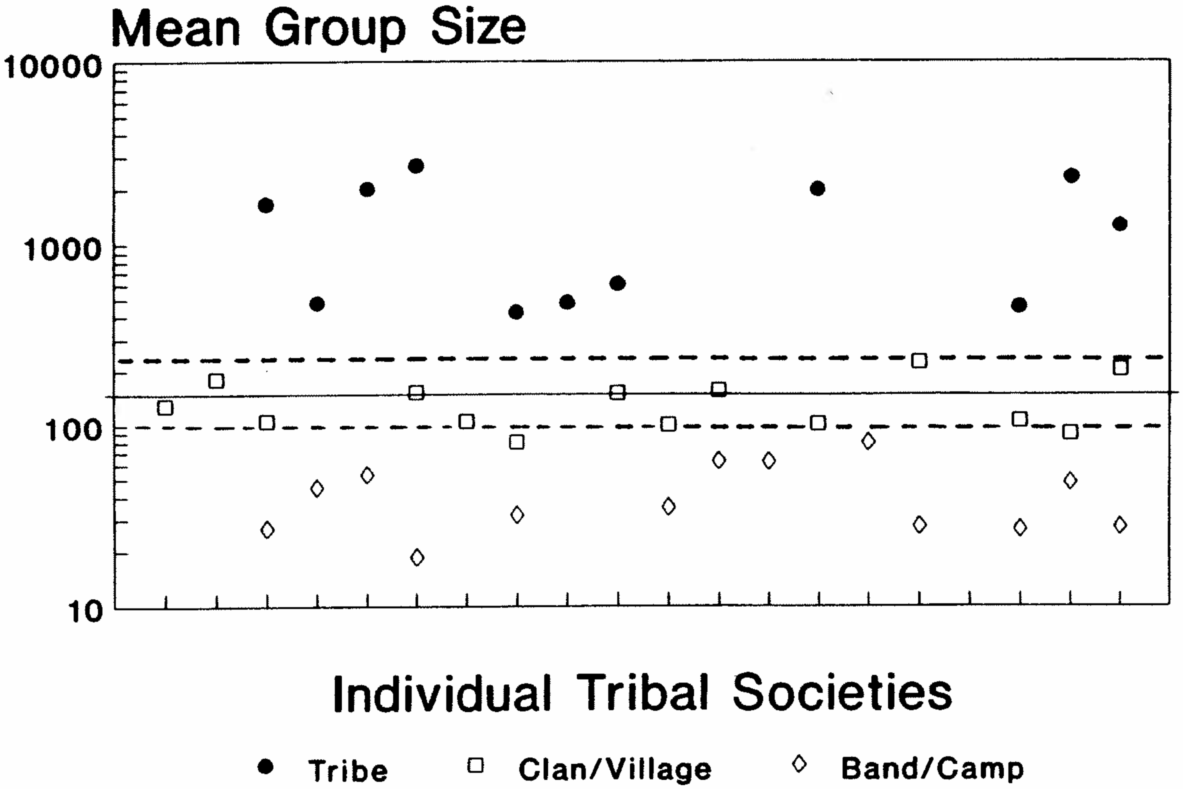

Figure 2. Distribution of group sizes for traditional societies. Individual societies are placed along the abscissa in arbitrary order. The group size predicted by equation (1) is indicated by the horizontal line; 95% confidence limits around this value are indicated by the dotted lines (*source:* Table 1).

tween 500 and 2,500 individuals, and an intermediate level of grouping (either a more permanent village or a culturally defined clan or lineage group) that typically contains 100–200 people. In a few cases (e.g., the Mae Enga and the Kaluli of New Guinea), more than three grouping layers were identified by the ethnographer. Most such groupings are organised in a hierarchically inclusive fashion, however, and I have accordingly identified the groupings closest to the senses defined above.

Plotting these values on a graph produces what appears to be a clear trimodal distribution of group sizes, with no overlap between grouping levels (Fig. 2). The average sizes of the smallest and largest grouping levels (means of 37.7 and 1154.7, respectively) correspond quite closely to the figures for bands (30–50) and tribal groups (1,000–2,000) that are widely quoted in the anthropological literature (e.g., Service 1962; Steward 1955). The level of grouping that appears to lie between these two, however, has been given little more than passing attention (even though the social significance of such groupings as clans has been discussed extensively). This is reflected in the large number of "?" entries in Table 1, indicating that the ethnographer discussed such a grouping but gave no indication of its actual size.

The average size of the intermediate-level groups for those societies for which accurate census data are available is 148.4 (range 90–221.5, $N = 9$). If all the available data are considered (taking median values in cases where only ranges are given), the mean is 134.8 ($N = 15$); if only nomadic hunter-gatherers are considered, the mean is 156.4 ($N = 4$). None of these estimates differs significantly from the predicted value ($z \leq \pm 0.431$, $p \geq 0.667$ 2-tailed). Indeed, with one exception (the Mae Enga of New Guinea), all the values shown in Figure 2 lie within the 95% confidence limits of the predicted value (and even the exception is only just outside the lower 95% confidence limit). More important, in no case does the mean size of any temporary camp or tribal grouping (i.e., the smaller and larger grouping types) lie within the 95% confidence limits on the predicted group size. Indeed, the mean values for the band- and tribal-level groupings are significantly different from the predicted value ($z = 6.401$ and $z = 9.631$, respectively, $p \ll 0.0001$).

Note that the coefficient of variation for the intermediate-level grouping is considerably smaller than those for either of the other two groupings (Table 1). This suggests that the constraints on the former are greater than those on the latter, as might be expected if the former is subject to an intrinsic (e.g., cognitive) constraint, whereas the latter are more often determined by extrinsic environmental factors. The size of hunter-gatherer "bands" (or night camps), for example, is known to be particularly unstable and adjusted seasonally to the group's resource base (Johnson & Earle 1987; Lee 1982; Turnbull 1968). In contrast, the greater variability in the size of the tribal-level groupings almost certainly reflects the impact of contact with modern (especially European) cultures and their attendant diseases; in many cases these have drastically reduced the size of indigenous tribes.

It is important to note that the intermediate-level groupings do not always have an obvious physical manifestation. Whereas overnight camps can readily be identified as demographic units in time and space and the tribal groupings can be identified either by linguistic homogeneity or geographical location (and often both), the intermediate-level groupings are often defined more in terms of ritual functions: they may gather together once a year to enact rituals of special significance to the group (such as initiation rites), but for much of the time the members can be dispersed over a wide geographical area; in some cases they may even live with members of other clan groupings. Nonetheless, what seems to characterise this level of grouping is that it constitutes a subset of the population that interacts on a sufficiently regular basis to have strong bonds based on direct personal knowledge. My reading of the ethnographies suggests that knowledge of individuals outside this grouping is generally less secure and based more on gross categories (a "them" and "us" basis as opposed to identifying individuals by name). More important, perhaps, in the case of New Guinea horticulturalists at least, the intermediate-level grouping seems to provide an outer network of individuals who can be called on for coalitional support during raids or the threat of attack by other groups (see Hallpike 1977; Meggitt 1965b). Thus, this intermediate level of grouping in human societies seems to correspond rather precisely in both size and social function to what we would expect on the basis of the nonhuman primate data.

In addition, estimates of the size of Neolithic villages in Mesopotamia are of about the same magnitude. Oates (1977), for example, gives a figure of 150–200, based on 20–25 dwellings as the typical size of a number of village sites dated to around 6500–5500 B.C. It turns out that figures in the region of 150 also occur frequently among a wide range of contemporary human societies. Thus, the mean size of the 51 communities (or *Bruderhoefe*) in the Schmedenleut section of the Hutterites (a fundamentalist group who live and farm communally in South Dakota and Manitoba) is 106.9 individuals (Mange & Mange 1980). According to Hardin (1988), the Hutterites regard 150 individuals as the limiting size for their farming communities: once a community reaches this size, steps are taken to split it into two daughter communities. Bryant (1981) provides another example from an East Tennessee rural mountain community (all of whom claim to be related to each other and regard themselves as a single social group): the total number of living members was 197 when the community census was taken at the end of the 1970s. Even academic communities appear to abide by this rule. Price and Beaver (1966), for example, found that research specialities in the sciences tend to consist of up to 200 individuals, but rarely more. Becher (1989) sampled network sizes (defined as the number of individuals whose work you pay attention to) in 13 academic subdisciplines drawn from both the sciences and the humanities and concluded that the typical size of the outer circle of professional associates that defines a subdiscipline is about 200 (with a range of 100–400). Disciplines apparently tend to fragment with time as their numerical size (and, of course, their literature) grows.

In addition, it turns out that most organised (i.e., professional) armies have a basic unit of about 150 men (Table 2). This was as true of the Roman Army (both before and after the reforms of 104 B.C.) as of modern armies since the sixteenth century. In the Roman Army of the classical period (350–100 B.C.), the basic unit was the maniple (or "double-century"), which normally consisted of 120–130 men; following the reforms instituted by Marius in 104 B.C., the army was reorganised into legions, each of which contained a number of semi-independent *centuries* of 100 men each (Haverfield 1955; Montross 1975). The smallest independent unit in modern armies (the *company*) invariably contains 100–200 men (normally three or four rifle platoons of 30–40 men each, plus a headquarters unit, sometimes with an additional heavy weapons unit; Table 2). Although its origins date back to the German mercenary *Landsknechts* groups of the sixteenth century, the modern company really derives from the military reforms of the Swedish king Gustavus Adolphus in the 1620s. Despite subsequent increases in size to accommodate new developments in weaponry and tactics, the company in all modern armies has remained within the 95% confidence limits of the predicted size for human groups. The mean size of 179.6 for the twentieth-century armies listed in Table 2 does not differ significantly from the 147.8 predicted by equation (1) ($z = 0.913$, $p = 0.361$ 2-tailed).

Table 2. *Sizes of the smallest independent unit (a "company") in selected professional armies*

Period	National army	Size
16th century	Spain	100–300
	England	100
17th century	Sweden/Germany	106
	England: c. 1650	110
	c. 1670	80
20th century	USA: 1940	223
	1945	193
	1960	212
	Britain: 1940	124
	USSR: 1940	139
	France: 1940	185
	Italy: 1940	198
	Germany: 1940	185
	1943	147
	Japan: 1940	190

Source: MacDonald (1955).

This fact has particular significance in the context of the present argument. Military units must function very efficiently in coordinating men's behaviour on the battlefield: the price of failing to do so is extremely high and military commanders cannot afford to miscalculate. Given that the fighting power of a unit is a function of its size, we might expect considerable selection pressure in favour of units that are as large as possible. That the smallest independent unit should turn out to have a maximum size of about 200 even in modern armies (where technology presumably facilitates the coordination of planning) suggests that this upper limit is set by the number of individuals who can work effectively together as a coordinated team. Military planners have presumably arrived at this figure as a result of trial and error over the centuries.

In the context of the present analysis, the reason given by the Hutterites for limiting their communities to 150 is particularly illuminating. They explicitly state that when the number of individuals is much larger than this, it becomes difficult to control their behaviour by means of peer pressure alone (Hardin 1988). Rather than create a police force, they prefer to split the community. Forge (1972) came to a rather similar conclusion on the basis of an analysis of settlement size and structure among contemporary New Guinea "neolithic" cultivators. He argued that 150 was a key threshold figure in community size in these societies. When communities exceeded this size, he suggested, basic relationships of kinship and affinity were insufficient to maintain social cohesion; stability could then be maintained only if formal structures developed that defined specific roles within society. In other words, large communities were invariably hierarchically structured in some way, whereas small communities were not.

Similarly, in an analysis of data from 30 societies ranging from hunter-gatherers to large-scale agriculturalists, Naroll (1956) demonstrated that there was a simple power relationship between the maximum settlement size observed in a given society and both the number of occupational specialties and the number of organisational structures recorded for it. His analysis suggests that there is a critical threshold at a maximum settlement size of 500, beyond which social cohesion can be maintained only if there is an appropriate number of authoritarian officials. Bearing in mind that Naroll's threshold is expressed as the maximum observed settlement size, it seems likely that the equivalent mean settlement size will not be too far from the value of 150 suggested by the above analyses.

Other evidence suggests that 150 may be a functional limit on interacting groups even in contemporary Western industrial societies. Much of the sociometric research on industrial and other comparable organisations, for example, has demonstrated that there is a marked negative effect of group size on both group cohesion and job satisfaction (as indicated by absenteeism and turnover in posts) within the size range under consideration (i.e., 50–500 individuals; see, e.g., Indik 1965; Porter & Lawler 1965; Silverman 1970). Indeed, an informal rule in business organisation identifies 150 as the critical limit for the effective coordination of tasks and information flow through direct person-to-person links: companies larger than this cannot function effectively without substructuring to define channels of communication and responsibility (J.-M. Delwart, personal communication). Terrien and Mills (1955), for example, found that the larger the organisation, the greater the number of control officials needed to ensure its smooth functioning.

Other studies have suggested that there is an upper limit on the number of social contacts that can be regularly maintained within a group. Coleman (1964) presented data on friendships among print shop workers which suggested that the likelihood of having friends within the workplace reached an asymptote at a shop size of 90–150 individuals. (The small size of the sample for large groups makes it difficult to identify the precise point at which "saturation" is reached.) Coleman explicitly argued that this was a consequence of there being a limit to the number of individuals within a shop that any one person can come into contact with. His results also seemed to suggest that the large number of regular interactants an individual could expect to have within a large work group limited the number of additional friendships that could be made outside the workplace.

Most studies of social networks in modern urban societies have tended to concentrate on specific subsets (e.g., support networks) within the wider network of friends and acquaintances (see Milardo 1988; Mitchell 1969). One exception to this has been the study by Killworth et al. (1984), who used a "reversed small world" protocol to determine the total network size (i.e., the total number of individuals known by name with whom a respondent has a degree of personal contact). Forty subjects were each given a dossier containing 500 fictitious (but realistic) target individuals living in different parts of the world and asked to name an individual among their own acquaintances who (either directly or via a chain of acquaintances of their own) would be able to pass a message to each of the targets. The number of different acquaintances listed was assumed to be an index of the subject's total social network. The mean number of acquaintances selected was 134 (although the variance around this figure was considerable). Since the number of nominated acquaintances seems to increase more slowly as the number of targets increases, Killworth et al. (1984) suggested that the asymptotic network size could be determined by extrapolation from the rate at which the curve of nominated acquaintances increases as the number of targets does. They calculated this value to be about 250. Although just outside the 95% confidence limits on the predicted value ($z = 2.29$, $p = 0.022$ 2-tailed), the latter estimate is not so far outside the range of likely values to be seriously worrying. For one thing, the difference between the mean and asymptotic values may well reflect the difference between the functional norm (i.e., the number of personal friends an individual has) and the maximum network size when more peripheral acquaintances are included. More research is clearly needed to clarify this.

3.2. Grooming and the evolution of language. Given that primate groups are held together by social grooming, time budget constraints on group size become an important consideration (Dunbar 1992b). Even if a species has the cognitive capacity to manage all the relationships involved in large groups, there may be circumstances under which the animals simply do not have the time to devote to servicing those relationships through social grooming. Relationships that are not serviced in this way will cease to function effectively; as a result, the group will tend to disperse and the population will settle at a new lower equilibrium group size.

A comparative analysis of the determinants of grooming by primates has demonstrated that grooming time is a linear function of group size, at least within the catarrhine primates (Dunbar 1991). The distribution of the data suggests that grooming does not necessarily function in such a way that each individual grooms with every other group member; rather, as noted earlier (sect. 1), it suggests that the intensity of grooming with a small number of "special friends" (or coalition partners) increases in proportion to increasing group size. Regardless of the precise way in which grooming functions to integrate large primate groups, we can use the relationship between group size and grooming time to predict the grooming time required to maintain cohesion in groups of the size predicted for modern humans.

Because our main concern is with how time spent grooming functions to maintain group cohesion, I have considered only those catarrhine species that do not have

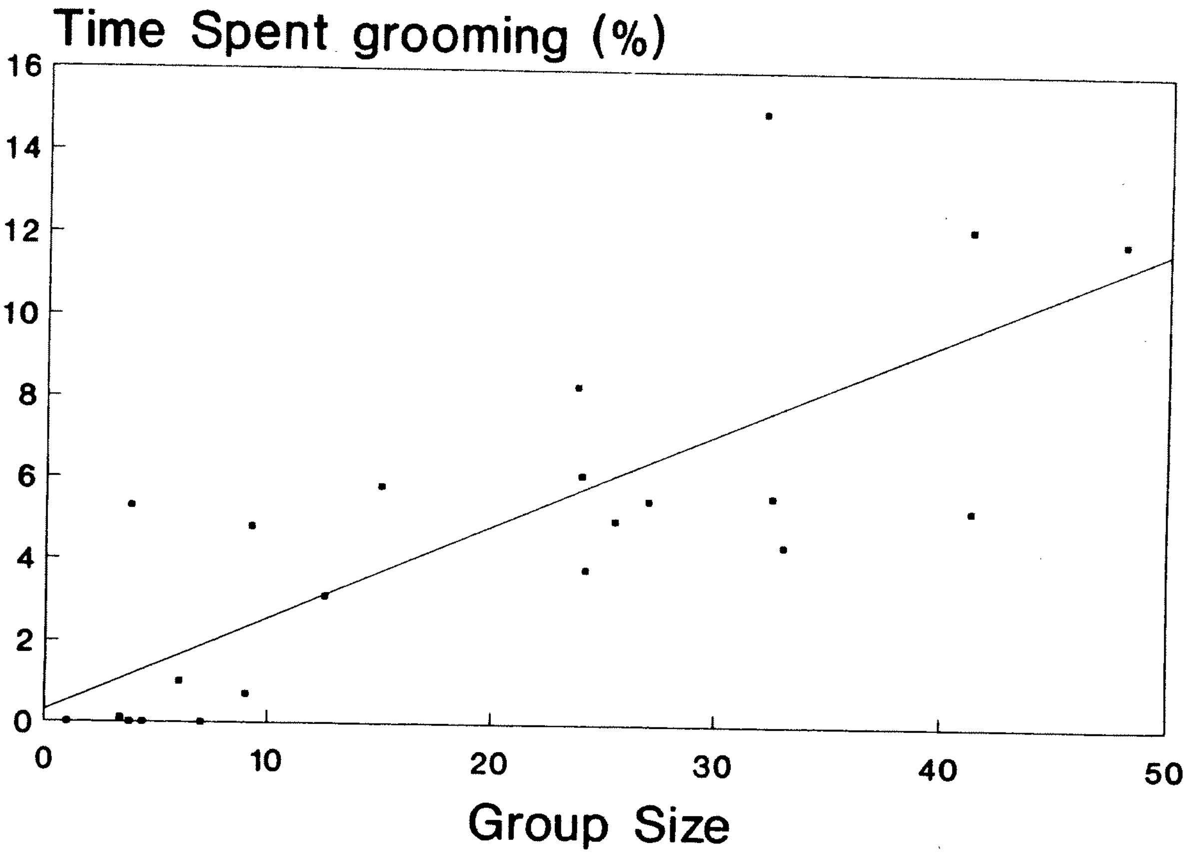

Figure 3. Mean percentage of time spent grooming plotted against mean group size for Old World monkeys and apes that do not have fission-fusion societies (based on data in Dunbar 1991).

fission-fusion social systems. For the 22 species listed in Dunbar (1991, Table 1) that are described as living in stable cohesive groups, the reduced major axis regression equation is:

$$G = -0.772 + 0.287\,N \tag{2}$$

where G is the percentage of time devoted to social grooming during the day ($r^2 = 0.589$, $t_{20} = 5.36$, $p < 0.001$; Fig. 3). (Transforming the data logarithmically does not affect the value of r^2 but produces impossibly high values of grooming time for some primate populations as a direct result of the transformation.) The highest recorded value for any individual species is 18.9% for one group of *Papio papio* baboons (Sharman 1981), but a number of other baboon and macaque groups exhibit grooming time allocations in the range of 15–18% (see, e.g., Iwamoto & Dunbar 1983). A figure of around 20% seems to be an absolute upper limit on the amount of time that primates can afford to devote to social interaction.[1]

The group size predicted for modern humans by equation (1) would require as much as 42% of the total time budget to be devoted to social grooming. (The 95% confidence limits on predicted group size would yield grooming times that range from 28% to 66%.) This is more than double that observed in *any* population of nonhuman primates. Bearing in mind that this figure refers to the *average* group size, and that many groups will be substantially *larger* than this, the implications for human time budgets are clearly catastrophic. A group of 200, for instance, would have to devote 56.6% of its day to social grooming. For any organism that also has to earn a living in the real world, this would place a significant strain on its ability to balance its time budget. This problem would clearly be compounded if thermoregulatory considerations forced individuals to take time out to rest in shade during the hottest parts of the day: among baboons, at least, temperature-driven resting appears to be incompatible with social interaction (Dunbar 1992b).

To place this in perspective in relation to relative neocortical size in the hominoids, I have calculated the equivalent figures for predicted group size and grooming time for all the genera of hominoids (Table 3). (That only the chimpanzees live in groups of the size predicted by equation [1] is not significant in the present context: this point is discussed in more detail in Dunbar [1992a].) The question I want to ask here is whether the size of the neocortex in nonhuman hominoids is large enough to yield group sizes that would lead to a time-budgeting crisis if the group's relationships had to be serviced by social grooming alone. Table 3 suggests that, although group size increases steadily through the hominoids, in no case is the grooming time requirement predicted by equation (2) excessive by the standards of other catarrhine primates. The figure of around 15% social time predicted for orangutans and chimpanzees compares very favourably with the values actually observed among baboons and macaques (see Dunbar 1991). Although larger-bodied apes would need to spend a rather higher proportion of their day foraging than smaller-bodied baboons, the predicted grooming time requirement does not suggest that it would place excessive pressure on their time budgets. Data summarised by Wrangham (1986) indicate that the

Table 3. *Grooming time requirements for hominoids, based on group sizes predicted by neocortex ratio*

Genus	Neocortex ratio[a]	Predicted group size[b]	Grooming time requirement (%)[c]
Gibbon	2.08	14.8	34
Orangutan	2.99	50.7	13.8
Gorilla	2.65	33.6	8.8
Chimpanzee	3.2	65.2	17.9
Human	4.10	147.8	41.6

[a] Based on neocortex and total brain volumes given by Stephan et al. (1981) or Dunbar (1992a).
[b] Predicted by equation (1).
[c] Predicted by equation (2).

various chimpanzee populations spend 25–43% of their time in nonforaging activities (mainly resting and social interaction). None of these populations would be forced to forgo any foraging time were they to spend as much as 20% of their time in social grooming.

The situation for modern humans is clearly very different, and such high grooming time requirements simply could not be met. In baboons it has been shown that when the actual amount of time devoted to social interaction is less than that predicted for a group of the observed size, the group tends to fragment easily during foraging and subsequently often undergoes fission (Dunbar 1992b). Faced with this problem, there are, in principle, only two solutions: either reduce group size to the point where the amount of grooming time is manageable or use the time that is available for social bonding in a more efficient way.

Given that minimum group sizes are ecologically imposed (see Dunbar 1988), there may be little that a particular species can do to manipulate its group size in a particular habitat. The only option will thus be a more efficient use of the time available for social bonding. In this context, the main problem with grooming as a bonding mechanism is that it is highly inflexible: it is all but impossible to do anything else while grooming or being groomed. In addition, grooming is an essentially dyadic activity; only one other individual can be groomed at a time.

Modern humans, however, do possess a form of social communication that overcomes both of these limitations very effectively: not only can speech be combined with almost every other activity (we can forage and talk at the same time), it can also be used to address several different individuals simultaneously. Thus, language introduces major savings by allowing an individual to do two different things at once. My suggestion, then, is that language evolved as a "cheap" form of social grooming, thereby enabling the ancestral humans to maintain the cohesion of the unusually large groups demanded by the particular conditions they faced at the time.

3.3. Language as a bonding mechanism. That language (and hence speech) might have evolved as a consequence of the need to increase group size raises the question of just how it functions as a bonding mechanism. Conventionally, language has always been interpreted in terms of the exchange of information, and this has usually been understood as being the exchange of information about the environment (e.g., the location of prey, the coordination of behaviour during the hunt). However, the social intelligence hypothesis for the evolution of large brain size in primates (see Byrne & Whiten 1988; see also Whiten & Byrne: "Tactical Deception in Primates" *BBS* 11(2) 1988) implies that the acquisition and manipulation of social knowledge is the primary consideration. The fact that language can be interpreted as fulfilling the same role as social grooming suggests that, rather than being the selective factor driving brain evolution, ecologically related information-exchange might be a subsequent development that capitalised on a window of opportunity created by the availability of a computer with a substantial information-processing capacity.

How might language function as a mechanism for social bonding? There would appear to be at least two possibilities. One is that it allows individuals to spend time with their preferred social partners, thereby enabling them to acquire information about each other's behaviour by direct observation. This appears to be one way in which social grooming itself might work (Dunbar 1988). That the intellectual content of human conversations is often trivial (and, indeed, many conversations are highly formulaic and ritualised) lends some support to this argument. The second possibility is that language allows the acquisition of information about third party social relationships, thereby enabling an individual to acquire knowledge of the behavioural characteristics of other group members without actually having to observe them in action. (I am grateful to R. W. Byrne for pointing this out to me.) This would have the effect of considerably widening an individual's sphere of social knowledge relative to what would be possible from direct personal observation. This suggestion meshes well with the social intelligence hypothesis and is given some support by the extent to which humans seem to be fascinated by gossip about other people's behaviour.

It is rather difficult to test either of these possibilities unequivocally. However, it is clear that if the second explanation is true gossip about third party social relationships must constitute an important component of human conversations. Table 4 summarises data on the content of conversations in a university refectory. Approximately 38% of conversation content was devoted to personal relationships (either of those present or of third parties) and a further 24% discussed personal experiences of a more general kind, both topics being clearly related to social knowledge. Considering the potential importance of academic and other intellectual topics of conversation in a university environment, these are remarkably high values. The acquisition and exchange of information about social relationships is clearly a fundamental part of human conversation. The implication, I suggest, is that this was the function for which language evolved.

3.4. Efficiency of language as a bonding mechanism. If language evolved purely as a form of vocal grooming in order to facilitate the evolution of larger social groups, its design properties should be of about the right efficiency relative to grooming to allow an increase in group size from the largest observed in nonhuman primates to those predicted for modern humans. By "efficiency" I mean the

Table 4. *Topics of conversation in naturally formed groups in a university refectory*

Topic	Percentage of conversation[a] males	females
Personal relationships	35.1	41.2
Personal experiences	23.2	24.2
Future social activity	6.4	9.0
Sport/leisure	8.6	6.7
Culture (art, music, etc.)	4.6	4.7
Politics, religion, ethics	3.1	4.1
Academic-related matters	19.0	10.1
Sample size	453	614

[a] Based on conversations sampled from 19 groups; the topic of conservation was determined at 30-sec intervals (for details, see Dunbar & Duncan, in preparation).

Table 5. *Human interactional group sizes*

Type of group	Mean group size	Source
Freely interacting groups[a]	2.7	Coleman (1964)
Subcommittees (U.S. Congress)	7.1	James (1952)
State and city board committees	5.5	James (1952)
Business corporation boards	5.3	James (1952)
Restaurant reservations	3.8	Cohen (1971)

[a] Individuals recorded interacting in groups (solitary individuals excluded) at the public beach picnic area in Portland (Oregon) in censuses carried out by James (1953).

number of interactants that can be simultaneously reached during a social interaction. In social grooming, this is necessarily only one, because grooming is exclusively a one-to-one interaction. Language would thus need to allow proportionately as many individuals to be interacted with at the same time as is necessary to raise the size of nonhuman primate groups up to that predicted for modern humans.

The observed mean group size for chimpanzees (presumably the closest approximation to the ancestral condition for the hominid lineage) is 53.5 (Dunbar 1992a). The predicted size of 147.8 for human groups implies that language (the human-bonding mechanism) ought to be 147.8/53.5 = 2.76 times as efficient as social grooming (the nonhuman primate bonding mechanism). (The figure would be 2.27 if we used the neocortex-predicted group size of 65.2 given in Table 3 for chimpanzees.) In terms of the argument outlined here, this means that a speaker should be able to interact with 2.8 times as many other individuals as a groomer can. Since the number of grooming partners is necessarily limited to one, this means that the limit on the number of listeners should be about 2.8. In other words, human conversational group sizes should be limited to about 3.8 in size (one speaker plus 2.8 listeners).

Table 5 summarises data on small group sizes from a number of studies. Cohen (1971), for example, took a census of group sizes from the reservations book for Novak's Restaurant in Brookline (Mass.) over a 98-day period in 1968. Although the distribution was double peaked (with near equal modes at 2 and 4, as might be expected), the mean size of 3,070 groups was 3.8. (If groups of less than three people were excluded on the grounds that they have concerns other than social interaction, then the mean of 2,020 groups is 4.8, but the modal group size is just 4 with a highly skewed distribution.) James (1952) collated information on the size of committees in a number of national and local government institutions as well as four business corporations in the United States: mean size varied from 4.7 to 7.8, with distributions that were highly skewed toward the low end. In a study of freely forming groups in Portland (Oregon), James (1953) found a mean group size of 2.7 (solitary individuals excluded) on a public beach area. Group sizes were slightly smaller, but comparable, in a variety of other social contexts (shopping precincts, open streets, bus depots, school playgrounds).

The most direct evidence, however, comes from a study of conversational group sizes carried out in a university refectory. Dunbar and Duncan (in preparation) took a census of conversational cliques that formed freely within interacting groups varying in size from 2 to 10 individuals. They found that the average number of people directly involved in a conversation (as speaker or attentive listener) reached an asymptotic value of about 3.4 (one speaker plus 2.4 listeners) and that groups tended to partition into new conversational cliques at multiples of about four individuals (Fig. 4).

It turns out that there is a psychophysical limit on the size of conversation groups. Because of the rate at which speech attenuates with the distance between speaker and hearer under normal ambient noise levels, there is a limit on the number of individuals that can effectively take part in a conversation. Sommer (1961), for example, found that a nose-to-nose distance of 1.7 m was the upper limit for comfortable conversation in dyadic groups; this would yield a maximum conversational group size of five individuals with a shoulder-to-shoulder spacing of 0.5 m between adjacent individuals standing around the circumference of a circle.

Theoretical and empirical studies of signal-attenuation rates suggest that as the circle of interactants expands with increasing group size, the distances between speaker and listeners across the circle rapidly become too large for conversations to be heard (Beranek 1954; Cohen 1971; Webster 1965). In addition, Webster (1965) found that a doubling of the distance between speaker and hearer reduces by about 6 db the level of background noise that can be tolerated for any given criterion of speech recognition accuracy, with the reduction proportionately greater for those with lighter voices (e.g., women). Cohen's (1971) analyses of these results suggested that at background noise levels typical of both offices and city streets, conversational groups would be limited to a maximum of seven individuals if they maintained a spacing distance of about 0.5 m apart even when they spoke with raised voices; groups of five would be the limit with normal voice levels.

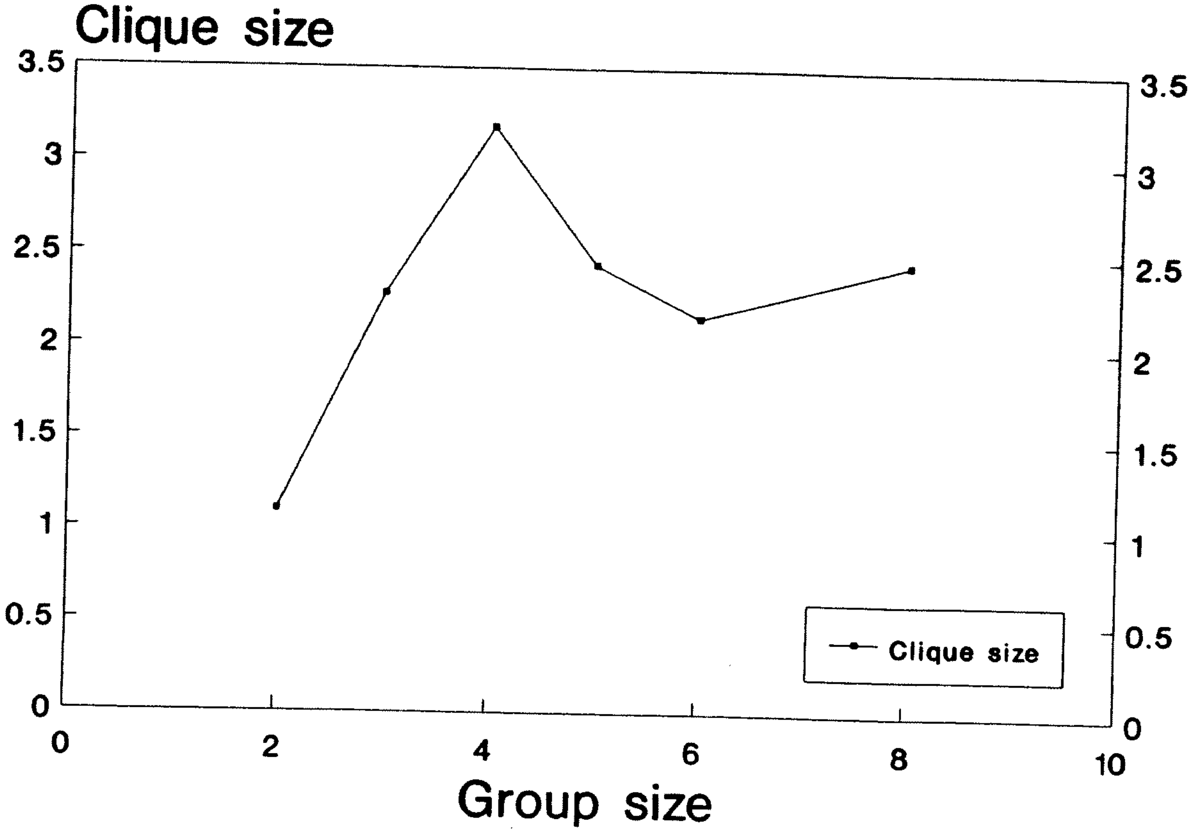

Figure 4. Mean size of conversational cliques (speaker plus attentive listeners) in groups of different size in a university refectory. The clique size census was taken at 15-min intervals (*source:* Dunbar & Duncan, in preparation).

Although background noise levels in natural environments are unlikely to approach those found on busy city streets, comparably high noise levels are commonly found in large interacting human groups. Legget and Northwood (1960) measured maximum noise levels at cocktail parties of 120–640 people (including a coffee party for librarians!); they found noise levels that were typically in the region 80–85 db in the mature stages of these parties. This is considerably in excess of the noise levels recorded in city streets and only just below the level sufficient to induce hearing impairment. At such levels speech recognition is close to zero, conversation becomes impossible, and maximum group size approaches one (see Cohen 1971, Fig. 7.1). Such noise levels may not be untypical of the periodic ritual social gatherings of traditional societies at which relationships are renewed and social gossip about third parties exchanged.

In summary, these results suggest that conversation does meet the requirements of a more efficient bonding mechanism and that it does so at about the level relative to social grooming that is required to facilitate an increase in group size from those observed in nonhuman primates. Moreover, the psychophysical properties of human speech provide some evidence to suggest that they are correlated with these demographic characteristics of human groups.

4. Discussion

My argument has been that there is a cognitive limit to the number of individuals with whom any one person can maintain stable relationships, that this limit is a direct function of relative neocortical size, and that this in turn limits group size. The predicted group size for humans is relatively large (compared to those for nonhuman primates) and is close to the observed sizes of certain rather distinctive groups found in contemporary and historical human societies. These are invariably groups that depend on extensive personal knowledge based on face-to-face interaction for their stability and coherence through time. I argued that the need to increase group size at some point during the course of human evolution precipitated the evolution of language because a more efficient process was required for servicing these relationships than was possible with the conventional nonhuman primate bonding mechanism (i.e., social grooming). These arguments appear to mesh well with the social intelligence hypothesis for the evolution of brain size and cognitive skills in primates.

Three points should be noted. The first is that there is no obligation for particular human societies to live in groups of the predicted size: The suggestion here is simply that there is an upper limit on the size of group that can be maintained by direct personal contact. This limit reflects demands made on the ancestral human populations at some point in their past history. Once neocortical size has evolved, other factors may of course dictate the need for smaller groups. Precisely this effect seems to occur in gibbons and orangutans: in both cases, neocortical size predicts groups substantially larger than those observed for these species, but ecological factors apparently dictate smaller groups (Wrangham 1979). Thus, the observation that Australian Aboriginal tribes living in the central desert regions lack the larger clanlike groups does not necessarily refute the hypothesis. The marginal habitats occupied by these peoples seem to dictate a foraging strategy based on small, dispersed groups living in very large territories; this almost certainly creates communication problems that preclude the formation of larger social networks. The hypothesis would be invalidated, however, if there were no evidence for clanlike groupings in more productive environments.

(It is worth observing, incidentally, that we might expect the upper limit on group size to depend on the degree of social dispersal. In dispersed societies, individuals will meet less often and will thus be less familiar with each other, so group sizes should be smaller in consequence; in spatially concentrated societies, on the other hand, individuals will see each other more often and group sizes should accordingly be larger.)

The second point is that the limit imposed by neocortical processing capacity applies only to the *number* of individuals with whom a stable interpersonal relationship can be maintained. This in no sense commits us to any particular way of structuring those groups (e.g., via kinship). Although the layers of grouping listed in Table 1 are often based on biological relatedness (involving the successive fission of what are usually termed *segmentary lineages;* see, e.g., Meggitt 1965b) there is no requirement that groups must be organised on genetic principles. Kinship is one dimension of primate society that is relevant to individuals' decisions about whom to group with and it often provides a convenient means of structuring a hierarchically inclusive pattern of grouping (see Dunbar 1988). However, even among nonhuman primates, it is not the only basis on which individuals choose whom to form groups or alliances with (see Cheney 1983). Primate groups are, strictly speaking, coalitions based on common interest, and any number of biological, economic, and social dimensions besides kinship may be relevant in individual cases (see, e.g., de Waal & Luttrell 1986).

Finally, it should be noted that this explanation clearly stands in direct contrast to the conventional wisdom that language developed in the context of hunting, to enable early hominids to communicate about the location of possible prey and to plan coordinated hunting expeditions. Indeed, the explanation for the increase in brain size within the hominid lineage on which my argument is based itself contradicts the conventional wisdom that these large brains evolved to enable humans to hunt or manufacture tools. Others (e.g., Wynn 1988; see also Blumenberg 1983) have already pointed out that the evolution of large brain size within the hominid lineage does not correlate well with the archaeological record for changes in tool construction. The markedly improved tool designs of the Upper Palaeolithic can thus be better interpreted as a consequence rather than a cause of enlarged brain size.

This analysis raises a number of additional questions. (1) At what point during the process of human evolution from the common pongid ancestor did such unusually large groups (and hence language) evolve? (2) How is it that, despite these apparent cognitive constraints on group size, modern human societies are able to form super-large groups (e.g., nation states)? (3) To what extent is language a uniquely novel solution confined to the hominid lineage?

With respect to the first question, the fossil evidence (see Aiello & Dean 1990) suggests that brain size increased exponentially through time within the hominid lineage, being well within the pongid range for the *Australopithecus* species and not showing a marked increase until the appearance of *Homo sapiens.* This suggests that neocortical sizes are unlikely to have been sufficiently large to push the grooming time requirement through the critical threshold at about 25–30% of the time budget until quite late in hominid evolution. Application of equations (1) and (2) to all the fossil hominids for which cranial capacity estimates are available identifies the appearance of archaic *Homo sapiens* at about 250,000 years B.P. as the point at which language most likely evolved (Aiello & Dunbar 1993). (It turns out that neocortex ratio is a simple allometric function of cranial capacity in all primates, including humans, with a very high coefficient of determination, thus allowing us to determine group sizes even for extinct species.) Language would thus have been a rather late evolutionary development. Just why early humans should have found it necessary to evolve such large groups remains uncertain, however, and there is little that can usefully be said to clarify this point at present (for further discussion, see Aiello & Dunbar 1993).

Let me forestall at least one line of criticism at this point by observing that our inability to provide a functional explanation for the evolution of a trait does not invalidate that such a trait has evolved: it merely signals our limited knowledge. Humans clearly have larger group sizes than nonhuman primates, and groups of that size cannot have appeared by magic for no good reason. Whether we can ever provide a functional explanation will ultimately depend on whether we can extract the relevant information from the fossil record. It will also depend, however, on our developing theories of sufficient complexity to allow us to understand the interactions between the various components within what is inevitably a complex socioecological system (Dunbar 1989b; Tooby & DeVore 1987).

The second issue, that contemporary human societies are able to maintain very large groupings indeed (in the order of several hundred million individuals in a modern nation state), evokes two observations. One is that the structure of these super-large groupings is not particularly stable through time, as has repeatedly been demonstrated in history by the eventual collapse of most large empires. The other is that language has two unusual properties that make it possible to form groups that are substantially larger than the 150–200 predicted by neocortical size: it allows us (1) to categorise individuals into types and (2) to instruct other individuals as to how they should behave toward specific types of individuals within society. Thus, we can specify that individuals identified as a class by a particular cue (for example a clerical collar or a sheriff's badge) should be treated in a certain, rather specific, way (e.g., with great deference). Naive individuals will thus know how to respond appropriately to a member of that class on first meeting even though they have never previously encountered that particular individual. This may be especially important in the case of those types of individuals (e.g., royalty, bishops, etc.) that the average citizen does not normally have the opportunity to meet. Later, more intimate interactions may, of course, allow the relationship to be fine-tuned in a more appropriate way, but conventional rules of this kind at least make it possible to avoid the initial risk of souring a potential relationship by inappropriate behaviour at the first meeting.

This ability to categorise individuals into types clearly makes it possible to create very much larger groups than is possible by direct interaction. One need only learn how to behave toward a general type of individual rather than having to learn the nature of each individual relationship. By structuring relationships hierarchically in this way, social groups of very substantial size can in principle be built up. The obvious example is, once again, the hierarchical structuring of military units. Notice that even in this case members of different groups are often given distinctive badges or uniforms to allow them to be identified easily: this applies not only to categories of individuals who are considered to be "important" (e.g., officers) but also to members of different types of unit who are of equivalent status in the hierarchy (e.g., military policemen, marines, different regiments, etc.).

It is significant, however, that larger groupings of this size appear to be much less cohesive than groups that are smaller than the critical limit. Language seems to be a far from perfect medium for acquiring detailed social knowledge about other individuals: secondhand knowledge, it seems, is a poor substitute for the real thing. Indeed, it is conspicuous that when we do want to establish very intense relationships, we tend to do so through the much more primitive medium of physical contact rather than through language. The kind of "mutual mauling" in which we engage under these circumstances bears a striking resemblance to social grooming in other primates – and suffers from all its disadvantages. One study of social grooming in a natural human population, for example, found that 92% of all grooming interactions were dyadic (Sugawara 1984). In this context, it is relevant to note that sociometric studies of "sympathy groups" suggest that we are only able to maintain very intense relationships with 10–12 other individuals at any one time (Buys & Larsen 1979).

The final issue is the purely phylogenetic one of how language might have evolved from the natural communication patterns of primates. Can we identify any features of nonhuman primate vocal communication that could function as a natural precursor for human language? The obvious analogy lies in the contact calls used extensively in many species of anthropoid primates to coordinate spacing between individuals of the same group. Although these calls have traditionally been interpreted as a mechanism for maintaining contact during movement (hence their generic name), it has become clear in recent years that there may be more subtle layers of meaning to these calls. Cheney and Seyfarth (1982), for example, found that vervet monkeys use contact calls to comment on events or situations as they occur. They were able to show experimentally that slight differences in the acoustical form of the calls allow the audience to infer a great deal about the event or situation on which the caller is commenting, even in the complete absence of any visual information.

So far, rather little work has been done on the phonetic structure of primate contact calls. The one exception here has been the gelada, whose vocalisations have been analysed in considerable detail by Richman (1976; 1978; 1987). Richman (1976) found that gelada are able to produce sounds that are similar to the vowel and consonant sounds (notably fricatives, plosives, and nasals as well as sounds articulated in different parts of the vocal tract such as labials, dentals, and velars) that were hitherto thought to be distinctive features of human speech. Furthermore, Richman (1987) has pointed out that the gelada's highly synchronised exchanges of contact calls (see also Richman 1978) have many of the rhythmic and melodic properties of human speech patterns. The conversational nature of these exchanges led Richman (1987) to suggest that gelada use these musical qualities to designate utterance acts so as to permit hearers to parse the sound sequence into smaller units in just the way that humans do when talking. He specifically related this ability to the social context, in particular, the need to resolve the emotional conflicts inherent in many social situations. It is significant that, in the gelada, calling and counter-calling between individuals is closely related to the strength of the relationship between them (see Dunbar 1988, p. 251; Kawai 1979).

At present we do not know whether the acoustic features identified by Richman are unique to the gelada. They might well not be. However, the conversational properties of gelada contact calls (in particular, their use in highly synchronised bouts, often involving intense emotional overtones) do seem to be unusual. It may therefore be significant that gelada live in the largest naturally occurring groups of any nonhuman primate: the average size of their rather loosely structured bands (a high-level grouping within an extended hierarchically organised social system based on a very much smaller stable reproductive unit) is about 110 (see Iwamoto & Dunbar 1983).

Clearly, the gelada have not evolved language in the sense we would use this term of humans, but then neither have they developed the large cohesive groups characteristic of our species. However, it may be that the large groups in which this species sometimes gathers forced the evolution of a supplementary vocal mechanism for servicing relationships in a context where they are already at the limit of available grooming time (see Dunbar 1991; Iwamoto & Dunbar 1983). It is worth noting that this much has been achieved without the need to increase neocortical size: indeed, the gelada have a rather small neocortex compared to their baboon cousins (genus *Papio*), which probably explains the lack of cohesiveness in their larger-scale groups compared to those of the baboons.

This suggests that many of the basic properties of speech and language were already available in the more advanced nonhuman primates. What was required was their close integration and elaboration, and this may have been dependent on a significant increase in neocortical size to provide the necessary computing capacity. My suggestion is that the evolution of this increased capacity arose out of the need to coordinate the large number of interpersonal relationships necessary to maintain the cohesion and stability of larger than normal groups.

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NOTE

1. Alternative forms for equation (2) using least-squares regression or the full catarrhine dataset yield equations that are similar in form, but whose coefficients vary somewhat. Although this affects the absolute values for the grooming time requirement, it does not affect their relative values; hence, the argument itself is unaffected. Equation (2) seems to give a generally better fit to the primate data; in particular, it yields a more accurate prediction of the amount of time devoted to social grooming in the very large groups typical of the gelada. I have preferred to use it here mainly for this reason.

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Behavioural constraints on social communication are not likely to prevent the evolution of large social groups in nonhuman primates

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The central hypothesis in the target article seems to be that social grooming is so important a source of social cohesion in primates that the increasing time that must be devoted to it with rising group size sets upper limits on the group size that can be attained in primates other than humans. Human language allows much larger groupings and was evolved in response to evolutionary pressures for large and complex societies.

The main challenges to this hypothesis I wish to consider are the following:

1. Group size and structure evolve to meet ecological demands; behavioural mechanisms are sufficiently flexible to offer little constraint.
2. The positive correlation between group size and time devoted to grooming is not a direct causal one.
3. Many of the social advantages conferred by language are available through vocalisation in nonhuman primates; the time devoted to social grooming (and close social contact like cuddling) is therefore potentially rather easily adjusted in response to evolutionary pressures.
4. It is impossible to make any simple single estimate of the upper limits of "typical" human social groupings.

The first point needs little amplification. Dunbar recognises that it is the conventional position he is attempting to refute. The issue is important, and the attempt is to be applauded. The final outcome may well be that both positions are partly true. It seems extremely probable that the evolution of human language allowed increased social complexity.

Correlations are notoriously difficult to interpret (point 2). It could be argued that free time allows social grooming and that differences between species reflect (at least in part) increasing free time in larger, highly social species. Positive correlation within a species between the amount of grooming and the likelihood of fission could reflect reduced grooming of individuals with whom social bonds are weakening, rather than an inability to sustain bonding because of time constraints on grooming. Issues of this sort need to be addressed, and there should be extensive consideration of crucial species. I would particularly have welcomed here some comment on the question of whether human societies are not best considered to be "fission-fusion," in so far as they can be compared with other primate societies. If they are "fission-fusion" then the use of Figure 3 to predict human "grooming time allocations" seems inappropriate.

Point 3 is the most important. It now seems likely that some primates are able to distinguish individuals by calls (e.g., *Saimiri*, Biber & Symmes 1991). In addition, kinship groups have common signatures in recruitment screams (*Macaca nemestrina*, Gonzoules & Gonzoules 1990), which would potentially allow distant individuals to decide whether or not to join in a dispute on the basis of a judgement of degree of relatedness to the participants. Here the sort of division of members of a complex society into categories ("my matriline" or "matriline X") that allows humans to cope with very large numbers of different individuals is at least available to nonhuman primates by the use of vocal communication.

Learning of properties of contact calls from the mother (*Macaca fuscata* and *M. mulatta*, Masataka & Fujita 1989) now seems likely. There is thus the potential for the evolution of the elaborate mate, sex, and kin signatures characteristic of complex bird societies (e.g., mynah, Australian magpie).

It could still be said that such distant communication could not substitute for grooming in maintaining bonds and in reconciliation. The essence of the argument, however, is that exactly such substitution has occurred in humans, with an irreducible minimum of grooming and similar behaviour being used alongside language. In addition, vocal interaction in gibbons may provide an example of the predominant use of vocal communication in social interaction in nonhuman primates. Again, comparison with birds is interesting. Australian magpies (Brown & Farnbough 1991) use group and pair singing very extensively but do not allopreen as adults. Here it seems likely that substitution of vocalisation for grooming has indeed occurred.

It thus seems likely that nonhuman primates have available to them at least some ability to exchange information about position in social structure by vocal means, and in the same way to maintain and manipulate social bonds. Probably other mechanisms are available too. It is therefore difficult to see how the time necessary for grooming can act as a rigid constraint on social evolution even in the absence of language.

Finally, a comparison of human and primate social structures using Dunbar's approach is clearly valuable, but it must do more than focus on single estimates of group size. I felt that the grouping chosen as representing the maximum number of interacting individuals (the "coffee party") was not particularly helpful. It ignores exactly the sort of division into subgroupings and the existence of conventions as to what is being communicated that allows for larger rallies and meetings, with simultaneous chanting of slogans (and consequent "bonding").

Independent contrasts analysis of neocortical size and socioecology in primates

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In this commentary I focus on the nature of the relationship between neocortical size and group size. There are two problematic aspects of Dunbar's analysis. First, it assumes that primate genera represent independent data points and it does not control for phylogenetic inertia; generally, we would expect closely related genera to be more similar to each other than to more distant relatives. Such nonindependence is a problem, because the logic of the comparative method depends on the identification of multiple cases of coevolution between character states (e.g., Harvey & Pagel 1991). In the present case, for example, we need to be sure that the statistical association between neocortical size and group size does not arise simply because strepsirhine genera have small neocortices and live in small groups relative to haplorhine genera (effectively $n = 2$ for the regression in Dunbar's Fig. 1). Second, the measure of neocortical size used, the ratio between neocortical size and the size of the rest of the brain or hindbrain, is confounded by overall brain size, itself a function of body size. This is because neocortical size increases with body size more rapidly than does the size of the rest of the brain; it is positively allometric relative to the size of the rest of the brain (Passingham 1982). Thus, large-bodied species will have higher neocortex ratios than small-bodied species. This scaling effect is conceivably due to ecological factors such as terrestriality in large-bodied species requiring larger group sizes. A more conservative procedure, however, that uses a measure uncorrelated with overall brain size, would be preferable. One approach would be to use the residuals from a linear bivariate regression of neocortical size on the size of the rest of the brain. These residuals could then be regressed on the independent variables of interest (e.g., group size). An alternative method, which is slightly simpler and analytically equivalent, would be to include the size of the rest of the brain with the other independent variables in a multivariate regression. It is the latter method I use here.

Recent developments in the comparative method allow the problem of phylogenetic nonindependence to be overcome (e.g., Harvey & Pagel 1991). In particular, Felsenstein (1985) provides a method that uses phylogenetic information to produce standardised contrasts in character states representing independent evolutionary events. These contrasts can then be subjected to correlation and regression analysis. The CAIC computer package, written by and available from Andrew Purvis (Zoology Department, University of Oxford, England), implements a version of this method incorporating modifications suggested by Pagel and Harvey (1988a; 1989), Grafen (1989), and Harvey and Pagel (1991). Like Dunbar, I have been analysing Stephan et al.'s (1981) volumetric brain structure data in relation to socioecological information from the literature, and the following analysis, using the CAIC package, is based on that database (see Barton & Purvis, in press, for further details).

Twenty-nine independent contrasts for neocortical volume, volume of the rest of the brain, body weight, breeding group size, and home range size were derived. The contrasts for neocortical volume were then regressed on those for the other variables using a stepwise procedure. The results, shown in Table 1, indicate a positive association between neocortical size and breeding group size once the size of the rest of the brain is taken into account. Neither body weight nor home range size explain any additional variance, the latter result arguing against cognitive demands of foraging as a selection pressure on neocortical size (for a different result on the hippocampus, see Barton & Purvis, in press). Thus, the central pillar around which Dunbar's arguments are constructed remains intact once phylogeny and allometry are taken into account.

Two aspects of these analyses require further attention. First, various features of the analyses (such as choice of neocortical measure, phylogenetic controls, and regression model) will affect the scaling exponent and hence estimates of "natural" group size in humans. There is no space here to explore this implication, but it would seem to be an important aspect for future consideration. Second, the ubiquity of the association between neocortical size and group size within particular primate taxa should be explored. I have repeated the above analysis for strepsirhines and haplorhines separately; the association is, in fact, present only in the haplorhines, and the strepsirhines as a taxon have significantly smaller neocortices (relative to the size of the rest of the brain). Thus, selection for social intelligence (Byrne & Whiten 1988) may have only got going after the split between these two lineages. [See also Whiten & Byrne: "Tactical Deception in Primates" *BBS* 11(2) 1988.]

Table 1 (Barton). *Stepwise multiple regression analysis of neocortical size in primates*

	Cumulative r^2	Partial *F*	Slope
Rest of brain	0.95	439.1***	+
Group size	0.96	6.9**	+
Home range size		2.1	
Body weight		0.1	

Note: The analysis is based on 29 independent contrasts (*sensu* Harvey & Pagel 1991) for each variable. Volumetric brain data from Stephan et al. (1981); ecological data from Clutton-Brock and Harvey (1977b) and Smuts et al. (1987).
***$p < 0.001$; **$p < 0.01$

Brain expansion: Thoughts on hunting or reckoning kinship – or both?

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What a thought-provoking gambit! It is probably not the final word on the matter of the coevolution of neocortical size and language in the human past, but it certainly represents another positive step in our efforts to understand the circumstances that led to the emergence of those intellectual and linguistic capabilities that separate all modern *Homo sapiens* so dramatically from their nearest nonhuman kin.

I do have a query to which I hope Dunbar can provide an answer. One of the questions that has always made me feel a little uneasy about arguments for the development of human intellect like the ones offered by theorists such as Humphrey (1976), Alexander (1990), and now Dunbar is: If it worked so well for humans why did it not work for other creatures as well? If the explanation has general value, what was the reason it only found its expression in the human line? Surely the ability to recognize and deal with larger immediate groups of both recognized relatives and supporters and opponents must have been just as valuable for other kinds of animals. Why, then, did it have such profound consequences only for the evolving human line?

There is one more observation that most anthropologists would be sure to add. This is that the expansion of the hominid brain from chimpanzeelike size to the nearly three-times-larger human norm took place over a million-year-plus time span, during which humans gradually adopted a form of subsistence behavior that is unique among the primates. This was the addition of regular and systematic hunting to the usual primate attention to gleaning (Brace 1991, pp. 116ff.; in press a).

By the time brain size stopped increasing, perhaps as long as 200,000 years ago, the archaeological record begins to show extensive evidence for the modification of foodstuffs by the application of heat – that is, the beginning of cooking (Brace 1991, pp. 155–57; in press b). Starting at the same time, the restricted regional distribution of particular stylistic elements in the period's stone tools begins to resemble what we now associate with areas characterized by related languages; it is hence hard to resist the suspicion that some approximation to articulate speech as we know it had emerged just at the time that brain expansion came to a halt.

Subsequently all kinds of techniques for food preparation were gradually added. These made it possible to extract nourishment from a spectrum of possible sources that had previously been of no use. The expansion in sheer numbers of human beings that ensued surely has to be related to these innovations. The end result was a creature that gained its sustenance in a most unprimatelike fashion when hunting had attained a major role in human subsistence activities. It is hard to resist feeling there had to be some connection between the selective pressures associated with adopting those unprimatelike approaches to subsistence and the correlated expansion of the hominid brain.

There is another aspect of maintaining structured forms of behavior between groups well below the size of Dunbar's calculation whose members meet only periodically, one that is fully compatible with the nature of the argument he is advancing and that should actually strengthen his case: this is the matter of time. The knowledge of kinship and acquaintance that stretches back for generations is often of vital importance in the nonmodern world. In the folklore of professional ethnology, Australian aborigines were famous for an interest in kinship that seemed quaintly arcane to their postindustrial European-trained observers. Although they should have known better, the anthropologists who studied native Australians always seemed bemused that the first thing two new acquaintances would do was to sit down and discuss kinship together.

Such behavior, however, provides a splendid example of why one might consider kin selection (Alexander 1977, p. 295; Hamilton 1964; Wilson 1975, p. 106) an important selective force behind the development of language. Because Australian bands were held together by bonds of male kinship whereas interband ties were maintained by a web of relationships determined by females who moved away from the natal band at marriage, the network of putative as well as real kinship bound people over long distances in a sparsely inhabited land. But the ability to reckon such relationships often involves tracing back for a number of generations to sort things out. The consequences could be of literally vital importance at times of resource scarcity or the threat of intergroup conflict.

My interjection of the association between brain expansion/linguistic development and Pleistocene subsistence strategies should not be seen as an objection to the explanation that Dunbar has offered. It is not a matter of either/or, because it is just possible that the extraordinary behavioral capabilities and associated anatomical developments that are involved were simultaneously influenced by the effects of selection from more than one source. At the moment it seems unlikely that we can point to any one thing and say "there, that is the sole reason we developed those extraordinary features that made us uniquely human."

Do larger brains mean greater intelligence?

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The striking idea that language originated during human evolution because it allowed gossip – gossip functioning as an efficient bonding mechanism and replacing the more labour-intensive grooming that is used by other primates – follows, in Dunbar's analysis, from the way in which nonhuman primates live in socially cohesive groups. He has shown that there are close relationships between a primate's typical group size and both the time it needs to devote to grooming its friends and the relative volume of its neocortex. Interpretation of this last fact is underpinned by the theory that living in a larger group selects for a larger brain, because this permits greater intelligence, and any increased intelligence benefits an individual's fitness in a complex social milieu: the Machiavellian Intelligence theory.

Dunbar is able to support his chain of argument with a range of interesting and provocative data, but the Machiavellian Intelligence theory remains untested – for good but entirely pragmatic reasons. Problems experienced by the other proposals, suggesting a selective pressure crucial to increases of brain size within the primate line (see Byrne 1994; Wynn 1988), have tended to increase general confidence in a socially grounded explanation. But the fact remains that it is very difficult to assess an animal's social intelligence, making problematic all attempts to relate this to any brain parameter. We cannot yet even claim that having a larger brain gives a primate greater intelligence of any kind.

The closest to an index of intelligence that is available for a wide range of primates is their manipulation of fellow social group members, seen in tactical deception (Byrne & Whiten 1985; 1990; Whiten & Byrne 1988c). These data are opportunistic observations and therefore biased by the amount of study devoted to each species and the observers' principal interests, but they are not "anecdotal" in the pejorative sense of uninformed, casual reports. We have recently attempted to take account of the bias in these data as far as possible by comparing the number of definite records of tactical deception in different functional categories against the null hypothesis that the frequency of reported deception is a function only of the number of field studies conducted on a species (full details are given in Byrne & Whiten 1992). The pattern of reported deception differed significantly from that null expectation, using a chi-squared test. This was shown to be largely because deception is overly common in *Pan* and *Papio* (but not *Macaca* or *Cercopithecus*, often the focus of detailed studies of psychologically relevant behaviour).

Can we correctly predict frequency in using deception by knowing brain size? The individual measures of "how much deception has been reported for a primate taxon more or less than would have been expected," summed to give the chi-square statistic, are a metric and can now be compared with the taxon's mean relative neocortical volume. When this is done, a relationship does emerge (Fig. 1, effect significant on 1-way

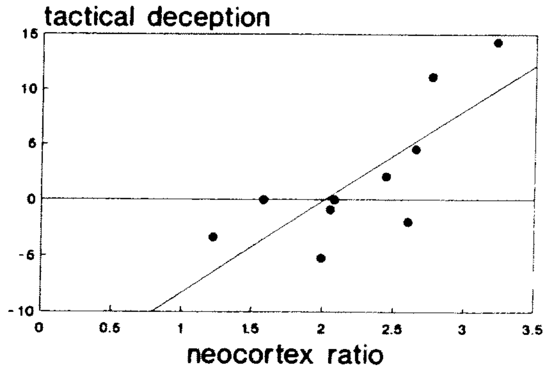

Figure 1 (Byrne). Regression of an index of social manipulation onto the mean neocortex ratio for 10 primate taxa. This index measures the over- or under-reporting of tactical deception, beyond that expected from the number of studies carried out. Neocortex ratios were kindly provided by R. Dunbar (personal communication).

ANOVA, $F(1,8) = 11.89$, $p < 0.009$). The linear regression to predict tactical deception from neocortex ratio is

$$td = -16.5 + 8.16\, nr$$

(where td = number of records of tactical deception observed minus number expected from frequency of studies, squared and divided by number expected; nr = Dunbar's neocortex ratio). Relative neocortical volume explains 60% of the variance in usage of tactical deception. Too much reliance should not be placed on the exact numbers, but it is encouraging that a relationship is present at all with such rough and ready measures.

First, this gives strong support to the belief that larger brains allow more intelligent behaviour – in this case more ready acquisition of socially useful tactics, probably by means of quicker learning. Second, it encourages confidence in the use of Dunbar's neocortex ratio measure for brain size, a measure which is not independent of body size and consequently not insensitive to absolute brain volume. This makes sense, if brains are to some extent "onboard computers," because computers – as approximations to Turing machines – are limited by their number of elements not the weight of their container. Finally, it gives increased confidence that primate tactical deception is partly a product of intelligence.

A gesture in the right direction?

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The Achilles' heel of Dunbar's thesis lies in the following sentence: "The fact that language can be interpreted as fulfilling the same role as social grooming suggests that, rather than being the selective factor driving brain evolution, ecologically related information-exchange might be a subsequent development that capitalised on a window of opportunity created by the availability of a computer with a substantial information-processing capacity." The mixed metaphor may not be too serious, given that computers these days *do* seem to have windows (but not heels). The more substantive problem is that there are powerful reasons, articulated by Pinker and Bloom (1990) among others, for supposing that language is designed precisely for the serial production of propositional communication and cannot be simply a matter of taking advantage of a general-purpose computer that evolved in some other context. Seidenberg and Pettito (1987) also warn against assuming that apes and humans differ simply in cognitive capacity; "the dichotomy between the apes' cognitive and linguistic capacities," they write, "is the single most important finding to have emerged out of modern ape research" (p. 284). In other words it is language, not general intellect, that truly sets us apart.

My guess then is that Dunbar's argument might be more plausible if inverted; the selective pressures for the evolution of language probably had to do with propositional communication, and this secondarily solved the problem of social grooming among large groups. Even granted our propensity for gossip and its role in social cohesion (although this might be disputed these days in royal circles), one is hard pressed to find any structural principles common to grooming and human language; it is a bit like seeking the origins of the eye, often compared to language for its calibration and functional intricacy, in the navel.

I can, however, offer one thought that might be of assistance. I have tried to revive the idea, originated by Condillac (1746/1947) and more recently championed by Hewes (1973), that human language may have originated in manual gestures (Corballis 1991; 1992). I think there are some arguments in addition to those offered by Hewes in support of this idea. One is that it is becoming increasingly clear that manual sign language such as ASL has all of the properties of a natural language (e.g., Poizner et al. 1987), including a critical period in development (Newport 1990). Deaf children exposed only to sign language even go through a "babbling" stage analogous to the vocal babbling of normal infants (Pettito & Marentette 1991).

I have also argued that language may have evolved as a primarily manual system from *Homo habilis* through archaic *H. sapiens*, and that one of the features that distinguished *H. sapiens sapiens* was the switch to a predominantly vocal mode (Corballis 1991; 1992). This switch would have freed the hands from involvement in communication, which may explain why the "explosion" in the manufacture of tools and other artifacts seems to have occurred well after the emergence of *H. sapiens sapiens* as a distinct species (Pfeiffer 1985).

It might be easier to sustain the view that language relates to grooming if it is also supposed that language was initially based on manual gestures.

Grooming and language as cohesion mechanisms: Choosing the right data

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Dunbar's hypothesis combines many sorts of information. I found the idea intuitively attractive, but the evidence was not altogether convincing. I shall limit my comments to two areas.

Is a special cohesion mechanism needed? Dunbar argues that a cohesion mechanism other than grooming was needed by ancestral humans because they associated in very large groups whose integrity and cohesion would have demanded an extraordinarily (and impossibly) large proportion of time spent grooming. This conclusion is based on extrapolation from a linear regression equation relating grooming time to group size in 22 extant primate species. These data were selected from an earlier paper (Dunbar 1991): only catarrhine species living in cohesive groups of stable size were included. But why should the four species with fission-fusion societies be excluded? After all, the human societies included in Table 1 are also characterized by hierarchical fission and fusion: this is why overnight camps can be distinguished from bands or villages. Our concern is behavior that maintains ties within larger social units whose members may meet infrequently. There are roughly analogous units in the excluded nonhuman species. Rather than exclude such species, it seems we should consider them with special interest.

Including these four species affects the relationship between group size and grooming time and hence the predicted grooming time for humans living in groups of 148.7. Although Dunbar acknowledges this fact parenthetically (sect. 3.2), and though his statements are strictly correct, it was not until I manipulated the data myself that I realized how much these four data points influence the picture. First, when they are included, the relationship of grooming time and group size looks more asymptotic than linear, mainly because of the points for species with group sizes greater than 100 (Fig. 1). This change exemplifies the danger of extrapolating beyond the limits of available data. Assuming that maintaining cohesion gets increasingly difficult in larger groups (which seems likely), the full dataset suggests that in very large groups, some behavior other than grooming operates to maintain cohesion. Possible candidates are distance-regulation behavior, monitor-and-adjust behavior (Rowell & Olson 1983), or postconflict reconciliation (de Waal 1989). Some nonhuman primates live in groups considerably larger than

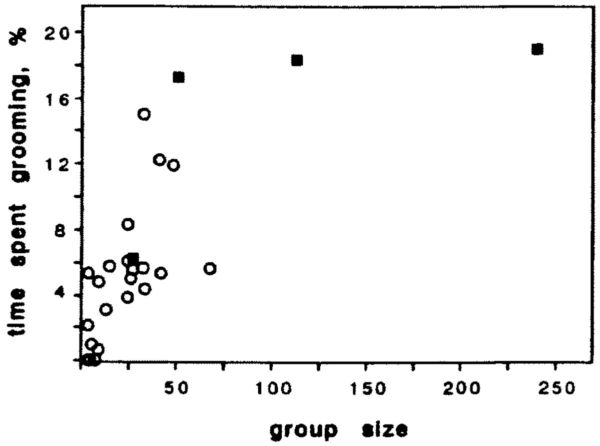

Figure 1 (Cords). Mean percentage of time spent grooming plotted against group size for 26 species of group-living catarrhine primates. Open circles indicate points included by Dunbar in generating equation 2; filled squares indicate the four fission-fusion species originally excluded from that analysis (data from Dunbar 1991).

those predicted for humans. For example, Japanese macaques can maintain cohesive groups of over 1,000 members; these groups are provisioned, however, so feeding time is reduced and more time should be available for social interchange. As far as I know, actual time budgets have not been published for these large groups. Wild Rwandan black and white colobus monkeys have also been reported to live in very large stable groups (up to 350 members, Vedder, personal communication). How these groups maintain cohesion is not yet known, but Vedder reports that neither grooming nor vocalization occurs especially frequently. If alternative mechanisms for maintaining cohesion operate in monkeys and apes, would language be necessary or even advantageous? It seems we should know much more about the alternatives: comparing language to grooming is only part of the task.

Second, if we overlook the apparent nonlinearity of the data (transformations do not improve the fit), the data points from fission-fusion species change the linear regression equations. Specifically, the predicted amount of time that ancestral human groups of 100–200 would spend grooming is *reduced*. Simple least squares regression on the full dataset predicts that humans should spend 16% of their time grooming; the 95% confidence limits on predicted group size yield grooming times of 12–23%. These values mostly fall within the range of those reported for living primates. (Reduced major axis regression gives percentages 2–6 points higher.) Thus even ignoring the possibility of alternative cohesion mechanisms, it is not clear that grooming could not do the job in fairly large groups of early humans.

Finally, we have assumed that early humans had time budgets quite similar to those of extant primates; if cooperative foraging or tool use improved efficiency, however, early humans might have had more time available for social grooming than most nonhuman primates have now, even if total energy requirements were greater because of their relatively large body size: who knows? Pinpointing the maximal amount of time that could be spent grooming seems a rather speculative exercise.

Language as a bonding mechanism. The theoretical argument that language is better than grooming for maintaining group cohesion because it allows the acquisition of information about group-mates not present and the classification of types of group-mates is persuasive. The data supporting the role of language in maintaining group cohesion, however, are not very convincing. First, I question whether conversations in a university refectory are representative of all conversations. Second, I find it hard to judge the proportion of time spent gossiping as being high without having some expectation of what it should be. What is the null expectation for the distribution of conversation across possible topics? Finally, even if language did evolve to allow gossip, language may not be used today for the same purpose; the hypothesis implies only that language could have been or can be used for this purpose. Thus the data on content of refectory conversations seem relevant only insofar as they show that social relationships are a possible subject. This "finding" is consistent with the hypothesis, but it certainly does not "imply" that the hypothesis is correct.

A further argument for language's suitability as a cohesion mechanism relates to its efficiency with respect to grooming. Dunbar limits the concept of efficiency to the number of interactants that can be reached in social exchange. Perhaps, however, we also need to consider how they are reached. Can we assume that one would learn as much about each of the three people in a conversation group as one would about a single grooming partner? Would one learn equal amounts in equal periods of one-on-one conversation and grooming? The idea of efficiency is vague because the information transmitted through social interchange has not been specified. That is, we do not really understand how social interchange maintains group cohesion. If Dunbar's hypothesis stimulates research directed at this question, it will have served an important purpose beyond the presentation of a new and interesting idea.

Confounded correlations, again

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In the last decade alone dozens of papers have endeavored to demonstrate that brain size (or the size of some brain structure) is correlated with some important socioecological variable (such as social structure, home range size, foraging strategy, diet, day journey, group size, etc.). It is presumed that discovering such a correlation will answer the question: What selects for increased brain size? I happen to think this is a misguided question. Dunbar (1992a) carefully debunks many previous claims for correlations between brain size, body size, encephalization, and various ecological variables, but at the same time he suggests another correlation: between relative neocortical volume (either total neocortical volume or else the ratio of neocortex to the rest of the brain) and social group size. His target article further extrapolates from this claim to suggest explanations for human brain evolution, social structure, and the origins of language.

Dunbar makes four principal claims:

1. Group size is a function of relative neocortical size in nonhuman primates.
2. Extrapolation from this regression trend predicts group size in traditional human societies.
3. Social grooming is a function of social group size in primates because it functions to maintain group cohesion by decreasing agonistic interactions that might otherwise split the group.
4. Language evolved as a more efficient means than grooming of maintaining group cohesion, thus allowing larger mean group sizes.

Together they lead to the principal hypothesis: our large neocortex ratio accurately predicts large group sizes in human societies, because the neocortex expanded to meet the information demands of the increased social interactions provided as language replaced grooming as a buffering mechanism.

The first claim is the starting point for all subsequent extrapolations and so its weaknesses ramify throughout the remaining arguments. Despite much care taken to test and control for the confounding effects of other correlates, the apparent correlation between neocortex ratio and group size in primates is not without methodological problems. Dunbar (1992a) compares a number of neocortical size statistics for their degree of correlation with group size in primate genera and finds that neocortex ratio provides the highest value ($r^2 = 0.764$), just edging out the correlations with neocortex/hindbrain ratio and neocortical volume. However, another test in that same paper controls for the contribution of gross size by regressing group size on the residual of neocortex with respect to body mass – producing an essentially null relationship ($r^2 = 0.003$) – and it controls for the effect of brain size by regressing group size in the residual of neocortex with respect to the rest of the brain – producing a weak but significant correlation ($r^2 = 0.286$; see Table 2, Dunbar 1992a). These residual correlations are tiny because neocortical size is strongly correlated with brain size minus neocortex ($r^2 = 0.974$, also in Dunbar 1992a, Table 2). Controlling for the effects of both body and brain size essentially eliminates any correlation. Dunbar's trick of using the ratio of the neocortex to the rest of the brain (a neocortical version of encephalization that controls for part/whole bias) inadvertently smuggles these confounding correlations into a dimensionless statistic, and the effect is not controlled for (the ratio further introduces a troublesome nonlinearity with unequal distribution of variance). A regression analysis of log neocortex ratio against log brain size in anthropoids (from the same original data source) shows that this ratio is indeed highly correlated with brain size ($r^2 = 0.843$); bigger brains have proportionately more neocortex. Subtracting the brain size effect from neocortex ratio leaves a residual that is as uncorrelated with behavioral ecology statistics as those Dunbar has already rejected.

The second claim appears to depend on a creative interpretation of group size data from human societies. Not being an expert in this field, I can only voice doubts about a selection criterion that assumes what it sets out to demonstrate and then searches through heterogeneous data to find a match. What is achieved by ignoring the variability and hierarchical complexity of human as compared with primate data? If the intent is to identify the unit that best approximates what is meant by "troop" in the primate behavior literature, I see no way of avoiding getting involved in arguments about criteria and definitions, as Dunbar hopes. On the one hand I find it quite plausible that what Dunbar describes as the "overnight camp" unit could be homologous with "troop." It is a foraging-feeding unit, a predator defense unit, to some extent a reproductive unit, a unit of mobility – perhaps the largest unit that can move from place to place cohesively – and it falls within a group size that is similar to many mid- to large body size social primates, including chimpanzees. On the other hand, who can doubt that language is a major factor in determining the incredible size ranges and hierarchical diversity of group structure in different human societies. The social anthropological literature offers a massive testament to the complex ways that kinship terms, myths, totemic symbols, mores, ceremonies, and so on (not to mention simple conversation) all play pivotal roles in defining and binding together large groups of people into nested corporate units that can grow to immense size. Dunbar concludes that the "true" unit of human group size is in between. I cannot help but conclude that the effects of language and material culture are the primary reasons for there *not* being any single human analogue to primate troop size.

The third claim is that grooming behaviors help maintain large group sizes by creating "friendships" that buffer potentially disruptive agonistic encounters. Observational evidence shows an expected increase with group size. Selection for increased group size may be driven by resource or predator defense needs, and this would, in turn, favor more extensive use of social mechanisms that help maintain larger groups by limiting the probability of potentially divisive interactions. But grooming is only one of many mechanisms. Vocalizations and postural-gestural signaling of arousal state, behavioral intention, or social status are also crucial mechanisms for maintaining stable group structure, and should also scale with respect to group size, for similar reasons. It is peculiar that these have been ignored, particularly since they seem the more obvious analogues for language.

The fourth claim is yet another in a long line of reverse logic, "just-so" stories about language evolution of the form: "Language makes *X* more efficient, therefore selection for *X* explains the origins of language." Substitute your favorite fashionable *X* from a large range of possible alternatives (more efficient foraging, better transmission of past experience to offspring, stronger social cohesion for intergroup competition, more subtle and devious social-sexual manipulation, closer bonds between kin and sexual partners, etc.). In fact, substitute "more efficient communication" for language and the argument remains the same. The generic quality of this argument excludes few alternatives and offers little in the way of explanation for the remarkable structural complexity and semiotic uniqueness of language as compared with other forms of communication. It should be pointed out that humans still groom one another in close affiliative relationships and use a wide range of other innate and learned gestural and vocal signals in addition to the use of language. Language may have assumed some of the social buffering functions of these other communicative behaviors, but its complementary role suggests it does something else that may be far more relevant to its unique evolution.

There is almost certainly some link between human brain size, disproportionate neocortical size, and the evolution of language, but I doubt it is to be found reflected in simple brain-ecology relationships. The error may be in assuming that human brain-language evolution is merely an extrapolation of some general evolutionary trend – an idea that a great many evolutionary theorists seem committed to. But what if it is not? Language is unique. What if it is the result of unique selection pressures? There may be no general trend out there from which to extrapolate. What then? Such fishing expeditions into brain size-socioecology statistics will have provided a valuable contribution even if they only serve to show that there are no fish to be had. Maybe phrasing the questions in terms of brain size, intelligence, and more efficient communication fails to carve the problem at the joints, so to speak. But to rephrase these questions we must contend with neurobiological and linguistic issues that brain-ecology statistics fail to address.

Vocal grooming: Man the schmoozer

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Dunbar's multifaceted model for the origin of language seems more reasonable at first glance than either of the two cited alternatives: it is hard to account for human neocortical size by selection for coordinated male hunting alone; and, few archeologists are now ready to say that the stone tool record provides strong support for an association between more complex tools and the increase in brain size seen in Middle Pleistocene *Homo sapiens*. In this light, Dunbar's hypothesis relating the origin of language to an increase in the potential overall number of interpersonal relationships seems preferable. Upon further consideration, however, it appears that there is no way to document the event or test the claimed model of causality.

The observed correlation between the rapid increase in human brain size and the large number of interpersonal relationships we maintain is intriguing. It may be that language had a crucial role in "allowing" group size to increase. Dunbar makes the stronger argument that the "need to increase group size at some point during human evolution" was the deciding factor in the origin of language. Whose or what need was this? Was there a particular environment that shaped this demand? On the evidence, how can we test this hypothesis? Dunbar's resort to the sociobiologist's tack of "ultimate causality" does not add to his hypothesis' rigor.

A similar extrapolation from observed correlation to causal explanation has guided many interpretations of primate social structure. The observation of sexual dimorphism in a primate population has traditionally been claimed as evidence of a polygynous social structure (Fleagle & Kay 1985; Kay et al. 1988). It was assumed that the process of sexual selection resulting in Irish elks and saber-toothed cats was at work universally. This correlation has been contradicted in several primate species (Plavcan & van Schaik 1992); patch size and graininess seem to be more useful predictors of social structure (Dean 1992).

Several passages that required similar leaps of faith gave me pause. Why should one assume a causal relationship between group size and neocortical size? Are differential brain structure and function mitigating factors? The existence of the large-brained but solitary orang refutes the posited relationship between group size and ecological factors as well as Dunbar's use of the reversal for prediction. Jumping from chimps to hunter-gatherers to military units to businesses, and so on, seems more like an exercise to fit the data to a preconceived model than an attempt to identify the physical and social constraints behind the "150 club" ceiling. Are there specific constraints on group size that language releases? Are Hutterite informant claims that peer pressure cannot be exerted in larger communities explanatory? Is it not just as likely a rationalization for the strains their culture, technology, and lifestyle put on larger communities?

A major portion of Dunbar's model involves the causal relationship claimed between "vocal grooming" and social cohesion. Nonhuman primate grooming clearly serves to release tension between troop members. Dunbar has carefully documented the correlation between nonhuman primate group size and time spent grooming. Assuming the causes are analogous, Dunbar presents observations that much of linguistic communication consists of gossip and other "stress-releasing" topics. That gossip may in some contexts be analogous to grooming is not the issue. Does gossip as a behavior maintain group cohesion, stability, and account for the origin of language, even indirectly? It seems the role of deception, currently a focus of many behavioral studies, especially avian and mammalian ones, has not been considered (Mitchell & Thompson 1986). While deception can occur in parallel with tactile grooming, the actual grooming act can incorporate little. Gossip does allow for the collection of information on individuals with whom the gossips may not come into contact. Much of the time this information is wrong, sometimes intentionally, possibly leading to violent misunderstanding. Is this the adaptation on which society rests?

Does gossip form the glue of social systems, providing another vehicle for Rousseau's social contract? As has been illustrated in every manifestation of the police state, vocal contact can devolve to pure suspicion. Foucault's discussion of the transition from the more brutal yet tactile forms of corporal justice, rarely involving incarceration, to the "Panopticon" prison model is relevant here (Poster 1984). Now aided by closed-circuit television, the nineteenth-century Panopticon prison architecture allows for one guard to watch all prisoners in a cell block with them unable to see him. In a similar way, all significant traces of our behavior, for example, credit card purchases, personal finances, magazine subscriptions, job and loan applications, criminal records, organization memberships, marriage records, electronic mail, and so on, are susceptible to invisible computer tracking. In situations of decreasing job security we have reason to be suspicious of the large numbers of people with whom we interact daily. Worry about saying too much is a tension-builder. In situations where we need to talk yet say nothing, perhaps most of what Dunbar would classify as stress-releasing endearment is simply white noise.

Perhaps Dunbar has been right in identifying a key limiting factor in human cognition and brain size, the ability to *track* interpersonal relationships. This clearly requires a certain number of well-wired neurons combined with the means and time to interface with colleagues. An interesting question arises in relation to the current increase in use of electronic communications. With greater potential membership, will there be a "natural" size-limit to the "virtual communities" that form via electronic mail? This medium allows one to interact with a far more diverse and potentially powerful group of people than through local vocal grooming.

On this point, Dunbar suggests it is the size of the networks to which we can connect, not the number of networks, that limits group size. This assumes that each parallel network must be self-sufficient. From fission-fusion social organization to virtual communities, it would seem that individuals can be successful given an environment with enough perceived and acted-on opportunities. The size and coherence of the network providing the opportunity is of little importance to the individual making gain from it.

Do grooming and speech really serve homologous functions?

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I have cited Dunbar's research in my own work (Donald 1991; see multiple book review of Donald's *Origins of the Modern Mind, BBS*, this issue) because he has constructed a provocative argument that language supports essentially the same core social functions in a wide variety of human cultures, from hunter-gatherers to postindustrial societies. Moreover, he has shown an intriguing correlation between brain expansion and group size in primates, which suggests that primates needed increasingly large brains to cope with the demands imposed by servicing more and more individual relationships. These are two fascinating results that deserve our attention. The question is: Are these two observations related?

Dunbar's main empirical link between these two observations lies in his extrapolation of the encephalization quotient (EQ)-group size regression line to humans and his data on the ubiquity of human conversational "grooming." The underlying reasoning appears to be: (1) human groups are just about the right size for our brains, according to his regression equations; (2) but human group size is so large that even with better brains the grooming time required to service so many relationships would have become unsustainable; (3) therefore humans evolved language to manage efficiently the more complex social bonding needed to sustain larger groups; and (4) the memory limitations on basic human group size have not changed, despite the superimposition of much higher levels of social organization following the agricultural revolution nor have the core social functions of spoken language.

This is a tempting theoretical package, despite the rather tenuous link between his primate and human studies. But there are feasible alternatives to Dunbar's interpretation of his data. One attractive alternative is that language evolved for multiple reasons, only one of which might have been social grooming. Other areas in which language had obvious immediate adaptive value might be: coordinated fighting and hunting, food classification, pedagogy, forming functional hierarchies, giving humans a newfound independence of the environment, integrative thought, and so on. Assuming that all of these functions were probably being supported concurrently by language capacity as it evolved, one would expect a thorough sample of conversational exchanges to reflect all the sorts of information that support these multiple functions, rather than focusing so much on personal information.

A thorough (comprehensive and representative) sampling of human conversational exchanges should cut across *all* of the putative applications for which spoken language might have evolved. However, a look at Dunbar's sampling methods is not reassuring on this score; for example, in one of his studies he sampled conversations in a university refectory, one of the few places where modern humans do indeed tend to talk more about personal relationships than anything else. I realize the problems involved in trying to find a good homologue to use as a "natural" human conversational setting in modern culture, but I wonder whether a broader sample would really continue to support Dunbar's hypothesis. Moreover, even if we dismiss the sampling problem, there is a further question about the way he determined the categories of his subjects' conversations: making category judgments on recorded conversations is somewhat subjective, and the same snippet of conversation might fall into more than one category.

The other link, the extrapolated correlation between EQ and group size, is open to obvious criticisms, all of which Dunbar has acknowledged. Undoubtedly his biggest problem was in choosing what level of organization in modern human society might be comparable to primate groups. His selection of army company size was very clever, and undoubtedly revealing; but of course armies lack most of the interpersonal dimensions of kinship groups. They have a very different age and gender balance, they lack a nuclear, or even extended family structure, they have a much more focused social hierarchy, and so on. I would expect the memory load imposed by social grooming in such a group to be much less than in a self-complete tribal group of the same size.

In conclusion, I find it difficult to accept the argument for extending an essentially similar theoretical framework from Dunbar's primate data to his human data. However, I think both these datasets are very interesting in themselves and are sure to generate more research into the important questions Dunbar has raised.

Language and levels of selection

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One of the most exciting recent trends in the social sciences is the breaking down of the walls separating evolutionary biology, cultural anthropology, and social psychology (Barkow et al. 1992; Boyd & Richerson 1985). Although the roads connecting these disciplines were, until recently, laden with landmines (set by all factions), it now appears that something of a demilitarized zone exists that is safe for travel. We applaud Dunbar for walking this perilous path.

Any attempt at generating hypotheses about the coevolution of neocortical size, group size, and the evolution of language is bound to draw criticism from experts in evolutionary biology, anthropology, and social psychology and no doubt Dunbar's target article will receive its share of such criticism. Here, however, we focus on a related issue raised by Dunbar, namely, the role of between-group selection and the "social bookkeeping" effect of language.

We begin our discussion of Dunbar's arguments at the point at which the physiological and anatomical structures needed for language exist; we will try to examine what evolutionary forces select for language as a replacement for social grooming. Our discussion focuses not on the evolution of language per se but on the function of language as a mechanism for keeping track of the actions (and intentions?) of many other group members. It must almost certainly be true that language allows individuals the ability to keep track of other group members in a somewhat efficient manner. As such, language allows you to know whom you can trust and whom you cannot. At the same time, however, language provides "cheaters" with a new, very efficient mechanism for deceiving others. Cheaters now not only have the opportunity to deceive many individuals at once but also to use gossip and rumors to further their goals (whatever they may be). It may in fact be the case that cheaters prosper when a certain level of anarchy, generated by their own actions, exists. Thus, although it is true that language has the potential to unite a group and increase its overall productivity, it also provides cheats with a means for intentionally impeding such a process for their own benefit. It is therefore possible that within a group language (as a social bookkeeping mechanism) favors cheaters, but that language is favored as a mechanism for producing "well-oiled" machines at the between-group level. Thus the ability of language to create honest bookkeeping within social groups may be a balance between within- and between-group selection.

The hypothesis that selection favors the social bookkeeping effect of language at the between-group level is not strictly semantic, as it generates at least two testable hypotheses. The first and most obvious is that between-group competition played a major role in Pleistocene times, and that groups acting in a coordinated fashion (because of the accurate bookkeeping of social interactions) were typically the winners in such competition. If the confusion, gossip, and anarchy caused by cheaters' use of language increased the probability of group disintegration, or a general decrease in group size, between-group selection would act against it. If this proves to be the case, then in addition to providing evidence that between-group selection favored the social bookkeeping effect of language, this hypothesis may provide some insight into what the initial selective force favoring large groups was in the first place (a point that Dunbar admits is not at all addressed by his hypotheses). For example, large group size may have been favored because of between-group competition for scarce resources. Second, if between-group selection is important, we would expect group-level rules to deal with cheaters who use language to deceive others and create group-level anarchy. [See Caporael et al.: "Selfishness Examined" *BBS* 12(4) 1989.] The Hutterites, as Dunbar notes, have just such a set of rules for dealing with cheaters (see also Wilson 1989). Whether such group-level rules suppressing cheating exist in all cultures is not yet known, but should they be, it would probably not be very surprising to many cultural anthropologists.

Mosaic evolution of the neocortex

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A conclusion of the target article is that the enlarged human neocortex evolved primarily to keep track of multiple social relationships in increasingly enlarged social groups. Although we agree with Dunbar's emphasis on language (see below), it is important to recognize that the neocortex has multiple functions. Below, we discuss some of the partitions and functions of the neocortex, reviewing relevant comparative and paleoneurological data.

The importance of "neocortex ratio" as an explanatory variable depends on its appropriateness as a scalar in an allometric system. The target article's focus on neocortex ratio is surprising, especially in light of the acknowledgment that "it turns out that neocortex ratio is a simple allometric function of cranial capacity in all primates, including humans." For this reason, the statement that neocortex ratio for humans is "about 30% larger than the maximum value for any other primate species" may be misleading. In fact, human relative neocortical size is unremarkable, that is, the amount of human neocortex is what would be expected for an ape brain of equivalent size (Passingham 1975). The use of ratios creates additional scaling issues and apparently, the reason for using neocortex ratio is that it provides the "best fit" with group size. The conclusion of such a strong relationship based on this *post hoc* rationale may yield a Type I error. We also analyzed the same dataset as in Stephan et al. (1981) and the Dunbar (1992a) data on group size, and found (as suggested in the target article) that brain weight, whole brain volume, neocortical volume, volume of brain other than neocortex, body weight (log transforms of each) and the ratio of log neocortical volume to log of other brain volume all predict log of group size. The "worst" predictor of this group was body weight ($r = .59$). The brain indices are all highly correlated with each other, and with body size, producing great difficulty in concluding causal directionality. We found that the log of "neocortex ratio" accounted for only 14% of the variance in log group size, after log body weight and log total brain volume were partialed out (squared semipartial correlation), a far cry from the 76% indicated in the target article. A relationship is nonetheless clearly present in this dataset, but the conclusion of a unique influence of relative neocortical size should at least be based on residuals from an allometrically corrected regression. The simplest conclusion is that larger primates tend to have larger brains and neocortices, and more often live in larger groups. Which is cause, which is effect, and which relationships are spurious are not questions that can be unambiguously answered from this dataset. Unfortunately, neocortex data for *Pongo* were apparently unavailable. One wonders what decrement in the correlation would be produced by including data for this solitary, large-brained ape. Extending the analysis to more species is therefore crucial.

Thus, although some debate can occur about the correct way of scaling neocortical size, Dunbar has demonstrated that a relationship with social group size is clearly present in primates. An outstanding finding regarding human neocortex is that it is three times the predicted size for an ape of equivalent *body size* (Passingham 1973), although it is precisely scaled for the relevant *brain size*. But what does this neocortex do, and did it enlarge uniformly or did different parts increase at different times? The recognition of familiar faces and the association of those faces with specific biographical information and names appear to be functions of three separate parts of the temporal lobes in humans (Szpir 1992). Association cortices of the frontal lobes, on the other hand, are important for facilitating tactile and verbal "grooming" (i.e., speech). Various lines of evidence suggest that frontal and temporal neocortices evolved at different times during hominid evolution (an example of mosaic evolution). For example, the Taung (*Australopithecus africanus*) endocast has already achieved summed lengths of temporal lobe sulci that are comparable to the human condition once allometric scaling is taken into account. However, the summed sulcal lengths in the frontal lobe of Taung relative to humans is below the prediction from humans (Falk et al. 1989). It therefore appears that frontal but not temporal neocortices expanded relatively late during hominid evolution. These findings agree with those based on comparative gyrification indices across a series of primates (Armstrong et al. 1991; Zilles et al. 1989) and with Passingham's (1973) comparative study regarding frontal association cortex.

From the above it is clear that the hominid neocortex did not evolve uniformly and that expanded prefrontal association cortices first appeared in early *Homo*. In keeping with this, the oldest known humanlike frontal lobe sulcal pattern is reproduced on an endocast from KNM-ER 1470, an approximately two-million-year-old *Homo habilis* specimen (Falk 1983). This pattern is on the left side of this specimen and appears similar to Broca's speech area in modern humans. From this, as well as from archaeological evidence related to handedness (Toth 1985), one may surmise that early Homo had at least the beginnings of speech, although brain size would not reach its modern capacity for another two million years (Falk 1983; 1992a; Tobias 1981).

We agree with Dunbar's assessment that language was an important factor during hominid brain evolution, that language is a social phenomenon, and that humans use language to "groom" each other. However, language is used to impart and absorb all kinds of information, in addition to the social. "Social intelligence" per se may not have driven hominid brain evolution for a variety of reasons. Nonhuman primates are highly social animals even though their neocortices are one-third the size of those of humans after allometric correction. Although monkeys have temporal lobe neocortices that permit them to recognize faces and voices of specific individuals, they lack the neocortical expansion and organization required for language. In short, evidence from paleoneurology, comparative neurology, and psychology converges on the hypothesis that if there was a prime mover of hominid brain evolution, it was language, with all of the cognitive benefits it entails (Falk 1992a; 1992b).

Ecological and social variance and the evolution of increased neocortical size

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A paper as stimulating and challenging as this demands two alternative responses. One is to take a fine-tooth comb through the data and the statistics and thus hope to dismantle the edifice that has been built. The other is to adopt a position of creative credulity and to explore some implications of the relationships proposed by Dunbar. I shall pursue the latter strategy.

Here and elsewhere (1992a) Dunbar has provided the first quantitative basis for the proposed relationship between social complexity and levels of intelligence (Humphrey 1976). In contrast, an equivalent relationship has been proposed between relative brain size (as a measure of intelligence) and dietary quality (as an outcome of ecological conditions) (Clutton-Brock & Harvey 1980; Foley & Lee 1991; Gibson 1986; Milton 1988). The triangle of relationships – brains, social complexity, and ecological conditions – is completed by pointing out that it is generally accepted that the structure of ecological resources influences social organisation and indeed is a strong factor in determining group size (Dunbar 1988; Wrangham 1979; 1980).

Although Dunbar has explored one side of the triangle, other relationships may be of considerable significance, for as things stand in Dunbar's model the evolution of larger group size, and by implication the evolution of language, appears to be an internally generated and almost directed evolutionary pattern. What is needed is a better understanding of the ecological conditions under which group size may increase and hence the opportunities to engage in social interactions may expand. This would explain the conditions under which human language may have evolved.

In this context intraspecific variation may be significant, for the implication of Dunbar's model is that those individuals who can best cope with the problems of larger groups will have a higher reproductive success; among humans, this would involve some increased capacity for social bonding through vocalisation. Among *Papio* baboons group size varies from a lower limit of 19 to a maximum observed of 247 (Dunbar 1992b). In that paper Dunbar himself shows that the maximum ecologically sustainable group size is dependent upon overall primary productivity – larger groups occur where resources are more abundant. The same is true of chimpanzees (*Pan troglodytes*). Community size varies from less than 30 at Mount Assirik and Bossou to between 80 and 90 at Budongo. Overall community size increases with increased productivity when measured through lessened seasonality in rainfall patterns (Foley 1993).

Where social groups are already large, therefore, further increases will tend to occur where resources are abundant, stable, predictable, or easily obtainable. These intraspecific trends imply that the conditions likely to promote the development of language are those involving greater ecological stability and resource predictability. The key link may turn out to be that a reliable and high quality resource base permits higher maternal input and hence more highly encephalised infants (Foley & Lee 1991). This suggests that life history parameters may be crucial in working out the details by which ecological conditions and social evolution are linked. In terms of hominid evolution it might be predicted that human language is most likely to make its appearance (or most rapid development at any rate) under conditions of ecological stability, that these will perhaps occur in the centre rather than on the margins of the species' range, and where climatic change is less effective. This might be consistent with the essentially tropical and African origins of *Homo sapiens* that have been proposed in recent years, and for which an ecological basis has been argued (Foley 1989). These ecological shifts in human evolution can be further used to model changes in social structure and group size (Foley & Lee 1989), which could fit with Dunbar's emphasis on social dynamics as one root to the language tree.

The effect of a change in life history parameters can be relatively simply estimated by the proposal that longevity increased at some point in the course of human evolution, from that of a large hominoid's 40 to 50 years to the more current human 60 and 70 years. Unless balanced by more frequent fissioning, such a change could increase the number of individuals interacting in, for example, a chimpanzee social group by considerably more than 10%, thus rapidly pushing the group beyond the upper limits on grooming time proposed by Dunbar. Life history thus provides another external biological dimension to provide a context for social evolution.

Whether such a shift in longevity is sufficient to take the number up to the magic 147.8 predicted by Dunbar is another matter, but this may not be that significant as the predictive value of the equations at these higher levels is likely to be limited. It is clear from Dunbar (1992a) that there is a good correlation between group size and neocortex ratio. The precise value of the linear regression used to derive a predictive equation from this correlation, however, will be affected by the species at the upper end of the range for social group size. It is these that will determine the slope of the regression. When we consider one of these highly gregarious species – chimpanzees – we find that they have a mean community size of 48.8 (Foley 1993). The coefficient of variation, however, is 42.4%, which is very high, higher than for humans (CV = 29.1%, Table 1 in Dunbar). This means that at the upper limits of the primate social range minor variations in the data may have an undue influence on the equations. Variance for the other highly gregarious catarrhine, *Papio*, is equally high (47.4%, based on Dunbar 1992b). These will not affect the strength of the association but can affect the quantitative predictions.

None of this may be of particular importance when it is noted that what highly social species such as chimpanzees, baboons, and humans face is not just the problem of coping with large social groups but dealing with this very variability. Given that the human "groups" Dunbar links to human neocortical size do not represent demographic units but are themselves social constructs, these are likely to be subject to exactly the sort of interindividual variation that is thought to promote evolutionary change.

Finally, it is a surprise to discover that Dunbar has overlooked the further implication of his model that would nicely wrap up all the problems of human evolution. A shift from grooming to language as the means of social lubrication is likely to have left a lot of itchy and parasite-infested fur, and the loss of body hair in human evolution may turn out to be the adaptive price our species has had to pay for its loquacity.

Group structure and group size among humans and other primates

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Dunbar's basic idea that neocortical size constrains "the number of relationships an animal can keep track of in a complex, continually changing social world" is appealing, but the notion that such a limit leads to a constraint on the size of the social groups in which the individual is embedded is less so.

The problem is in Dunbar's casual treatment of groups. Over 30 years ago Floyd Allport (1961, p. 195) pointed out that because "a group is a phenomenon so familiar to everyone that it is not a question of what a group is, but only of how it works," researchers had simply "assumed the existence of groups." This is precisely what Dunbar has done.

Dunbar's notion that the limit on an individual's information processing capacity imposes a limit on group size depends on how the group is conceived. He defines a group as a subset of a population of conspecifics that "interacts on a sufficiently regular basis to have strong bonds based on direct personal knowledge." For their knowledge to be personal, each individual must interact "on a sufficiently regular basis" with each and every other individual in the group. A subset that is maximal with respect to that property has been formally dubbed a "clique" (Luce & Perry 1949).

The properties of cliques can be specified in exact terms. Given a finite collection of individuals $A = (a,b,c, \dots)$ along with a symmetric relation I that links those pairs of individuals in A that interact on a sufficiently regular basis to have "strong bonds," suppose that each individual in A has the relation I with n other individuals; n is then the number of others with whom an individual has a "personal" tie. Suppose further that we find a clique in A of size m.

If Dunbar is right, there must be a relationship between n and m. But the value of m only sets a lower limit on n, $n \geq m - 1$. The upper limit of n depends on the arrangement of the ties linking individuals in A, and there is *no* necessary connection between the number of others with whom an individual has a personal tie and the sizes of the "groups" in the sense they were defined by Dunbar.

Dunbar may, however, have had other (unstated) restrictions in mind when he talked about groups. In his groups, for example, he may have assumed that "friends of friends are friends." In that case, the relation I would be transitive and each group would be a special kind of clique that Davis (1967) called a *cluster*. All individuals within each cluster would be directly linked, and no individuals falling in different clusters would be. In that case, $n = m - 1$, and individual network size would be inextricably tied to group size.

But, at least in the case of human primates, interaction frequencies are certainly not transitive (Freeman 1992b). Humans do display some tendency to strain toward transitivity in their relations with each other, but their interaction patterning is by no means as simple as Davis's clusters would suggest.

It turns out, however, that human observers of interaction patterns seem to *want* to see them as transitive (DeSoto 1960). Indeed, there is growing evidence that human observers impose transitivity on their observations and thereby construct a simplified and exaggerated image of group structure (Freeman 1992a; Freeman & Webster 1993).

Given this tendency, one cannot help but wonder about the accuracy of the data on group size used by Dunbar. Primate ethologists take it for granted that virtually all anthropoidea organize themselves into groups (Maryanski 1987). This assumption suggests that the groups they report may have little to do with actual interaction frequencies. Indeed, the one study that compares systematic observations of interaction frequencies (among mantled howler monkeys [*Alouatta palliata*]) with an ethologist's classification of them into "troops" showed very little agreement between the two (Sailer & Gaulin 1984).

For similar reasons, the ethnographic reports on human group sizes used by Dunbar must be viewed with suspicion. With respect to humans, we would certainly be on firmer ground if we forgot about groups entirely and examined data on frequencies of individuals' interpersonal contacts.

Fortunately, such data are available. Gurevich (1961) reported a study in which he tried to estimate the *acquaintanceship volume* for a sample of 27 humans. An individual's acquaintanceship volume was defined as the number of others whom that individual meets repeatedly in such a way that each recognizes the other and each can identify the other by name. This is very close to Dunbar's concern with the number of others an individual is able to keep track of.

To estimate this number, subjects were required to keep a diary for 100 days, recording every person they contacted on a given day who met the criteria. The number of different persons contacted in the 100-day period ranged from 72 to 1,043. Of course, many of these were contacts that were repeated again and again. Indeed, the number of contact events varied from 377 to 7,645. The pattern of repetition and the rate of introduction of new names were used to estimate the number of acquaintances who would have been listed had the diary been kept for 20 years (de Sola Poole & Kochen 1978). That number is 2,130; it is a full order of magnitude greater than Dunbar's estimate of 147.8. Yet these are all individuals who meet Dunbar's criteria; they are all known personally by the subjects and known well enough that the subjects could recall their names and faces.

The discrepancy between Gurevich's estimate and Dunbar's is huge, but it does not indicate that Dunbar's basic thesis is wrong. Such a discrepancy could result from the fact that the nonhuman primate data are records of group sizes and Gurevich's human data are records of individual interaction patterns. To determine the implications of Dunbar's ideas for data on individual interaction we would need comparable data on nonhuman primate interaction patterns. Such data are rare and difficult to collect.

I think Dunbar's view is important enough to deserve a more rigorous development and more reliable data. His idea of group requires a more systematic and contemporary treatment. My guess is that he will end up having to consider not only group size but also structural complexity. And on the data question, he will need not the impressionistic reports of ethologists and ethnologists but matrices representing records of systematic long-range observations of interaction frequencies among conspecifics. Only then will these ideas be given the careful consideration they deserve.

Do gossip and lack of grooming make us human?

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Dunbar's two major premises seem shaky and make unacceptable simplifications. First, the fact that the median primate group size is related to neocortical volume may be due to correlations between relative neocortical size and habitat or social structure (Sawaguchi 1989; 1992). Surprisingly, Dunbar does not refer to either of these papers. It is inadmissible at this stage of our knowledge of very complicated morphological and physiological parcelation of the mammalian neocortex to speak about the global size of the neocortex in relation to speech function. In many experimental and clinical studies, beginning in the nineteenth century, it has been shown that only limited areas of the neocortex in the human brain relate directly to language function (see Markowitsch 1988). It was well documented that in a morphophysiological sense mammalian neocortex can be divided into two major subdivisions: one that relates to more elementary bodily functions, and the other that relates to higher functions, including speech in humans (Hofman's [1982; 1985] "extra" cortical volume, Jerison's [1973] "extra" neurons). Thus, Dunbar's parallel between the *global* size of the neocortex and the size of sociobiological groups in primates is inaccurate, because only specific parts of the neocortex pertaining to higher nervous activity increased phylogenetically, whereas the other regions (so-called primary areas) were relatively diminished (Blinkov & Glezer 1968). Sawaguchi (1989) has shown that the size of monkey troops is only secondarily correlated with the size of "extra" cortical volume (Ve) and "extra" neurons (Nc), whereas the major factor for this correlation is ecological grouping (polygynous or monogynous). Apart from the ecological grouping, other factors play an important role in determination of neocortical size in mammals, including energy resources, biomechanics of the brain, gestation length, and so on (Hofman 1985; 1988; 1989; Kruska 1987; Little 1989).

Second, the statement that "the relationships that maintain group cohesion . . . are serviced by social grooming" is not valid for New World monkeys, and in general Dunbar does not take the neotropical primates into account. "Grooming" is not the social glue in platyrrhine primates that it is in the Old World. For example, muriquis (*Brachyteles arachnoides*) rarely groom (Strier 1992), although their group size is large, 25–49; titi monkeys (*Callicebus*), which groom extensively – an average of more than three hours a day (Kinzey & Wright 1982) – have a group size of 2–5 individuals. Howler monkeys are seldom thought to groom (Crockett & Eisenberg 1987), and *Aotus palliata*, *A. pigra*, and *A. seniculus* rarely groom. But there is considerable variability in the genus since, in contrast, *A. fusca*, and *A. caraya* in both the field and captivity, are frequent groomers (Neville et al. 1988).

Because grooming is not the social glue for all primates, a prediction for humans based on this premise is probably not valid. The main problem has to do with monogamous groups. Since the vast majority of humans marry one spouse at a time (monandry and monogyny; Fisher 1989), this premise is especially problematical for humans. We do agree with Dunbar's final sentence, that in "the evolution of this increased capacity" of the neocortex there was a "need to coordinate . . . interpersonal relationships . . . to maintain the cohesion and stability of larger than normal groups." We believe this was equally necessary "to communicate about the location of possible prey and to plan coordinated hunting expeditions."

Overall, Dunbar equates the social role of grooming with the social role of language and posits a direct causal relationship between evolutionary changes in global size of the neocortex and the evolution of human speech. Last, he makes the size of social groups in nonhuman primates directly dependent on relative volume of neocortex. We believe that these suggestions do not accurately reflect the known facts on neocortical evolution, neurophysiology, and behavior studies in primates.

Anthropological criticisms of Dunbar's theory of the origin of language

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Dunbar's target article stimulates but, especially because of its handling of anthropological data, it does not convince. I begin with some background problems of definition and theoretical orientation.

Primate groups typically seem to be small and unstable in the sense that individuals frequently switch groups and entire groups frequently fission. Attributing – without operationally defining and measuring – properties such as "cohesion" and "integrity" to such apparently incoherent and poorly integrated entities is a fundamental problem. The need for operational definition glares when, for instance, Dunbar (sect. 4, para. 9) asserts that modern nation states are "not particularly stable through time," despite the fact that membership shifts and fission are certainly far rarer than in small-scale human or infrahuman societies generally.

Is grooming necessarily instrumental in bringing about whatever "cohesion" typical primate groups may be said to have? It seems as plausible, a priori, that cohesion fosters grooming, or that both cohesion and grooming result from some underlying third factor. The assumption that a trait (grooming) satisfies some presumed "need" of a social structure (cohesion) bespeaks a theoretical orientation which, while having little explanatory power, is littered with pitfalls (e.g., Hempel 1965, pp. 297–330).

Anthropologically, Dunbar's claim that groups averaging around 150 were critically important in human evolution is weak. The case is disturbingly resistant to archaeological refutation, given that such groups may have left no "obvious physical manifestation" (sect. 3.1, para. 16). His crucial Table 1 severely distorts the ethnographic evidence it purports to present. Idiosyncratic use of the term "overnight camp" for what is generally termed a band, and "band" for – apparently – what is generally termed a descent group, is misleading. "Overnight camp" is an entirely inappropriate description, for example, of the Shoshone and Ammassalik groups *as described in Dunbar's own sources;* indeed, the latter were patrilocal longhouses within a winter settlement numbering 413 (Service 1963, p. 94). Merging descent groups of some societies with horticultural villages of other societies renders the "intermediate-level groupings" distressingly heterogeneous; after all, village membership and descent-group identification are fundamentally different and often cross-cutting forms of affiliation (e.g., Chagnon 1974, pp. 133–41). And the data for at least one of this category's members are patently an artifact of colonialism: the Walbiri "band/villages" are described, in the original source, as "government settlements" (Meggitt 1962, p. 31). More generally, the assertion that "swidden horticulturalists . . . may reasonably be considered to be settled hunter-gatherers" (sect. 3.1, para. 11) is anthropologically heterodox, and, in this context, sounds like special pleading: food production originated far too recently for horticultural villages to have had anything to do with the origins of language, and probably under conditions radically altered by the completion of global hominid expansion (Cohen 1977). In sum, it is unclear that Table 1 deserves to be taken seriously.

Of the serendipitous juxtaposition of pacifistic Hutterite colonies and professional army companies, because both happen to have the "right" mean size, one can only note that it certainly is in keeping with an avowedly "exploratory rather than explanatory" enterprise (sect. 3.1, para. 2).

But if the empirical case for the Paleolithic existence of groups of 150 is weak, the theoretical case for their adaptive significance is weaker yet: on this topic, Dunbar (sect. 4, para. 7) admits, "little . . . can usefully be said . . . at present."

More forcible than this involved argument, I think, is simply the salience of gossip in human conversation; yet the uses to which a trait is put are not a reliable indicator of its origin. After all, a naive observer of the uses we modern humans make of our ability to rotate our arms fully would conclude that this trait evolved for recreational and athletic reasons rather than for survival in the trees. Besides, is it safe to assume that gossip's net effect is integrative rather than divisive?

Another anthropological heterodoxy is the suggestion that hominid brain size showed no "marked increase until the appearance of *Homo sapiens*" (sect. 4, para. 7). Expert consensus holds, on the contrary, that "the majority of cranial expansion in hominid evolution occurred in *Homo erectus*, whose earliest representatives have cranial capacities between 800–900 cc and whose latest representatives have skull sizes well within the range of modern humans, more than 1,200 cc" (Staski & Marks 1992, p. 450).

Dunbar's penchant for peculiar anthropological interpretations and his faith in a regression extrapolation he admits is methodologically dubious appear to stem from his commitment to the "social intelligence hypothesis," which proposes that the human brain expanded to sustain larger groups rather than "to enable humans to hunt or manufacture tools" (sect. 4, para. 5). Yet we have impressive, concrete evidence that *Homo erectus*, with its expanding brain, made generally better tools, obtained control of fire, and, concomitantly, greatly expanded the geographical range of hominids; there is, at the same time, nothing generally accepted as definite evidence for increase in average group size. Indeed, significant growth in human societies (in a form recognizable in space and time) appears to have depended on substantial increases in density, which seem to have been avoided, through territorial expansion, until the planet was full of foraging peoples around 10,000 years ago. (A speculative – but very elegant – hypothesis is that the mean number of people per society then began increasing with the square of density; e.g., Graber 1991.)

It should be added that biological anthropology's "conventional wisdom," with its stress on the significance of making and using tools, helps explain not only brain expansion but also the two other, more ancient hallmarks of hominid anatomy: bipedalism and canine reduction. The social intelligence hypothesis remains comparatively unattractive, then, in terms of both hard evidence and theoretical parsimony.

Dunbar's brief comments on the integration of modern societies miss the mark by mentioning sheriffs' badges but not their guns. The existence of ever larger human societies is heavily indebted not only to density increase but also to coercion (e.g., Carneiro 1970; 1988).

Despite these criticisms, I am not entirely unsympathetic; this is a most provocative paper, and I heartily share Dunbar's underlying assumption that what fundamentally needs explaining, in primate social evolution, is the growth of larger societies, not, as he formerly implied (Dunbar 1987, p. 248), the proliferation of small ones. His previous position did furnish me with a convenient foil for presenting my "inertia law" of mean societal size (Graber 1993), but I welcome the change and look forward to his future contributions.

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Brains, grouping and language

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Robin Dunbar has suggested two original and stimulating ideas about limits to group size and the origins of language. First, brain size limits the number of relationships that primates can monitor, and therefore limits group size. Second, language did not start with males talking about the hunting environment but with females talking to, and about, each other in order to cement friendly social relationships.

Dunbar opens his target article with the statement that primates are the most social of animals, and continues with the proposition that large brains and consequent intelligence evolved for processing information about the social rather than the physical environment. His argument depends crucially on these precepts. But what is meant by "social" in this context, and what evidence is there that the large-brained primates are using their extra processing ability for social ends? After all, a number of nonprimates live in large, stable, social groups with multiple levels of different sorts of social relationships (Moss & Poole 1983).

Primates certainly are socially complex (Byrne & Whiten 1988; Cheney & Seyfarth 1990; Harcourt & de Waal 1992), but until recently statements that they were more complex than nonprimates were almost entirely unsubstantiated. However, it seems that primates might form uniquely complex alliances (de Waal 1992; Harcourt 1992; Wrangham 1983), as might some members of that other big-brained taxon, the toothed whales (Connor et al. 1992). Thus, only primates are known to cultivate actively alliances with others (by grooming them, for instance) on the basis of differences among those others in their ability or readiness to give useful help, such as during fights (Harcourt 1992).

Dunbar supported his contention about the importance of social intelligence and the constraint that information-processing ability imposed on group size with the observation that the size of the neocortex correlated with group size. However, both brain size and group size correlate with how animals use the environment: primates that rely largely on fruit have larger brains than do the leaf-eaters and they also live in larger groups (Clutton-Brock & Harvey 1977a; Sawaguchi 1990). And, of course, resource patches are not infinitely large. Is social intelligence separable from environmental intelligence as a selective force, therefore? And is brain size or resource-patch size the limiting factor on group size?

It is easy to see how environmental and social intelligence would be necessarily linked and logically very difficult to separate. Larger resources are rarer and more widespread, and so more difficult to find (Milton 1988). At the same time, larger resources allow larger groups, which mean a greater number of competitive and cooperative relationships to monitor and service. That having been said, improved ability at complex manipulation of the social environment by one animal cooperating with others for its own or its relatives' competitive benefit will cause a process of positive feedback, as other members of the social environment respond, that presumably proceeds at a far greater rate than can result from interaction with the physical environment (Harcourt 1992).

Turning to limitations on group size, abundant observational and experimental evidence shows that one constraint is the size of the resource patch that group members can simultaneously use. Another constraint is the time available for the social interactions maintaining the bonds between individuals that cause the group to cohere, which is determined by availability of resources (Dunbar 1992b). Now Dunbar appears to argue that ability to monitor relationships, rather than service them, is the ultimate limiting factor. I do not see how that can be the case, but we can test the idea more directly by discovering how often individuals have time to service as many relationships as they can monitor, which in turn depends on how many more they can monitor than service.

I know of only one study designed to test limits to primates' knowledge of group members. Mori (1977) found that in groups of less than 300 animals, individuals were confident about whether or not to attempt to obtain a peanut thrown between them and another monkey, as if they knew not only the identity of the other but also their relative competitive ability; above that group size, they were hesitant. Three hundred is much higher than Dunbar's postulated maximum group size for any primate. Admittedly, the knowledge tested by Mori is relatively simple. At the same time, the fact that fairly stable groups of several hundred macaques were available for Mori's study appears to be strong evidence against Dunbar's hypothesis.

The crux of Dunbar's second main hypothesis, about the origins of language, is that language functions in the same way we think grooming does, namely, to cement, and perhaps monitor, social bonds (i.e., cooperative relationships) between group members. The reason grooming functions in this way is that it is potentially useful to the recipient who, the argument goes, later reciprocates the service (Cheney & Seyfarth 1990). Much communication is potentially useful to the recipient, some so useful that animals are punished if they do not communicate (Hauser 1992c), but is there any evidence that vocalizing enhances social bonds in the way Dunbar suggests?

Directedness is a crucial feature of arguments about the origins of reciprocally cooperative relationships because these can evolve only if donors distinguish those who reciprocate from those who do not, and continue to service only the former (Axelrod & Dion 1989; Boyd 1992). Whereas grooming is manifestly directed, vocalizations are less obviously so. However, if prairie dogs are more likely to give alarm calls in the presence of close relatives (Hoogland 1983), the potential is there. Furthermore, monkeys can vocally communicate information about their relationships, giving different screams depending on the identity of opponents (Gouzoules et al. 1984). But, can animals communicate nonverbally about others' relationships, or does that ability arise only after language has evolved?

The functions of grooming and language: The present need not reflect the past

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Chomsky has argued that human language is possible because we are equipped with a piece of neural machinery that permits complex combinatorial manipulations of grammatical structures. From Chomsky's perspective, the communicative function of language is purely accidental. Robin Dunbar's provocative hypothesis contrasts with the Chomskian view by arguing that language is an adaptation, its function being to service the complexities of our social lives. In this commentary we begin by pointing out two theoretical problems with Dunbar's hypothesis. We then discuss issues where additional data are needed and conclude with some comments on how several of Dunbar's statements may be inconsistent with published data.

Current function need not reflect initial function, especially given changes in the environment that shape the adaptive landscape. Dunbar explicitly states "that language evolved as a 'cheap' form of social grooming, thereby enabling the ancestral humans to maintain the cohesion of the unusually large groups demanded by the particular conditions they faced at the time" (sect 3.2, last para.). Given the data presented, we agree that a powerful function of language is to service a large number of complex social relationships. This does not, however, entail evidence that language evolved *in order to* service such relationships. Dunbar's hypothesis is best seen as an explanation for one of the many functions of language in modern humans (i.e., current function) and not an explanation for why language evolved (i.e., origins), whenever it did.

Our second conceptual problem with Dunbar's hypothesis concerns the function of grooming. We disagree with the basic premise that grooming functions to maintain group cohesion. Although time spent grooming may increase with group size, and although there is sufficient evidence to argue that grooming maintains and builds social bonds, there is no evidence to suggest that primates groom more individuals or groom in a more egalitarian way as group size increases (Cheney 1992). In other words, there is no evidence to suggest that primates are forced to increase the size of their social networks as group size increases. Many other explanations could be given for the relationship between group size and time spent grooming. Therefore, there is no reason to argue that a new mechanism was needed to service more relationships in a more efficient manner.

Even if it were possible to demonstrate that grooming functions to maintain group cohesion, we see two related problems with Dunbar's hypothesis. First, language may not be a good substitute for grooming as a bond-servicing mechanism because of the differential costs involved in the two behaviors. Grooming may function to strengthen bonds (between certain individuals) precisely because it is costly to produce and thus reliably signals the groomer's intent to invest in the relationship. In contrast, language is a relatively cheap form of investment, making it more difficult for the receiver to detect cheaters. Second, because Dunbar never defines what he means by a "relationship," it is difficult to assess why big brains and language are necessary for servicing a relatively large network of social interactions. Intuitively, it seems clear that some relationships are more costly to service than others. For example, factors such as loyalty and kinship are likely to make relationships relatively cheap, whereas power relationships such as those that exist between bosses and employee are likely to be more costly. Consequently, future empirical tests of Dunbar's hypothesis will first require a more rigorous depiction of the quality/nature of each relationship so that a more accurate discussion of cognitive demands can be evaluated. This is important because an individual with 200 "relationships" may be able to add on additional ones because a large proportion of the current relationships is cost-free. The possibility of a cost index for social relationships may allow us to explain more properly why the relatively small-brained black and white colobus monkey can live in groups of up to 200 individuals whereas the relatively large-brained orangutan is solitary.

In attempting to follow the logic of the theory presented there were a number of places where we were unsatisfied with the level of detail. We would very much like to hear Dunbar's thoughts on the following comments: (1) He considers neocortex ratio to be the most important neural structure for keeping track of complex social relationships. Why the neocortex? If memory is crucial, why not look at the hippocampus or the prefrontal cortex? Evolutionarily, one of the major differences in comparative neuroanatomy between humans and all other vertebrates lies in the prefrontal cortex. Goldman-Rakic (1988) and others have pointed out that the prefrontal cortex is the primary center for working memory and is thus likely to play a critical role in the dynamics of an individual's social environment. The hippocampus is likely to be critical for long-term storage of information. (2) By excluding fission-fusion societies, Dunbar has ignored what is socially and cognitively one of the most complex primate species: the chimpanzee. Where do chimpanzees and the other apes fit on the neocortex-ratio group-size regression? In addition, humans are often depicted as a fission-fusion species (e.g., Rodseth et al. 1991), which gives added justification for including fission-fusion species into the analysis. (3) Even if grooming could be argued to be an important factor in social cohesion, it is surely not the only factor. Is it possible to perform a multivariate analysis of grooming as well as other factors, such as the distribution of resources, to look at the relative contribution of each while holding the others constant?

Finally, there are four statements we believe are inaccurate. First, Dunbar defends his use of mean group size as the relevant variable for comparison by claiming that fissioning occurs when group size reaches a maximum and thus represents a size beyond the hypothesized cognitive constraints. This generalization is based on a few genera (e.g., Catarrhinae) and does not reflect the demographic patterns of other species in his sample (e.g., *Alouatta, Gorilla*), which show fluctuations in group size due to individual dispersal rather than group fission. Since the mean is highly vulnerable to extremes (such as newly formed groups), we suggest that the maximum group size represents a more accurate estimate of cognitive constraints on group size. Second, Dunbar's calculation of human group size is distorted by his underestimates of prosimian social network size (Bearder 1987); and, we believe, inappropriate log-log transformations. If one uses data on prosimian sleeping group size rather than foraging group size, the regression equation predicts a human mean group size of 71.5 (log-transformed data) or 58 (raw data). This predicted group size does not coincide with the empirical data reported by Dunbar. Third, it is stated that the only paper on the phonetic structure of primate contact calls is Richman's (1978; 1987) work on gelada baboons. There are several studies on species such as rhesus monkeys and vervet monkeys showing formantlike patterns (Owren & Bernacki 1988), prosodic contours (Hauser & Fowler 1991), and nasality (Hauser 1992a). These are all important features of human speech. Fourth, Dunbar claims that the conversational structure of geladas is unique. Not only have other studies provided evidence of conversations among group members, but they have documented more convincingly than Richman both the mechanisms underlying conversational turn-taking (Hauser 1992b) and the social function of conversations (reviewed in Snowdon 1990).

In summary, Dunbar has presented some intriguing ideas on how brain size may constrain social complexity and how different behavioral mechanisms have evolved to deal with the intricacies of primate social relationships. Although language is clearly used to service our social relationships, it is also used for several other functions. Reconstructing the original function of language is likely to remain a highly speculative endeavor.

Another primate brain fiction: Brain (cortex) weight and homogeneity

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Dunbar's is a very interesting hypothesis that carries much further some speculations I once made regarding the link between neural and behavioral complexities (Holloway 1967; 1981), which I still believe evolved in a positive feedback relationship. The suggestion that language might be viewed as a "cheap" form of social grooming is particularly fascinating, and Dunbar deserves a lot of credit for bringing together so many seemingly disparate elements. My comments must be brief, so I will limit them essentially to the role of the neocortex in language and its relation to other measures such as encephalization coefficients, extra cortical numbers, and the like, even though I suspect that many critical questions should be aimed at the behavioral and ecological data brought to bear on this question from so many different sources in primatology.

The criticisms I have are probably minor but deserve articulation. The first one relates to the problem of how to falsify the hypotheses Dunbar proffers. Some of the limits are so large on each side with respect to numbers of social actors and a concomitant narrowness of neocortical values that it is difficult for me to understand how any more exacting hypotheses can be framed for empirical testing. Dunbar's Figure 1 plots neocortex ratio against mean group size for nonhuman primates and the values for an exceedingly narrow range of the former, roughly between 2.0 and 3.0, appear to vary in mean group size between roughly 3 and 75 actors. That is, group size, with roughly equal neocortex ratios, varies by a factor of roughly 25. Surely the variances must be very unequal between the two variables. Similarly, Figure 3 gives the impression of only a poor correlation between percentage of time spent grooming and group size, going from 4% to 16% at a group size of roughly 32 or 33.

A second criticism is perhaps more serious, and that is the tendency of Dunbar and many others to treat the neocortex (or brain weight) as a homogeneous whole that has not undergone any regional evolutionary changes in its organization. It might be useful to consider the neocortex as composed of several organs, and we should not overlook the fact that the neocortex has numerous "parts," for example, primary sensory, primary motor, secondary primary and motor regions, and so-called association cortical areas, which include very complex polymodal integrative interactions between the frontal, parietal, and temporal lobes in concert with the sensorimotor components (e.g., as between Broca's and Wernicke's areas, supramarginal and angular cortex). Then, of course, the cortical regions have numerous two-way connections with the thalamus and each other.

The point is, should we believe that all these components are without any organizational differences between various primate species? Is the neocortex of *Homo* really the same as that of a rhesus monkey or a chimpanzee but simply larger? Deacon's (1984) studies admittedly suggest considerable homologies between the cortical fiber systems of humans and macaques, but then the numerous cortical maps being derived from recent techniques suggest that although the basic ground plan is similar for all primate cortical maps, they vary in degree of parcellation and areal distributions and also give evidence of differences in exuberant neuronal and selective cell death processes that are responsible for such parcellations.

Neuroembryology is thus a must in trying to understand any phyletic processes involving the brain, with regard either to its size or its organization. This is surely to be expected, since each primate species is an extant surviving species with a unique evolutionary history reflecting different selection pressures on feeding modes, locomotion, hand-eye coordination, manipulative skills, and social behavior, with its variegated thresholds for aggression and cooperation, which is far more complex than simply avoiding social overload or inventing language to control social grooming. The evolutionary trajectory of brain-behavioral evolutionary change for *Homo* was surely very different from that of *Pan* or *Gorilla* or *Hylobates* or *Pongo*, which in turn were very different from *Papio* and *Macaca*.

The paleontological evidence, albeit controversial, must eventually be settled as to when in hominid (or hominoid) evolution primary visual striate cortex underwent a relative reduction, whereas posterior parietal association cortex increased in relative size. It cannot and should not ignore the evolution of the frontal lobe or the evidence for hemispheric specialization as suggested by cerebral asymmetries. The same database (Stephan et al. 1981) that Dunbar draws upon for the size of the cerebral cortices in various primates also provides evidence for this reduction in Brodmann's area 17 (primary visual striate cortex) in the human brain, as I have shown elsewhere (Holloway 1992). Why would such a reduction (or its concomitant relative increase in peri- and parastriate cortex) only be related to language as a buffer against social stresses when visuospatial aspects are also of great importance in adapting to environments, both social and material? This could well have occurred during Australopithecine times, prior to the reorganization seen in the frontal lobe of the East Lake Turkana KNM-ER 1470 *Homo* specimen.

The above means that one should be very cautious about simply accepting the weight of the neocortex as a homogenous batch of jelly that can be regressed against total brain weight or body weight, or, as Dunbar has offered, as a ratio to the rest of the brain, medulla, or brain stem. These exercises are only approximations and may be lumping many different apples with oranges, tangerines, and clementines. The usual log-log regression of neocortex against brain weight is fraught with problems since in the higher primates (apes and humans) the neocortex represents between 65% and 76% of total brain weight. It is thus hardly surprising that the correlation coefficient is on the order of 0.99+. I have the same problem with life-history biologists that continually plot brain weight against social densities, feeding, or locomotor modes, as if the correlation coefficients were somehow directly translatable into causal relationships. These analyses completely overlook that the brain of each and every species is somewhat different from its closest neighbor; each has a unique history of natural selection, drift, migration, neural ontogenesis (hierarchy, see Holloway 1979), and ecologically determinant constraints on both ontogenesis and phylogenesis, whether gradualist, punctuated, or some mixture of both. They also overlook species-specific behavior.

A third criticism relates to the fictitious and probably meaningless concept of "extra cortical neurons," or N_c, as derived by Jerison (1973), and as recently abused by Tobias (1987). Once again, I find that my criticisms of this concept (Holloway 1966; 1974; 1979) are consistently ignored. Why does Dunbar believe that those derivations, including many cephalization quotients (Holloway & Post 1982), are anything more than the production of fictional numbers? That in the past some psychologists found it useful when comparing different orders (as suggested by Tobias 1987) is hardly convincing when the underlying assumptions regarding the functioning of so-called vegetative and behaviorally complex cerebral cortices have yet to be demonstrated. The neural densities of the various regions of the cerebral cortex are different from each other, and any averaging of them overlooks the fact that the relative size of the distributions has changed in the course of cortical evolution. Martin's (1983) more accurate regressions of primate brain and body weights provide an exponent of approximately 0.76, which is quite different from Jerison's earlier derivations of 0.66, suggesting that the earlier equations estimating N_c's are questionable. And because the "extra cortical" neurons are basically residuals from a double exponent body-brain weight relation, one must explain why the extra cortical neurons differ within species (as between males and females) and what that means for handling social density or behavioral complexity. What applies to intergeneric comparisons can, by the same logic, be applied to within-species variation, however much we may not wish otherwise. For example, the Australian Aborigines, with their lower brain weights and thus smaller neocortices (Klekamp et al. 1987), should be expected to have a more difficult time in substituting language as a "cheap" form of social grooming.

Size of human groups during the Paleolithic and the evolutionary significance of increased group size

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In general terms I agree with Dunbar's theory of the coevolution of neocortical size, group size, and language in humans. The thesis that large brains evolved for social reasons has been suggested before (Humphrey 1976) but has not been widely accepted, and Dunbar's target article provides new and substantial empirical support. The purpose of this comment is twofold: first, to caution against what I perceive to be an attempt to overquantify the relationship between neocortical volume and group size; second, to provide what Dunbar suggests is missing, namely, an evolutionary function of increased group size.

Dunbar correctly asserts that the modern brain size evolved about 250,000 years ago and suggests that in order to understand group size of that period it is necessary to examine modern hunter-gatherer groups, as their lifestyle is the nearest equivalent to archaic humans. Two points of detail are useful. The first is that the earliest remains of *Homo sapiens sapiens* date from about 100,000 years ago; the dominant *Homo sapiens* subspecies of 250,000 years ago were the Neanderthals, *Homo sapiens neanderthalensis*, who are almost certainly not ancestors of *H. s. sapiens* and who became extinct about 40,000 years ago. The average brain size of the Neanderthals based on 9 specimens (Trinkaus & Tompkins 1990) is 1,518.9 +/− 169.5 cc, which contrasts with early *H. s. sapiens* (based on 16 specimens of 1566.9 +/− 122.5 cc. These figures are slightly larger than those of modern humans (Dunbar quotes the figure of 1,251.8cc, Trinkaus and Tompkins suggest 1,300 cc to 1,350 cc) probably only because Paleolithic humans are physically more robust (the "meat-head hypothesis") than modern humans. Despite the similarity in brain size (though there are differences in cranial morphology, Trinkaus & Tompkins 1990) between the two *Homo sapiens* subspecies, there is a variety of archeological evidence (Gamble 1986; Trinkaus 1986) to support the idea that the Neanderthals had a socially simpler culture than archaic *H. s. sapiens*. Thus, the simple assumption that two *Homo sapiens* subspecies with similar brain sizes have similar levels of social complexity is not supported by the archeological evidence.

The second point of detail relates to group size of archaic groups. Dunbar correctly notes that group size is a slippery concept, as groups have a dynamic that may involve fragmentation into hunting parties and occasionally larger groupings. Group size in prehistoric peoples is inferred by calculating the ratio of people to camp-site size in modern hunger-gatherers and then applying that ratio to sites of archaic groups. This inferential process is likely to err on the side of overestimation as camp sites are used repeatedly, and repeated use may involve lateral shift in location – giving the impression of a larger group than actually ever inhabited that site. With this caveat in mind, comparison of Neanderthal and early archaic *H. s. sapiens* sites suggests that the latter are characterised by greater "variation in site, form, size and location, which suggests more organization of activities across the landscape" (Trinkaus 1986, p. 208). Neanderthal sites are of a size to suggest groups of about 25 persons, similar to the average of Paleolithic *H. s. sapiens* apart from terminal Paleolithic cultures where larger sites begin to appear (Hassan 1981). Hassan concludes his review of Paleolithic sites:

> The area of archaeological sites during the Paleolithic was small and . . . residential population units were in most cases between 11 and 31 persons, with an average of 22 persons. . . . During the Mesolithic/Epipalaeolithic period large sites emerge, reflecting a change in settlement strategy that might have been associated with socioeconomic changes. The smaller sites of that period, however, reflect an average of about 23 persons. The population size of the larger sites is difficult to determine, but at least in one case the population could have been as large as 150. (Hassan 1981, p. 92)

Dunbar notes that Neolithic villages in Mesopotamia are of the order of 150–200 persons, and indeed this is a characteristic of a number of longhouse occupations. Nevertheless, the site size of Epipaleolithic, Mesolithic, and Neolithic cultures include those that are substantially greater than sites indicative of about 25 persons, which characterised humans during the first 200,000 years that they had large brains. There may well be a biocognitive limit of groups of about 150 persons, but people evolved in smaller groups of about 25 persons.

Turning now to the evolutionary significance of group size, Dunbar says, "just why early humans should have found it necessary to evolve such large groups remains uncertain." Earlier he suggests that language did not evolve within the context of hunting. The archeological evidence, however, provides a different picture. The major development in brain size between *Homo erectus* and *Homo sapiens* was accompanied by a qualitative shift in hunting pattern – as inferred from the kind of animal bones associated with camp sites. *Homo erectus* was a scavenger and stalker of small prey (except for limited instances in late *Homo erectus*). *Homo sapiens*, by contrast, hunted large dangerous animals (e.g., mammoth, bear, wolf), the lithic and bone remains of the Neanderthals being consistent with close-quarter cooperative hunting and the lithic and bone remains of archaic *H. s. sapiens* being consistent with distance cooperative hunting (Geist 1978). Early humans were able to exploit dangerous animals as a resource by developing an organizationally complex strategy of killing. Thus, the increase in brain size and group size was accompanied by a change in hunting style where the larger group size was appropriate for the new type of hunting: large groups are needed to kill large animals. Furthermore, cooperative hunting requires emotional bonding between people as the safety of any one individual depends on the actions of others, and language may therefore not have had just the informational transfer properties suggested by Dunbar but a role much more tied up with the formation of affectionate bonds, emotional support, and synchronization of emotions (Buck & Ginsburg 1991).

The evolutionary trend toward greater group size and social sophistication enabled the human species to exploit new forms of resources; it enabled humans to become, as a group, the most dangerous regional animal during the Paleolithic and to exploit the benefits of agriculture from Neolithic times onward. It is instructive to note that modern humans did not evolve from the robust australopithecines but from the gracile branch. Moreover, modern humans are not the descendants of the more robust Neanderthals but a more gracile form of *Homo sapiens*. In the end it was the weaker, more socially sophisticated specimens that survived. In terms of evolution, humans were following a strategy that had been tried many times before, and most notably by hive bees: the weak become strong when in sufficient numbers. And just as bees need a language to synchronize their behavior, so do humans. However, humans had a problem that was not experienced by bees. Because the human Paleolithic environment was so variable, humans needed a means of ensuring cooperation that was not based on simple rule following. The human language needed to be much more complex to deal with synchronization of behavior under a variety of different and changing environmental conditions.

In conclusion, the archeological data provide no evidence that the evolution of large brain size in humans 250,000 years ago coincided with any social groups of 150 persons. Evidence of groups of 150 persons occurs from the Mesolithic onward. However, group size is an interaction between biological and social factors and archaic humans may have already evolved the capacity for complex social organization, a capacity that may not have been fully exploited. Dunbar should consider that it is not group size per se that signals social complexity but the quality of interactions with the group. Finally, the coevolution of increased neocortical size, group size, and language in humans are all consistent with an evolutionary strategy (Wilson & Sober 1989) where members of a species start to function as a group rather than as a set of independent individuals, thereby improving the chance of individuals surviving in such cooperating groups.

Sizing up social groups

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In suggesting an evolutionary relationship between group size, language, and neocortical volume, Dunbar contributes significantly to an ongoing discussion of factors linked to encephalization (see Falk 1990). Several parameters have been shown to correlate with relative brain size in primates and other mammals, including life history (e.g., lifespan, neonate weight, interbirth interval), ecological factors (e.g., home range area, dietary quality), and social interactions (e.g., social complexity, communication) (summarized in Foley 1990). Dunbar's proposal extends the long list of suggested explanations for encephalization that are considered "prime movers," such as hunting (Washburn & Lancaster 1968), tool use (Darwin 1871), throwing (Calvin 1982), thermoregulation (Falk 1990), and topographic mapping of the environment (Allman 1990). As noted by Foley (1990), however, each "prime mover" explanation is often simplistic and deterministic because, depending on one's perspective, each can serve as a condition, cause, constraint, or consequence of neocortical evolution.

Although the relative evolutionary contribution of social grooming to encephalization cannot be determined with any precision, it is certainly as plausible as any other prime mover candidate. Additional support emerges for Dunbar's position if one accepts that, within reasonable limits, (1) an increase in group size is linked to an increase in social complexity, and that (2) an increase in social complexity results in a more challenging environment for the organism. Thirty years of research on animals placed in novel and challenging (i.e., "enriched") environments has revealed a variety of neural changes, including (1) increased cortical thickness and brain weight, (2) altered cortical histology, neurophysiology, and neurochemistry, and (3) increased dendritic branching (for review, see Diamond 1988; Renner & Rosenzweig 1987). Enriched animals consistently outperform their nonenriched counterparts on a variety of behavioral measures. Such neurobiological and behavioral changes may also obtain from in utero and parental enrichment. Here, it is important to note that recent research on humans corroborates the findings of such studies and underscores the importance of epigenesis for shaping neural structure at the microanatomical level (e.g., Jacobs et al. 1993). Accepting that neural responses to a socially complex environment result in cognitive advantages for the organism, one may extend this principle to interspecific comparisons of organisms separated in space and time and thereby support the view that, evolutionarily, encephalization is related to social interaction.

Despite our positive impression of Dunbar's proposal, we believe that there are several limitations inherent in his argument. Dunbar appears to rely on social grooming as a primary measure of social cohesion. The concept of social cohesion is complex and difficult to characterize with a single measure, even one with as much face validity as grooming. Other behavioral measures that might partially capture the concept of social cohesiveness include spatial proximity (Kummer 1968; Scott & Perryman 1991), foraging patterns (Felleman et al. 1991; Menzel 1991), coordination of troop movement patterns (Boinski 1991; 1993; Würsig et al. 1991), selectively aiding group members in agonistic coalitions (Bradbury 1986; Dunbar 1988; Krushinskaya 1986; Raleigh & McGuire 1989), and territorial defense (Cheney 1992; Krushinskaya 1986). The use of multiple behavioral measures may result in characterizations of group cohesion different from that resulting from grooming alone.

Although neocortical size may limit the number and complexity of relationships animals can maintain over time, it is important to note that other measures may more directly reflect neural function in extant species. These include cerebrospinal fluid monoamine metabolites in human beings and other primates (Higley et al. 1992; Raleigh et al. 1992; Roy et al. 1989; Virkkunen & Linnoila 1990), endocrine parameters and other measures that may indirectly reflect neural activity (Ziegler & Bercovitch 1990). These measures are often evaluated to assess indirectly the contribution of different neural mechanisms to psychiatric and behavioral disorders. Despite the largely clinical nature of this literature, there is substantial evidence that differences in monoaminergic function contribute to individual and species differences in temperament, social competence, and behavioral style (Clarke et al. 1988; Cloninger & Gilligan 1987; Jacobs & Azmita 1992). Obviously, none of these physiological measures leave clear indicators of their presence in the fossil record. However, combining physiological data from extant species with the discussion of cranial capacity evolution would have tightened Dunbar's argument.

Finally, Dunbar's proposal can be characterized as *primatocentric*, a common shortcoming of many discussions related to (human) brain evolution. The discussion, ultimately, should not be limited to primates. Dunbar's position would be greatly strengthened, we believe, if the question of social cohesion and language were extended from terrestrial to aquatic animals, specifically the cetaceans. Although the cetacean neocortex is qualitatively different from the neocortex of land mammals (Garey et al. 1985; Ferrer & Perera 1988; Morgane et al. 1985; 1988), the cetacean brain remains one of the largest of any living mammal (whether one uses the Extra Cortical Neurons Index, the Encephalization Quotient, or the Neocortex Ratio; cf. Ridgeway 1986). Encephalization in cetaceans far exceeds what is required for sensorimotor adaptation and may be related to a neural system designed for elaborate detection and cognitive processing of echolocation signals. This "reality construction system" may in turn result in a kind of "communal cognition," whereby each animal could share both raw and enhanced sensory data with others (Jerison 1986). As Jerison notes, "A perceptual world constructed from shared raw data would permit unusual group cohesion . . . and might actually change the boundaries of the self to include several individuals" (p. 160). With our current knowledge, the existence of such communal consciousness is entirely speculative; even so, it could profoundly affect group size and the concept of social grooming as proposed by Dunbar.

Indeed, social aggregations of Cetacea constitute discrete, complex, and fluid social units. The size of such social units varies enormously across and within species, depending on location (e.g., inshore vs. open sea), ecological factors (e.g., food availability), and group activity (e.g., feeding, courtship, migration) (Evans 1987). For example, smaller dolphins (e.g., bottlenose dolphins, *Tursiops truncatus*) in coastal waters live mainly in small groups (i.e., 2–25 animals); pelagic dolphins (e.g., common dolphins, *Delphinus delphis*) form groups as large as several thousand; orca (*Orcinus orca*) travel in pods averaging approximately 30–40 animals (for review, see Ballance 1990; Evans 1987; Hansen 1990; Krushinskaya 1986; Norris & Dohl 1980; Pryor & Norris 1991; Scott & Chivers 1990; Würsig 1989). Comparisons between the social organization of cetaceans and primates are not new (cf. Saayman & Tayler 1979; Tayler & Saayman 1972), but combining perspectives on cetacean cognition and social cohesion may provide interesting material for future research and speculation.

NOTE

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Primate group size, brains and communication: A New World perspective

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Dunbar's provocative target article relies on two major points: (1) that large human neocortical size implies that early human group sizes were much larger than those of any extant nonhuman primate, and (2) that large group sizes force large commitments by individuals to grooming or other means of cementing bonds between social allies. Dunbar reasonably proceeds by restricting much of his analysis phylogenetically to Old World primates or to hominoids. Nevertheless, some interesting insights may be obtained by seeing whether parallel trends hold for the New World primate radiation, and if not, why not.

Dunbar starts by reasoning that primates that live in large social groups need high social intelligence, which he suggests relates to a high neocortex ratio (NR = neocortical volume divided by volume of other brain structures). However, NR is a measure of brain *composition*, not of relative brain size adjusted for body mass, as are the remaining indices of "braininess" cited by Dunbar. For example, the New World squirrel monkey (*Saimiri*) has a high NR and large social groups but a rather small brain relative to body mass (from data in Dunbar 1992a). Should such a species be more intelligent than a gibbon with a lower NR but a relatively larger brain? Whatever the answer, this example suggests that there may be nonsocial sources of selection for large overall brain size (independent of brain composition), as already suggested by the analyses of Clutton-Brock and Harvey (1980). To the extent that human intelligence relates to our large brain size in addition to our relatively large neocortex, its evolution may be due to selection from factors over and above social ones.

Dunbar may be right that early humans maintained larger social networks than any living nonhuman primate, but the statistical basis for this conclusion is weak. Some statistical authorities do not recommend using reduced major-axis regression-equations to predict unknown values (as does Dunbar, sect. 3.1), even if, with caution, they permit such extrapolations using conventional Y-on-X regression (Sokal & Rohlf 1981). This objection does not substantively alter Dunbar's conclusion, however, because the predicted human group size using conventional regression (100.7, from data in Dunbar 1992a) is still larger than that of any other primate. However, the confidence limits for the predicted human group size appear to be calculated incorrectly (Rayner [1985], cited by Dunbar, is concerned with confidence limits on regression slopes). Using Dunbar's (1992a) data on NR and group size in a conventional regression, the 95% confidence range for the predicted human group size at NR = 4.1 is from 22.73 to 446.2 (using row 4, Box 14.2, Sokal & Rohlf 1981)! This range covers more than ⅔ of all hunter-gatherer "group sizes" cited by Dunbar, as well as 9 of the 22 diurnal nonhuman primate genera in Dunbar's Figure 1. Thus, the neat fit between band/village group sizes and the supposed confidence limits for the predicted human group size is more apparent than real, and the extrapolation does not allow a confident claim that early human "group sizes" should have been larger than those of extant nonhuman primates.

Even if we accept that early humans had large social networks, Dunbar's claim that such groups would impose an intolerable grooming burden on individuals is only one of several possible results. The basis of his claim – the strong positive relationship between group size and grooming time in Old World primates – does not hold well for New World primates (Dunbar 1991). In particular, several species seem to have solved the problem of maintaining large social networks without resorting to high commitments to grooming. What solutions do these species use?

First, there are two fission-fusion genera, *Ateles* and *Lagothrix*, which live in relatively large communities of 15–30 individuals, yet devote less than 3% of their daily time-budget to all friendly social interactions (for *Ateles*, see Klein & Klein 1977). The key to these solutions seems to be the ability to fragment into small foraging groups, which limits both the opportunity and the necessity for maintaining strong competitive alliances. Spatial coordination among subgroups does occur and is mediated by very loud vocalizations of seemingly complex structure (van Roosmalen 1985).

Second, the case of squirrel monkey *Saimiri* is especially instructive, as it has the largest cohesive groups (30–40 animals) of any New World primate and a relatively large NR and yet devotes almost no time at all to social grooming (excluding time spent by mothers grooming infants; Janson, unpublished data). In one species, *Saimiri oerstedi*, the low commitment to grooming could be understood within Dunbar's framework as a result of the low level of aggression between females, thus eliminating the need to maintain allies (see Mitchell et al. 1991). However, this explanation would not work for the other species, *S. sciureus*, as females have frequent aggressive interactions and maintain large networks of allies (Boinski & Mitchell 1992; Mitchell et al. 1991).

Two alternative explanations are possible: (1) the average distance between neighbors is small enough (a few meters) so that preferred partners are never very far from each other (cf. Boinski 1988), or (2) vocalizations, perhaps differentiated with respect to allies, maintain contact between preferred partners (Boinski & Mitchell 1992). Given the latter prospect, it is interesting that the most hypertrophied part of the *Saimiri* neocortex is the occipital lobe, devoted mostly to auditory processing (Hershkovitz 1977).

These examples suggest that the burden of cultivating social alliances depends on several factors beyond group size. Maintaining strong social bonds is not needed, even in a large community, when most interactions concern only a few individuals at a time and possibilities for recruiting help are limited. Conversely, if groups are extremely cohesive, the maintenance of social bonds may be important but may not require great or exclusive efforts directed at allies. Even in large groups, the need for allies may be sufficiently low that little effort is needed to maintain social bonds by grooming. Allies may be unnecessary either because conflicts are rare (as in *Saimiri oerstedi*) or because they are resolved by relatively impartial third parties (as in most large human groupings). Thus, there are many ways in which large primate social networks can exist without providing the intense time pressure to maintain social allies that Dunbar postulates in Old World primates.

Even if the evolutionary origin of language in humans cannot be uniquely attributed to the maintenance of social alliances, it is equally implausible that language evolved without serving a social function. The vocalization studies of *Saimiri* reinforce the fact that the vast majority of communication between members of primate groups is "social" in the sense of maintaining cohesion or spacing between individuals (Boinski 1991; Boinski & Mitchell 1992). Thus, a predominantly social function for primate communication should be considered the primitive (plesiomorphic) condition, from which human language almost certainly derived. Given the complexity of human language, it would be fascinating to know whether the complexity of social "contact" calls scales with group size and cohesion among extant primates.

Hunter-gatherer sociospatial organization and group size

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R. I. M. Dunbar is to be commended for a compelling and provocative analysis. The range of information mustered in support of his thesis is impressive and speaks to the merits of interdisciplinary scholarship. The idea that language evolved as a "cheap" form of social grooming to integrate the large groups thought to be characteristic of our human ancestors in the late Pleistocene has much appeal. It is certainly preferable to simplistic notions of hunting and tool use as the prime catalysts for enlarged brain size, notions that are confounded by contradictory evidence and, not infrequently, androcentric interpretations of prehistory (Conkey & Spector 1984).

Even if we accept the strength of Dunbar's regression equation between neocortex ratio and mean group size for a variety of primate species, however, there is a problem in inferring the direction of causality. Is the cognitive capacity of the brain setting an upper limit on the number of individuals that can be bound together in intimate social relationships, or have the sizes and structures of groups as they have adapted to a variety of extrinsic conditions over time influenced the processing capabilities of the brain? Did language arise to solve a time-budget crisis, freeing humans from the costs of social grooming in large groups, or did the appearance of language, spurred by a complex of yet unidentified environmental and behavioral pressures, make social communication in large groups more efficient, which in turn selected for enlargement of neocortical volume? Even if one is sympathetic with Dunbar's argument, many scenarios are supportable with the statistical associations presented thus far.

Information on recent hunter-gatherer societies is offered as a means of approximating the social life of ancestral *Homo sapiens* circa 250,000 B.P. Dunbar's passing comment about the "disrupted" condition of these societies is surely an understatement. Considerable research in the past 20 years has documented how the lives of hunting and foraging peoples have been rearranged in complex ways, and over considerable time periods, by the political economy of markets, missions, national governmental policies, and related forces (Krech 1984, Leacock & Lee 1982; Lee 1992). This growing literature may not be welcome to researchers who desire uncomplicated ethnographic and ethnohistoric analogues for the prehistoric past, but the work cannot be dismissed as "fruitless definitional argument."

Since Dunbar's neocortex ratio for humans generates a predicted group size of 147.8, it then becomes a question of identifying this number in the real world. At first glance, Table 1 is impressive, because the average size of the "intermediate-level groups" for his list of hunter-gatherer societies is 148.4. The quality of the sample remains in doubt, however. Dunbar claims to have included cases for which adequate census data exist, although he draws mostly from sources published in the 1960s and 1970s. The bulk of the more recent literature on hunter-gatherers, at least some of which has useful ecological and demographic information, is omitted (Cashdan 1990; Ingold et al. 1988; Winterhalder & Smith 1981).

There is also, I believe, a misreading of the nature of sociospatial organization, at least for the subarctic and arctic hunter-gatherers. What Dunbar terms an "overnight camp" is, in many instances, an enduring residential grouping of close kin who live in face-to-face association for much of the year. Indeed, such units are more commonly referred to in the literature as "local bands," "microcosmic bands," or "staging communities." They are *not* the smallest or most ephemeral units, as Dunbar's Table 1 implies, but rather the most critical intermediate stages of social existence bridging larger aggregations ("regional bands," "macrocosmic bands," etc.), on the one hand, and more focused production or work units ("task groups," "hunting encampments," etc.), on the other (Helm 1968, p. 120; Honigmann 1946, pp. 64–65; Irimoto 1981, pp. 67–74; James 1983, pp. 12–17; Jarvenpa & Brumbach 1988, pp. 602–6; Rogers 1963, pp. 54–58; Sharp 1977; Smith 1978).

Among the southern Chipewyan, for example, five to ten nuclear and extended families (or 20 to 50 people) typically lived together in winter "staging communities," or *eyana'de*, from the freeze-up period in late October to the break-up period in late May-early June. Such communities served as general purpose processing and maintenance centers where bilaterally linked families socialized and nurtured children and where they fine-butchered, processed, and stored the mammals and fish retrieved from smaller dispersed bush camps. A number of these staging communities aggregated in loose form for about one month at midsummer fishing and trading locales. Among other functions, the latter gathering was a way for farflung families and kindred to reaffirm their identity as *kesyehot'ine* or southern Chipewyan. This larger regional band exceeded 300 people in the late nineteenth century (Jarvenpa & Brumbach 1988, p. 601).

The foregoing case simply raises the question of what sociospatial unit among hunter-gatherers should be targeted for comparative analyses of "group size." In recent history, the southern Chipewyan spent the bulk of their social existence in staging communities. Those units best exhibit the salient qualities of daily face-to-face interaction, bonding, and social intimacy that Dunbar sees as characteristic of human groups, yet their average size of about 35 falls far below his magic number of 150. The more enduring but less intimate regional aggregation, the *kesyehot'ine*, is significantly larger than his predicted value. Dunbar may be on the right track. I am only suggesting that one would like to see a larger sample of cases and a more probing treatment of the behaviors and social systems from which "group size" numbers are retrieved.

Number our days: Quantifying social evolution

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Dunbar's is a serious, appropriately documented analysis that improves our understanding of the forces that molded the evolution of the brain. I have some reservation about its behaviorist slant in the discussion of social organization, which I think weakens the central concept of "social knowledge." There are also too many significant figures in the numbers. In other respects, even if Dunbar's scenario is wrong, it raises the right issues. I will discuss the numbers and some of these issues and present a few alternatives to Dunbar's scheme.

I am always impressed by numbers when they make sense, and in Dunbar's hands they do. I accept the correlations, too, in the spirit in which they are offered, as challenges to our understanding rather than as definitive answers. We need more and better data on the size and organization of social groups. We also need more and better data on the size of the brain and its parts. I wonder how much longer we will have only Stephan and his colleagues (1981) for appropriately large samples of measures of the brain. We have the technology (Mazziotta et al. 1991) to extend Stephan's laborious analysis to many more vertebrate species. In addition to its other virtues, Dunbar's article is a model of how to use and interpret such data on the brain in conjunction with other quantitative information. It was depressing, if not surprising, to see the question marks in Table 1, which are evidence of our innumeracy but also illustrate the importance of efforts like Dunbar's in telling us what we need to know to write proper theories.

Is Dunbar putting us on when he reports that language is (precisely?) 2.76 times as efficient as social grooming as a mechanism for social bonding in primates? Anyway, I accept the point that we might scale the utility of language on the bonding dimension to show that it is more effective than grooming, even if the decimal point is not the point. I think Dunbar is more serious about the magic number 150 (plus or minus 50?), and that inspires me to contribute an oddity. Using a standard mathematical model of phenotypic evolution, I evaluated the hypothesis that brain enlargement in hominids was simply the result of genetic drift (Jerison 1988; I outline and document the argument but do not present it in detail). It turned out that the theoretical maximum size of the initial breeding population was about 150 individuals. Now a breeding population is not exactly the same as a social group, but it is nice to find the magic number coming up again. On the other hand, this also means that in current models of evolution there need have been no natural selection for neocortical sociality, language, or anything else to cause the brain to enlarge. I take this as evidence that current models are weak rather than that brains ballooned in a random walk across an evolutionary landscape. But it should also warn us that selectional scenarios for brain size may be unnecessary. It may be that like Topsy the brain just "growed."

Does neocorticalization truly constrain group size, or is the correlation a result of hidden variables? The fossil evidence cannot be read in primates, but there was a strong trend for neocorticalization in carnivores and ungulates during the past 50 million years. Also, the order Carnivora was more neocorticalized than its contemporary "archaic" carnivore order Creodonta (Jerison 1990; 1991a). There was evidently selection for neocorticalization in these orders of mammals. The capacity for social organization and increased group size as discussed by Dunbar may be part of the explanation. I would suggest a hard look at our ideas, however. We like the concepts, because social organization and group size can be described objectively, behaviorally. But behaviorism can mislead. There is nothing specific about neocortical function that identifies it as controlling social behavior. Do we need to be reminded of the complex social organization of insect societies to recognize that social organization can be affected in many ways? Although neocortical evolution in mammals may make mammalian social behavior possible, it may be through a circuitous causal path. My preferred analysis (Jerison 1991b) is to recognize neocortex as expanded in connection with the development and enlargement of sensory-perceptual and motor systems in nonhuman mammals. We can think of these as cognitive (i.e., "knowledge") systems. I would suggest that it is in the knowledge base for social behavior ("social knowledge" in Dunbar's words) that we may find the neocortical correlate for his analysis. Moreover, I think that although the social dimensions of knowledge should be recognized, knowledge also has other dimensions that may be equally important. Your knowledge of these words as you read them may have a social dimension, but its perceptual dimension may be intuitively more impressive. I am arguing for experience rather than behavior as the point of reference for cognition and for its theoretical analysis, although the evidence for any theory would, of course, have to be objective behavioral data.

I was puzzled by the identification of language as a functional equivalent of grooming without a suggestion of how and why this equivalence should initially have evolved. When I have speculated on the origin of language (Jerison 1991b), I have emphasized new environmental selection pressures for specialized cognitive capacities, an adaptational problem that could be solved (at the neural level) by neocortical enlargement. I do not see group enlargement as a pressure but rather as a possible response to pressure, so it remains a problem to identify the selection pressure. The problem in identifying language with grooming is that there is no neurological link. (Gestural theories of language origins can be criticized for the same reason.) Because of its neural localization, language probably first evolved as a control system, or knowledge system, as it were, and only after it appeared in some useful form could it have served the same social function as grooming, eventually to replace grooming in effecting the function. I see no simple route to initiate the sequence of events that Dunbar requires, though once initiated the role of language could have progressed according to his scenario. I agree with Dunbar's rejection of the conventional interpretation of language as an exchange of information. In my speculation I suggested that it began as a variety of cognitive mapping and was a preadaptation, as it were, for communication. It is hard for me to see it as related, except indirectly, to grooming, because I do not see the cognitive dimension of grooming.

The strength of Dunbar's argument is in his presentation of unusually correlated objective data. The accompanying theoretical analysis would be stronger, I think, if it were buttressed by neurobiological as opposed to sociobehavioral concepts. The evidence can be both behavioral and neural but the theory might be stronger if it were developed with respect to the brain's work as a control system, including its control of social functions that are constraints on group size. A brain-based theory might be the ideal, but lacking more information on the brain and its workings, I am satisfied with Dunbar's relatively behavioristic statements. The theory as he presented it led to the unusual and impressive conjunction of datasets that he pulled together and analyzed, and that is enough justification for any theory.

Group size, language and evolutionary mechanisms

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Dunbar's hypothesis seems to rest on four main claims: (1) a mutation producing larger cortex size in early humans caused or contributed to the development of language; (2) the development of language contributed to larger group size; (3) larger group size caused increased fitness; and (4) no other effects of neocortical size or language contributed enough to fitness to ensure their persistence in the population. I have serious doubts about all four.

Dunbar's evidence for (1) and (2) comes primarily from finding that human group size is consistent with the neocortex-group size ratio in other primates. There are at least the following reasons to worry that this evidence is of quite limited value:

(a) The 95% confidence interval for the predicted group size is so large that it is hard to put much weight on positive instances.

(b) The hunter-gatherer data show arguably 7 data points, not 1, as Dunbar maintains; this contradicts his hypothesis: the Central Eskimo size of 100 is outside the predicted range and 5 other data points show group sizes outside the predicted range; to count these as positive instances because they are close, because the data are an approximation (as in the Central Eskimo), or because the upper range of the mean group size does fall in the range is really stretching, given how imprecise Dunbar's prediction is to begin with.

(c) Naroll's (1956) data on maximum settlement size do not show that the mean settlement size "will not be too far from the value of 150." Without further evidence, we just cannot tell what average group size is; nor can we infer that it is not outside the predicted range; the latter is seemingly just as likely as not. Moreover, the data certainly show that group size is sometimes outside the predicted range; and it is not clear why that fact should not disconfirm Dunbar's hypothesis.

(d) Dunbar cites data about mean group size, yet his hypothesis is that language helped increase the limit to group size. Given this, it is not clear why mean group size rather than absolute group size is key. Of course, the observed limits might not be the real limit "imposed" by neocortical size, for other factors might cause actual limits to be below potential ones, as Dunbar suggests. Yet allowing that possibility leaves us in a quandary, for then any group smaller than 221.5 would count in favor of Dunbar's claim, threatening to make an already very imprecise test even less so. Furthermore, the upper limits in Dunbar's data are not all below his predicted range in the first place.

(e) The test based on group size depends crucially on the assumption that the neocortex-group size relation is linear when extended to all primates, *Homo sapiens* included. Given the wide confidence intervals for Dunbar's regression and the plausible idea that increases in brain size may bring about qualitative shifts in abilities, linearity cannot simply be assumed.

(f) For data about group size to support both (1) and (2), we need evidence that linguistic ability is the causal intermediary between neocortex and group size. If the intermediate-size groups that Dunbar cites are not somehow the product of language, then there is no reason to use data about intermediate groups rather than data about small or larger human groups, thus undercutting Dunbar's test. Moreover, Dunbar's data will not support the hypothesis that neocortical size determined group size by increasing linguistic ability rather than by increasing some other cognitive process not requiring language. Since Dunbar at times suggests that it is the ability to process information that limits group size, and since this factor can presumably operate separately from language, the second worry should not be just hypothetical. Pointing out that we can talk to more people than we can groom leaves these problems untouched. Dunbar needs evidence that groups of the predicted size are mediated by linguistic limits.

Given these questions, it is hard to see that Dunbar has given us much reason (or even any) to believe claims (1) and (2). The situation is no better for (3) and (4). What evidence is there that larger group size was or would have been selectively advantageous? Dunbar grants that this is unknown if not unknowable. Yet his hypothesis is speculation without some evidence along these lines, for language could then have evolved for many other uses, with group-size limits as a pleiotropic by-product. At the very least we would like to have evidence that a mechanism is not unlikely, but there are worries here as well. One scenario suggested by Dunbar is that language makes groups more cohesive, and cohesive groups outcompete noncohesive ones. That scenario, however, invokes the suspicious process of group selection. If we look for an individual-level analogue, then the question is, crudely put, who did they talk to? How did individuals with greater linguistic ability get to be part of larger groups than their inferior cohorts, especially if the groups were of fixed size and more or less separate? Maybe a plausible story can be told here, but it surely has to be, if Dunbar's hypothesis is to be more than mere speculation.

Finally, Dunbar frames his hypothesis as a competitor to accounts that link neocortical size to, for example, the evolutionary advantage of tool making. But these hypotheses need not be mutually exclusive. Larger neocortical size could have contributed to toolmaking and increased group size, with both contributing to fitness. Similarly, language could have contributed to larger group size as well as to other factors increasing fitness. There is nothing we know about evolution that requires such a simple causal picture. Such all-or-nothing claims may be more exciting, but they are not thereby more plausible.

Comparative studies, phylogenies and predictions of coevolutionary relationships

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The accuracy of Dunbar's predictions of human group size and time spent grooming depends to some degree on assumptions regarding the evolutionary histories of the nonhuman primate species used to develop the predictive regression equations. One of the assumptions of regression (and most other statistical tests) is that the data points are statistically independent of one another. In other words, we should have no a priori expectations regarding relationships among the data points used in the statistical analyses. In the case of Dunbar's data, for example, we should have no reason to expect the neocortex ratios of New World monkeys to differ from those of Old World monkeys, or for mean group sizes of Callitrichids to differ from those of great apes based on any information other than the variables being considered in the analysis. In evolutionary terms, Dunbar's analyses assume that all the nonhuman primates used in this study diverged essentially instantaneously from a single point in the distant past, and that they have been evolving independently ever since.

Dunbar (1991) argues that although taxonomic differences may have a major impact on the variables considered, the validity of incorporating phylogenetic information into statistical tests (as suggested by Cheverud et al. 1985; Felsenstein 1985; Grafen 1989; Lynch 1991; Maddison 1990; see Harvey & Pagel 1991 for review) will depend in large part on the accuracy of the available phylogenetic information (Dunbar 1992a). Primate phylogenies are still undergoing substantial revision, and it is difficult to determine phylogenetic relationships without error. Nevertheless, I was able to obtain a rough estimate of the phylogenetic relationships among the species used in this study from Schwartz (1986) and Ford (1986) (leaving unresolved polytomies whenever necessary and estimating branch lengths from the topological structure as shown in Fig. 1). Although these phylogenetic hypotheses are unlikely to be entirely accurate, I propose them as a reasonable alternative to Dunbar's implicit assumption that primates diverged instantaneously in a "star" radiation. As failure to incorporate phylogenetic information in interspecific analyses can lead to very poor statistical estimates and high levels of Type I and II error (e.g., Felsenstein 1985; Grafen 1989; Martins & Garland 1991), it seems worthwhile to see what impact phylogenetic relationships might have on the predictions made in Dunbar's study. Martins and Garland (1991) showed that even when the available phylogenetic information is highly inaccurate Felsenstein's (1985) technique is unlikely to cause greater errors in estimation than the implicit assumption of a star phylogeny; I accordingly applied Felsenstein's method to the data presented in Dunbar (1991; 1992a) to predict human behavior phylogenetically.

Felsenstein (1985) suggested that although species data are not statistically independent of one another, the differences or "contrasts" between historically nonoverlapping pairs of species are independent. He then describes how to standardize these contrasts, creating independent, homoscedastic variables that can be used in any standard statistical test. Thus, I calculated Felsenstein contrasts for the data on neocortex ratios and group size for 36 species of primates presented in Dunbar (1991) using the phylogeny in Figure 1A, and then regressed standardized contrasts in group size on standardized contrasts in neocortex

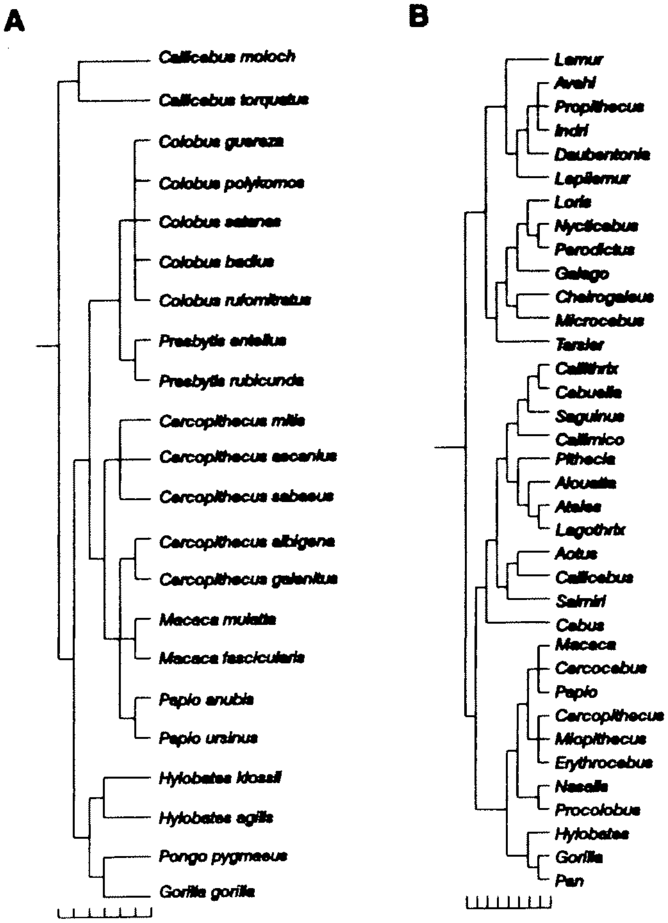

Figure 1 (Martins). Hypothesized phylogenetic relationships as developed from Schwartz (1986) and Ford (1986) for the relevant species (leaving unresolved polytomies whenever necessary). Branch lengths are in units of expected variance of change as required for use with Felsenstein's (1985) method. These were estimated by setting all branches between internodes on the phylogeny to the same length and setting branches leading to species such that the same total length is expected for all species. A: Phylogenetic relationships of 36 nonhuman primates used in Dunbar (1991). B: Phylogenetic relationships of 22 nonhuman primates from Dunbar (1992a).

ratio (regressing through the origin as required by Felsenstein's technique; Fig. 2). The least squares equation resulting from this analysis is:

$$\text{group size} = 10.47 * \text{neocortex ratio}$$

($r^2 = 0.13$; $p < 0.03$). The poor fit of this equation to the data is due in part to the large group sizes reported for *Miopithecus* and *Pan* in comparison to their closest relatives (these account for the largest and two smallest contrasts in group size). Contrasts in neocortex ratios were more homogeneous, with *Pithecia* and *Nasalis* showing slightly smaller neocortex ratios than expected given their phylogenetic histories.

Using a neocortex ratio of 4.1 for humans, the above equation predicts a human group size of about 42.9. This figure corresponds to the smallest level of societal groupings of modern hunter-gatherers (i.e., overnight band/camp), to the size of army rifle platoons (both as reported by Dunbar), and to what is generally considered an upper limit for a classroom with interaction between teacher and students. However, 43 is much smaller than the 148 predicted by Dunbar's regressions, and falls below the range of most of the cultural groups reported by Dunbar (e.g., Hutterite villages, military units, social networks, village size of modern hunter-gatherer societies). Furthermore, contrasts between humans and their nearest phylogenetic relatives (chimps and gorillas) in both neocortex ratio and predicted

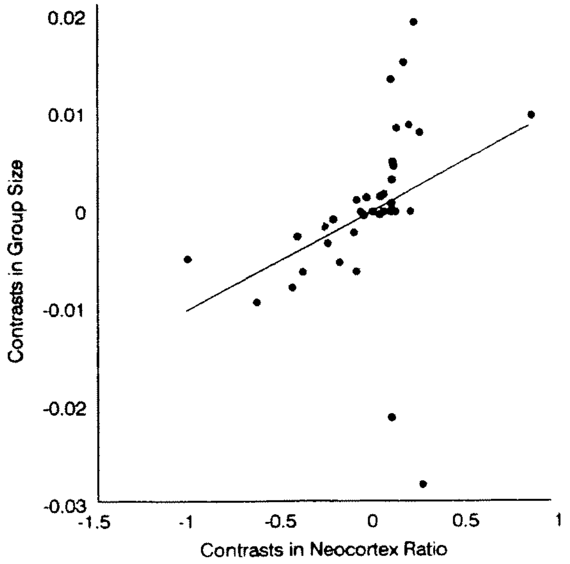

Figure 2 (Martins). Relationship between Felsenstein contrasts in neocortex ratio and group size in 36 species of nonhuman primates after correcting for phylogenetic relatedness (data as in Dunbar 1992a). Felsenstein's (1985) method was used to create 35 standardized independent contrasts between pairs of species. Least squares regression through the origin yielded the prediction equation: group size = 10.47 *neocortex ratio (r^2 = 0.13; $df = 34$; $p < 0.03$). Human neocortex ratio of 4.1 yields a predicted group size of 42.9.

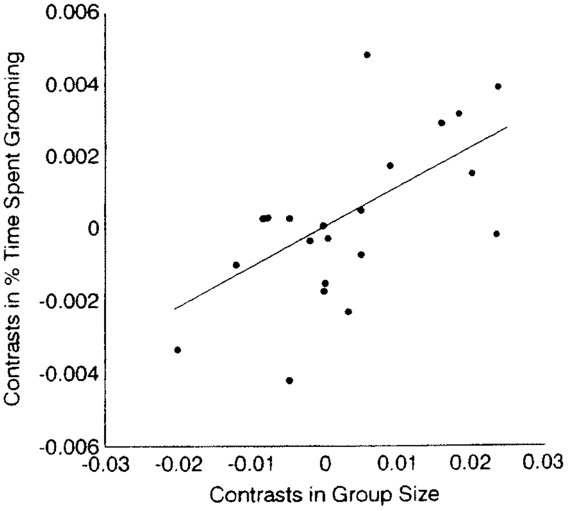

Figure 3 (Martins). Relationship between Felsenstein contrasts in group size and percentage of time spent grooming for 22 species of nonhuman primates after correcting for phylogenetic relatedness (data from Dunbar 1991). Use of Felsenstein's (1985) method with least squares regression techniques yielded the equation: % time spent grooming = 0.12* group size ($r^2 = 0.39$; $df = 20$; $p < 0.002$). Using the phylogenetically predicted human group size of 42.9, this equation predicts that humans would spend 5.15% of their time grooming each other. Using Dunbar's nonphylogenetically predicted human group size of 147.8, the predicted proportion of time spent grooming is 17.74%.

group size fall well within the range observed for other primate species, suggesting that no further explanation for large human neocortex ratio is needed.

A similar sort of analysis can be used to predict from their group size the proportion of time humans should spend grooming. Applying Felsenstein's (1985) method to the data in Dunbar (1992a) and using the phylogeny in Figure 1B, I found that the equation

$$\% \text{ time spent grooming} = 0.11 * \text{group size}$$

yields a reasonably good prediction of nonhuman primate behavior ($r^2 = 0.39$, $p < 0.002$; Fig. 3). Using the phylogenetically predicted human group size of 42.9, this leads to a predicted human grooming time of about 5.15%. Even using Dunbar's predicted group size of 147.8, the predicted proportion of human grooming time is only 17.74%. Both of these figures fall well within the range of nonhuman primate behavior and far below the 42% predicted by Dunbar. Thus, they do not require any explanations regarding the use of language as a time-saving mechanism of maintaining social bonds.

In summary, by considering a phylogenetic hypothesis that differs from Dunbar's implicit assumption of a "star"-like relationship among the primate species, we find that human neocortex ratio and predictions of group size and time spent grooming (or its human analog) are not particularly unusual and may not require any explanation beyond the phylogenetic relationship of humans with their evolutionary relatives. Until more accurate phylogenies are available, analyses with several possible phylogenies may be necessary to determine the range of results possible with any comparative study.

A developmental look at grooming, grunting and group cohesion

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The causal relationships Dunbar proposes link ecological demands, neocortical size, and living-group size for various primate species and are primarily of theoretical interest. Yet he treats his primary theses as subject to empirical validation (sect. 4, para. 8), even to the point of being willing to predict living-group sizes for extinct species from cranial fossil evidence. Although Dunbar cites evidence linking grooming time to group size, those reports (Cheney & Seyfarth 1982; Dunbar 1984) seem to reflect single species analyses. To provide evidence that group cohesion demands larger percentages of grooming time as living-group size increases, actual grooming time should be analyzed in relation to varying group sizes within and across species.

In applying these interpretations to modern humans, Dunbar skirts statistical limitations in predicting beyond the range of the datasets from which his regression equations were derived. He justifies this extension on the basis of the resultant wide confidence intervals and the exploratory nature of the analyses. Paradoxically, he wishes to argue by example, demonstrating that many human groups do fall into the predicted interval. The larger the interval the more likely that this procedure will meet with success.

Despite these technical difficulties, the theoretical notion of an overlap in function between grooming and vocal communication that might have facilitated the evolution of language in humans is interesting. The proposed underlying function is a "bonding mechanism" (sect. 3.4). It is common to argue either side of the thesis that ontogeny recapitulates phylogeny. Of equal interest is the idea that every evolutionary change proposed must have entailed developmental mechanisms to ensure that the adult behavior would emerge in new members. Considered from a developmental perspective, both touch and vocalization are effective in developing maternal/infant bonds across species. The success or failures of such bonds has been demonstrated to influence adult development.

Werner and Kaplan (1963) proposed a motivational system for the development of representation and language in human infants that emphasizes the influence of social bonds in the context of gradually increasing cognitive capacity. This view may prove fruitful in considering the question of development in both modern-day and extinct primate species; regardless of a given species' phylogenetic developmental ceiling, the adequacy of bonding and communication in adults must be ensured. [See also Kraemer: "A Psychobiological Theory of Attachment" *BBS* 15(3) 1992.] This developmental view supports the representational aspect of language evolution recently emphasized by Bickerton (1990; see also Bickerton: "The Language Bioprogram Hypothesis" *BBS* 7(2) 1984) and provides a rationale for linking representational and communicative development. Werner and Kaplan proposed that expanding cognitive capacity necessitates an implicit recognition of separateness on the part of the infant and concomitant efforts to ensure continued contact, first through primitive communicative activities and eventually through representational ones. They suggested that "call-sounds," more recently identified as "grunts" (McCune 1992), are a primary prelinguistic vehicle promoting the onset of language. Finding that referential language emerged in children who had previously demonstrated phonological readiness and a capacity for mental representation soon after grunts were used communicatively, McCune proposed that such grunts, originally occurring with abrupt glottal release as an involuntary accompaniment to movement or effort, might become dissociated from their original contexts and serve in the "effort" to communicate with adults.

In seeking an evolutionary source for language in natural primate communication Dunbar targets "contact calls," termed "grunts" in the nonhuman primate literature (Cheney & Seyfarth 1982; Struhsaker 1967), as a possible nonhuman primate analog to human social conversation. McCune et al. (submitted) summarize literature indicating the common occurrence of this form of communication across modern primate species, including vervet monkeys (*Cercopithecus aethiops*, Cheney & Seyfarth 1982; see multiple book review *BBS* 15(1) 1992), chimpanzees (*Pan troglodytes*, Goodall 1986), and mountain gorillas (*Gorilla gorilla beringei*, Fossey 1972; Schaller 1963). Struhsaker (1967) provides a comparative review of field studies indicating that some grunt forms are also used communicatively by baboons (*Papio sphinx*), platyrrhine monkeys (*Aotus trivirgatus*), and gibbons (*Hylobates lar*) (see Struhsaker 1967, Table 8, pp. 320–21).

These calls most commonly function to predict or regulate movement or to acknowledge conspecifics, sometimes with the grunt form varying in relation to the animals' rank. Data reported by Cheney and Seyfarth (1990, p. 129) suggest a three-year course in the development of the adult form and function of vervet grunts, with the possibility that they originated in accompanying movement (McCune et al. submitted).

Of particular interest in relation to the target article is Andrew's (1976, p. 675) report of the baboon's tendency to "superimpose such grunts on the tongue and lip movements of grooming or incipient grooming" yielding a modulated humanoid grunt display that "is derived from intention movements of grooming and apparently serves much the same function as mutual grooming, but can be performed at a distance," a view similar to the dissociation hypothesis noted above. Andrew also presents acoustic evidence that these glottally produced calls reveal resonances of the vocal tract, and thus the potential for developing discriminate grunt forms. Cheney and Seyfarth (1982) presented acoustic evidence suggesting that grunts recorded in four functionally distinct situations are discriminable when played back out of context to other animals in the troop.

In adult human conversation gruntlike vocalizations persist and are among the forms that indicate continued attention to the speaker on the part of the listener (Schlegoff 1972; Woods 1978); they thus seem to serve a "cohesive" function like the one suggested by Dunbar. There is no reason to suppose that a single vocal form will provide a missing link between language and prelanguage. However, a form that is similarly produced across modern species, including humans, provides one possible starting point for exploring its range of use and developmental course.

Grooming is not the only regulator of primate social interactions

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Dunbar's intriguing hypothesis uses the correlations among neocortical size, group size, and grooming rates in nonhuman primates to argue that the primary selective pressure acting on the evolution of human language was the need to develop a more efficient method than grooming for establishing and maintaining social bonds. Dunbar is one of the leading theoreticians in the study of primate social structure, but in this case his hypothesis seems premature.

There are good reasons for suspecting that grooming plays a major role in regulating social bonds in nonhuman primates, but in this target article grooming assumes paramount importance, at least in part because no other patterns of behavior are really entertained. It is especially curious that in discussing the evolution of human language most of the target article dismisses those aspects of primate behavior that are probably most similar to the antecedents of human language – the vocalizations of contemporary monkeys and apes.

With the exception of a few concluding paragraphs, Dunbar's discussion ignores virtually all research on the vocalizations of nonhuman primates. (Indeed, these last paragraphs appear almost as an addendum, and come perilously close to contradicting Dunbar's contention that social relationships are maintained by grooming rather than by vocalizations.) By erroneously implying that the only analysis of the acoustic structure of primate "contact" calls has been conducted on geladas, Dunbar dismisses with scant discussion the growing literature on both the phonetic structure of primate vocalizations and the role of vocalizations in regulating social relationships among contemporary monkeys and apes. The statement that "among primates, the cohesion of groups is maintained by social grooming" implies that vocalizations are *known to play no role* in the regulation of primate social relationships. Dunbar further implies that selection began to act on vocal communication – and ultimately led to the evolution of language – only as group size increased beyond that typical for contemporary monkeys and apes, when grooming no longer sufficed as a mechanism for maintaining social bonds. Consequently, the selective pressures acting on vocal communication in monkeys and apes today cannot be similar to those that acted on the evolution of human language.

We still know very little about the relationships among group size, encephalization, size of vocal repertoires, rates of vocalization, vocal exchanges, or the specificity of call meaning in nonhuman primates. This lack of information, however, should not be taken as an indication that nonhuman primate vocalizations are unimportant in the maintenance of social relationships, even when groups are small. No study has yet determined the relative importance of grooming, as opposed to vocalizations, in the establishment and maintenance of social relations in nonhuman primates. In his brief discussion of monkey vocalizations, Dunbar remarks that social bonds among geladas may be manifested in part through vocal exchanges; he suggests that the large size of gelada groups may have favored the use of vocalizations as a supplementary mechanism to regulate social relationships. Such supplementary mechanisms may be unnecessary in smaller primate groups. Gorillas, however, also exchange calls at high rates (Seyfarth et al., in preparation), even though group size rarely exceeds 15 adults and there is presumably little constraint on grooming time. Should we conclude that vocal exchanges serve a different function for gorillas than they do for geladas?

It seems likely that vocalizations – like grooming – have always played a major role in structuring the social relationships of monkeys and apes. This in turn means that our speculations about the evolution of language may well become more informed if we are able to uncover the general rules that link social organization, group size, and patterns of vocal communication – just as Dunbar and others have done in their analysis of grooming.

The difference between this and Dunbar's original presentation may seem subtle, but it constitutes a major shift in focus away from grooming as the *sole* regulator of nonhuman primate social relationships, and a major shift in the way we think about – and study – the vocalizations of contemporary nonhuman primates. Here is an example of what we mean. Dunbar (with acknowledgment to Byrne) suggests that language might function better than grooming as a mechanism for social bonding, because language "permits the acquisition of information about third party social relationships" and allows one individual to learn about others without interacting with them directly. However, as both Dunbar and Byrne know well, there are many studies showing that nonhuman primate vocalizations (though not a language) permit monkeys and apes to learn about social relationships in which they are not themselves involved (reviewed in Cheney & Seyfarth 1990). Moreover, even observational studies have documented that monkeys and apes routinely exchange vocalizations in the absence of any other behavioral interaction. Grooming, in other words, is not the only means by which primates regulate their social relationships (for a number of other examples, see Seyfarth 1987; Snowdon 1988), and at least one of the "unique" social benefits Dunbar attributes to language is already present in the vocal communication of contemporary nonhuman primates.

A second point – not discussed by Dunbar – concerns the cognitive demands placed on individuals as group size increases. Humans, we know, think about social relationships not only in terms of the particular individuals involved but also in terms of concepts or categories: types of social relationships that do not depend on any single perceptual feature. When someone mentions a father, colleague, or boyfriend, we immediately know something about this relationship even before meeting the individuals involved. By thinking of social relationships in terms of categories, humans are better able to transfer their knowledge to new stimuli and to predict the behavior even of those they have never met. Dasser's (1988) experiments suggest that monkeys also think of social relationships in terms of abstract categories (see also Cheney & Seyfarth 1990, pp. 86ff.), but to date the evolutionary advantages of social concept formation – and the selective pressures that gave rise to it – have rarely been considered.

It seems probable that the selective pressures favoring the formation of social concepts will be particularly strong under three conditions: when group size is large, when individuals transfer between groups or interact at high rates with the members of other groups, and when the formation of alliances is common (Seyfarth & Cheney, in press).

In relatively small groups, for example, an animal can easily memorize all the interactions he has seen and can form associations of different strength between different individuals. As group size increases, however, the number of dyadic relationships increases algebraically, placing severe constraints on an individual's ability to remember the specific characteristics of every social bond. Faced with the problem of remembering an increasing number of separate entities, both human and nonhuman primates (e.g., Swartz et al. 1991) typically recode items into larger units. The result is a measurable improvement in recall and prediction. Similarly, among group-living primates, increasing group size may place increasingly strong selection pressure on individuals to organize social relationships into types. Interactions among many groups further increase the number of animals with whom an individual must interact, while transfer between groups favors those individuals who can predict the behavior even of those with whom they have not previously interacted. Finally, in groups where alliances are common, an individual who attempts to gain a social and reproductive advantage must be able not only to predict other animals' behavior but also to assess their relationships with other individuals (Harcourt 1992; Seyfarth & Cheney, in press).

We therefore suggest that increasing group size is likely to have affected many aspects of social behavior not discussed by Dunbar. As just one example, larger groups are likely to have affected not only the use of vocalizations to regulate social behavior but also the cognitive mechanisms that underlie the perception and classification of social relationships.

The rest of the story: Grooming, group size and vocal exchanges in neotropical primates

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For some reason most writers attempting to formulate theories relating the behavior of nonhuman primates to that of human primates restrict themselves to discussing a very limited subset of Old World monkey and great ape species. This is true of recent reviews of male aggression toward females, of dispersal, of mate choice, and now of the relationship of grooming to the origins of language. While these authors compile interesting "just-so" stories based on a limited selection of species by presenting only part of the data, they effectively ignore the diversity of primate behavior that should lead them to develop more complex, sophisticated, and thus scientifically more useful theories than they do. The present target article is no exception.

New World primates in particular have been excluded from consideration for the present article, which is a pity, because some easily obtained data on New World primates directly falsify some of Dunbar's assertions. Social grooming is said to be involved in maintaining group cohesion and reducing intragroup aggression in Old World primates. Dunbar also claims that there is a linear relationship between amount of social grooming and group size. Yet data from neotropical monkeys directly contradict this assertion. Terborgh (1983) reports a negative correlation between group size and rest time, with pairs of *Callicebus torquatus* resting 54% of the day, the cooperatively breeding tamarins (*Saguinus* ssp.) resting 25–45% of the day and the large groups of squirrel monkeys (*Saimiri sciureus*) and capuchin monkeys (*Cebus* ssp.) resting only 11–18% of the day.

One might argue that resting time is not a true measure of grooming. This is true, but Dunbar cites resting time in chimpanzees as an approximation for grooming time. Studies that have explicitly investigated grooming in New World primates report that *Callicebus torquatus* grooms an hour a day (approximately 10% of the active day) (Robinson et al. 1986). Howler monkeys (*Alouatta* ssp.) that live in somewhat larger groups spend only 2% of the day grooming (Crockett & Eisenberg 1987), and muriquis (*Bracyteles arachnoides*) living in groups of 20–48 have never been observed to groom during a 10-year longitudinal field study (Strier 1992). Not only is there a negative correlation between group size and time resting or grooming, there is also a negative correlation between body size and grooming. Although body size does not specifically predict neocortical size, the great variation in body sizes among neotropical primates suggests a likely inverse relationship between grooming and neocortical size.

So how can we interpret these data? Terborgh (1983) also reported a positive relationship between group size and time spent foraging and feeding. Animals that must travel widely to find food will have much less time to engage in social grooming. What is the relationship between group size and time spent foraging in those species selected by Dunbar? Foraging demands may provide a more parsimonious explanation for grooming than either group size or neocortical size.

Dunbar cites Richman's (1976; 1978; 1987) work on vocal exchanges in gelada baboons as indicative of a possible nonhuman primate precursor to gossiping. He further notes that geladas live in relatively large groups. However, Dunbar has ignored the large body of data indicating extensive vocal exchanges in New World primates, where the rate of vocal exchange is not clearly related to either group size or body size. Snowdon and Cleveland (1984) described conversational turn-taking behavior in the pygmy marmoset (*Cebuella pygmaea*), the smallest monkey. Smith et al. (1982) described a call used by female squirrel monkeys that was exchanged only between females who had a close friendship. Robinson (1982) described a set of vocalizations used by capuchin monkeys (*Cebus olivaceus*) to regulate spacing within foraging groups. Titi monkeys (*Callicebus moloch*) have elaborate duets between mates each morning similar to the singing behavior of gibbons (Robinson 1981). Indeed, the New World primates have a complexity of vocal structure and complex vocal sequences that appears to be unmatched by any Old World primate studied to date (see Snowdon 1989, for review). If the grunts of vervet monkeys and the contact calls of gelada baboons are possible functional precursors of human gossip then one cannot ignore the much larger literature concerning calls with similar functions in New World primates.

Even among Old World primate species the data presented appear to be limiting. Although the names of the species contributing to Figure 3 are not presented, the upper limit of group size at 50 suggests that certain interesting species were not included. There is a subspecies of black and white colobus found in the Nyungwe Forest in Rwanda that has a stable travelling group of 300–350 members. Japanese macaque (*Macaca fuscata*) groups can be as large as 300 before fissioning into separate groups. It would also be interesting to know what proportion of the species in Figure 3 are arboreal. The one common feature of neotropical primates is that they are all arboreal. I suspect the pressures of an arboreal life are more likely to lead to complex vocal interchanges among group members than either group size or neocortical size.

Because of the limited data presented I am left unable to evaluate the theory presented here. Had Dunbar reviewed the broader literature to include New World primates and arboreal Old World primates he would have been led to raise questions similar to those I have raised here. He would have been either able to provide a refutation of these points leading to a stronger defense of his theory or forced to develop a more complex theory. As it stands, I am unable to determine whether this theory is science fantasy or science fact until I am presented with the rest of the story.

Social complexity: The roles of primates' grooming and people's talking

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Social complexity and brain power: What complexities still evade us? Dunbar's work raises study of the evolution of social intellect to new levels. In 1988 Byrne and Whiten were able to assemble a substantial range of findings that fleshed out what it means to say that anthropoid primates are socially complex, with social intellect to match. [See also Whiten & Byrne: "Tactical Deception in Primates" *BBS* 11(2) 1988.] However, no strong claim could be made to test the Machiavellian Intelligence hypothesis (that cognitive ability is explicable principally as a social adaptation) against the principal alternatives, which appeal instead to the challenges of primate feeding ecology. Thus, together with the findings of Sawaguchi (1990), Sawaguchi and Kudo (1990), and Barton (see his accompanying commentary), Dunbar's demonstration that the best correlate of neocortical ratio is group size and not variables related to foraging represents an important advance in testing of the prediction made by the Machiavellian hypothesis.

It is important to emphasize at this juncture, however, that although it is becoming common to refer to *the* Machiavellian Intelligence hypothesis (or social intelligence hypothesis), several hypotheses should really be distinguished (Whiten & Byrne 1988a). Two in particular have very different implications, but they are elided in tests that rely on the size of the brain or the gross size of major brain components such as the neocortex. The first of these subhypotheses is that intellect, considered as a set of generalised but high-level cognitive abilities, was selected for primarily by the complexity of anthropoid primates' societies. The second subhypothesis is that such selection has led to an element of intellect specialised for dealing with the social world (a social cognitive module) so that individuals might be more sophisticated in their cognitive dealings with the social world than with the nonsocial world. Cheney and Seyfarth (1988; see also multiple book review of "*How Monkeys See the World*," *BBS* 15 [1] 1992) have attempted to test this second alternative with what they interpret as positive results. However, the tests using brain volumes have not been able to make the distinction between general and socially dedicated processing. Perhaps with more understanding of the processing of social information in the brain (Brothers 1990) these subhypotheses will one day be differentiated in such analyses. We should also remember that "intellect" is itself a complex of elements that need to be distinguished before any sophisticated understanding can be gained of the linkage with aspects of social complexity (Whiten & Byrne 1988b), and analyses resting on gross size of brain parts are thus a relatively crude if important building block in the study of Machiavellian intelligence.

Where does social complexity lie? The measure of social complexity that Dunbar's analysis relies on is the number of individuals in the group. But there are many other sources of social complexity in primate groups that may select for advanced cognitive ability. A few candidates include the frequency of polyadic interactions; the rate of change of various classes of relationship; the number of factors required to predict the outcome of interactions; and variations in interactant's responses. We have barely begun to develop measures of these (one of our current projects is attempting this, for baboon groups of different size), but as such measures *are* developed, it should be possible to insert them into multivariate analyses of the type Dunbar reports. Kudo et al. (in preparation) have taken one important step in this direction by focussing on the size of primary networks or grooming cliques.

Dunbar could be clearer on where exactly he proposes the group size effect operates. Do I detect a slippage in what is proposed, particularly between the crucial analyses of nonhumans and humans? Discussing primates, he argues that the group-size/grooming-time relationship reflects time invested by small subsets of friends, the payoff for which is buffering with respect to the antagonism of other group members, which is greater in bigger groups. But in introducing the human language argument, there is a shift to talk of "cognitive capacity to manage all the relationships involved in large groups" and "time to devote to servicing those relationships," with the assumption that "grooming functions to integrate large primate groups." This seems a different function from the one implied by the earlier conflict-between-primary-networks formulation, and this conflict formulation does not seem consistent with what we may assume to underlie the operation of many of the human groups Dunbar refers to. In the military company or the business organisation the magic number of about 150 presumably reflects the size within which everybody pulls together, rather than, as implied by Dunbar's primary network logic, the size of the group within which small bands of friends need to spend a lot of time "bonding" to withstand harrassment by their colleagues. Whether the underlying bonding argument is one relying on cooperation across the optimal group size or conflict within it needs to be clarified.

What are the payoffs to the individual of grooming, or talking? No doubt it is unintentional, but Dunbar often argues in a way that may be taken by some as the sort of group-selectionist reasoning they feel comfortable with! Thus, amongst possible examples we have: "groups are held together by social grooming." But surely the benefits of grooming must be to individuals? And "grooming is used . . . to service . . . friendships." But what does "servicing" really mean here? We cannot assume that "friendships" and "bonding" are selected for in their own right, but rather through their benefits to individuals who treat grooming or being groomed as the basis of a "bond" that has future payoffs such as reciprocated grooming or help in fights. This becomes critical when we come to the hypothesis that talking replaced grooming. Why should an individual *A* accept being chatted to by *B* as the basis for adopting an attitude of being "bonded" to *B*, so that *B*'s chatting reaps future benefits through some form of future aid by *A*? In both cases it would seem that the grooming or the chatting must be *worth something* to *B*. The cleansing function of grooming could count here (Barton 1985), but what of talking? The first of Dunbar's suggestions, that it facilitates spending time with the partner, seems unconvincing because that can be done without any talking or grooming, and indeed one can easily observe 4 or 5 baboons quietly sitting together and observing each other as much as they wish. The second suggestion, Byrne's "gossip about others" (Emler 1990), and indeed all the talk about personal experiences and relationships so nicely revealed by the refectory study, are much more plausibly worth something to the Machiavellian individual: however, this would appear to rely on language having reached quite sophisticated levels of syntax, so I remain to be convinced that this could explain the *origin* of language – the critical issue of what could have been "the first utterance" (Whiten 1993). It seems more likely that simple presyntactic utterances could have been used to clarify those intentions that grooming already suggests: grunt-*A* signalling my preparedness to act as your friend in future contexts perhaps; grunt-*B*, with a glance at another individual, signalling my intention that our friendship be directed against him. Some primate vocalisations already carry information about attitudes to different categories of interactant (Gouzoules et al. 1984).

Finally, however, there is a simpler alternative that could act as a springboard for such developments, or perhaps function usefully in its own right: that simply *to be seen by others* grooming with high-ranking *A*, or chatting with high-status *B*, is worth something to the individual because of what this advertises with respect to future coalition. In this case, however, both interactants would need to reap the payoffs elsewhere than in immediate benefits of grooming or chatting per se.

Did primates need more than social grooming and increased group size for acquiring language?

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Dunbar's assumption that "social grooming" provides the preadaptation for the origin of linguistic communication is certainly a fresh, elegant, and scientifically sound approach to solving the puzzle of language origins. His method of reconstruction, however, although it nicely combines anthropological, biological, and primatological data, seems to leave a few questions unsatisfactorily answered.

I did not fully understand Dunbar's solution to the central chicken-egg question here, that is, what came first: neocortical size increase or the increased need for grooming? Such a question could of course be solved most elegantly by finding an ecological trigger that initiated one of the two and that worked only in one particular group of small-brained hominids ancestral to the *Homo* lineage. For example, in section 3.3 Dunbar states: "speech . . . might have evolved as a consequence of the need to increase group size." Could speech not have allowed group size to increase? Also, in section 4 Dunbar speaks of this "need" as occurring at some point in human (does he not mean "hominid"?) evolution. His even more strongly anthropomorphically colored statement later in that section seems to contradict his earlier ones: "Just why early humans should have found it necessary to evolve such large groups remains uncertain." Proposing some selective (e.g., ecological) force might have been helpful here. (In the subsequent paragraph Dunbar states: "Humans['] . . . larger group sizes . . . cannot have appeared by magic for no good reason." I assume that his using "reason" here is a consequence of loose use of the English language, that is, indicating "cause" rather than anthropomorphic tendencies.)

What are the consequences for Dunbar's theory of taking into account the differences in deleterious effects of inbreeding between the different-sized primate groups? Retropolating from modern clinical and extrapolating from primatological genetical data might assist in answering this question. Why does Dunbar speak (in sects. 1, 3 & 4) of the "evolution" rather than the "origin" of language? Does he really assume that language originated first and only changed after neocortical size had increased? Why would the increase in brain size have only become "marked" after *Homo sapiens*, and not after early *Homo* (*habilis* and *erectus*) originated (i.e., as compared with *Australopithecus*; sect. 4)?

In sections 3.3 and 4 Dunbar suggests that conventional wisdom has it that language arose from the need to exchange information (such as promoting hunting and toolmaking). Apart from other direct selective pressures that might have led to language, like increasing cognition, there undoubtedly were many more evolutionary processes that have added to the origin of language and speech. Some years ago I attempted to illustrate a number of processes that must have played a role in the origin of speech during primate evolution; see Figure 1. Further suggestions have been made in the publications that have originated from the meetings of the Language Origins Society (see von Raffler-Engel et al. 1991; Wind et al. 1990).

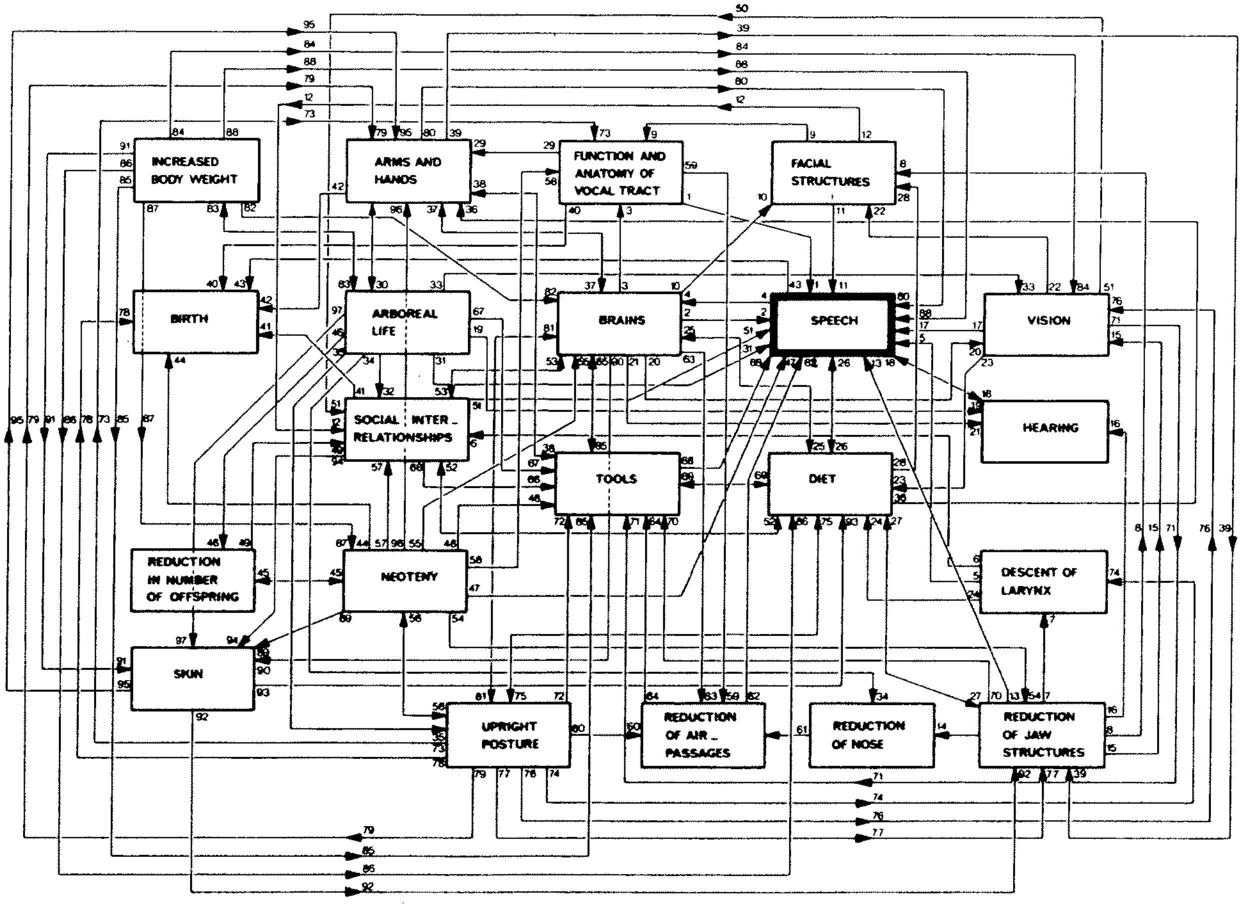

Figure 1 (Wind). A summary of a number of processes that must have played a part in the emergence of speech during primate evolution (from Wind 1983).

Author's Response

On the origins of language: A history of constraints and windows of opportunity

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> No one can keep all the problems and details clear, including me, and everyone has to mumble, guess, and handwave about large parts of the problem.
> Daniel Dennett (1991) *Consciousness Explained* (p. 255)

The commentary on the target article was so diverse that I have to begin with an apology. To respond in the detail that most of the commentaries deserve, I would need to write a book. This, in many respects, was the problem with the target article itself: for reasons of space I was obliged to gloss over many issues, some of which had been dealt with in previous publications. Unaware of this, many commentators raised points they interpreted as unsubstantiated assertions. I shall endeavour to clarify these here. However, limitations of space mean that, in my response, I can deal with only a small fraction of the points made: except for direct challenges to key points or serious misunderstandings of my argument (of which there are several), I have limited my responses to issues that were raised by at least three commentators.

The argument developed in the target article consists, as many commentators noted, in four principle assertions, and it is inevitably on these that most comments have focussed. I propose to deal with them in their natural logical order in the following four sections. In addition, a number of commentaries raised more general issues concerning evolutionary arguments. Some of these are fundamental points that apply widely beyond the scope of this article. I deal with these in the final section.

R1. The relationship between neocortical size and group size in primates. The first proposition is that group size correlates with neocortical size in primates and that this reflects a cognitive constraint on the number of individuals with whom an animal can maintain a coherent stable relationship. The justification for this claim was presented in detail in Dunbar (1992a), and I simply took the relationship as given here. Perhaps the most fundamental issues raised in the commentaries concern the indices used in deriving that relationship.

The fact that the neocortex cannot be treated as a single neurological unit was raised by a number of commentators (**Falk & Dudek, Glezer & Kinzey, Holloway**). I would not pretend otherwise, but the problem (highlighted by both Holloway and **Jerison**) is that the data are simply not available for a finer-grained analysis. I can only invite the neuroanatomists among you to give us better data so that we can tackle the problem in more detail. That much having been said, however, the extent to which the data fit the regression line (see also below) calls for explanation: we cannot ignore this fact merely on the grounds that treating the neocortex as a unit does not happen to fit our preconceptions of how things ought to be. There may be good neurobiological reasons why (at least for the kinds of problems considered here) it *should* be treated as a single unit, even though from a neurological point of view it should be compartmentalized. We surely know too little about the brain to prejudge the issue.

The converse problem of how to measure social complexity was raised by **Andrew, Deacon, Freeman, Hauser et al., Jacobs & Raleigh, Jerison,** and **Whiten.** I am as aware as anyone else that group size is ultimately an inadequate measure (see Dunbar 1989a), but, once again, it is the only one we have that can easily be quantified. This time it is up to us field biologists to do better; however, we do need to know what it is that we should be measuring. If the least to emerge from our analysis is a better idea of what we should look at, this will have been a profitable exercise. We are, in fact, already working on this problem: Kudo et al. (in preparation) are analysing grooming networks in just the manner suggested by Freeman. In addition, **Byrne** provides us with evidence that the use of deception correlates with relative neocortical size. Other studies need to be encouraged. That much having been said, however, it would be naive to suppose that group size has nothing at all to do with social complexity: it does at least capture one aspect of the problem, namely, the number of dyads that an animal has to keep track of.

In this context, and given my emphasis on cognitive constraints, it seems reasonable to question my use of mean rather than maximum-ever-observed group size (**Hauser et al., Kincaid**). I can only reiterate the discussion of this point in Dunbar (1992a): if primates were dungflies, then group sizes would follow an ideal free distribution, where the largest ever observed would be the largest that the animals could keep together. Primates (or at least the catarrhine primates I am familiar with) are not dungflies: their groups depend on bonding between specific individuals who cannot easily leave on their own to find a smaller group whenever group size exceeds the optimal one (see Dunbar 1988). (I am concerned here primarily with the philopatric sex – usually females – since in primates it is these individuals who give social groups their structure and coherence.) Before such groups can undergo fission, they have to achieve a size that will ensure that the smaller of the daughter groups exceeds the habitat-specific minimum for survival. This will commonly result in groups exceeding their ideal size for a significant period of time, during which they will invariably be socially fragmented (for evidence, see Dunbar 1992b).

We are interested here in the largest group that a species can hold together as a coherent unit for an indefinite period of time (in the absence of increases in size), not the largest number of animals that can remain momentarily in one place (irrespective of the coherence of their relationships). Social coherence is not an all-or-none affair, but a probabilistic phenomenon that presumably tends to zero in the largest-ever-observed group. I suggest that mean group size will yield a better estimate of the critical limiting value (if only because it will partial out some of the habitat-determined variance in group size). In addition (and this is crucial for the use of regression analysis), mean group size is less likely to be subject to sampling error than the largest observed group size (which will underestimate the true maximum except when very large numbers of populations have been censused). I do not claim that the observed mean group size *is* the limiting group size; merely that, for the moment, it is probably the best index we have.

Jacobs & Raleigh are worried about the apparent primatocentrism of my argument, observing that this is a common failing in analyses of (human) brain evolution. For once, however, the primatocentrism is deliberate (and unavoidable). The Machiavellian Intelligence hypothesis that underpins my argument is specifically concerned to explain why primates have significantly larger brains than all other animals; it hinges on the unique nature of primate groups (tightly bonded relationships made possible by deep social knowledge). Only if these conditions are met would my argument be expected to apply to nonprimates. Having worked extensively on a number of species of the Order Artiodactyla (see, for example, Dunbar & Dunbar 1980; 1981; Dunbar et al. 1990; Dunbar & Roberts 1992), I can reassure Jacobs & Raleigh that I am unimpressed by the social skills of the members of this particular taxonomic group. I am sure they are right in suggesting that the Cetaceans would be an appropriate group on which to test the hypothesis (Joan Silk and I are in the process of trying to do so), but such an analysis is not strictly a test of the theory: it merely concerns whether the theory *also* applies to Cetaceans. Would they want to insist that theories intended to explain the evolution of mammary glands are only valid if they can be shown to apply to reptiles as well as to mammals? If it is any consolation, however, it does seem that the relationship applies in at least some other orders: R. Barton (personal communication) has found that relative neocortical size is significantly larger in those species of bats that live in stable social groups than in those species that live in unstable aggregations. The problem is not an unwillingness to test the hypothesis on other groups but the lack of appropriate data. I fully endorse **Jerison**'s suggestion that we exploit the technology now available to determine brain part volumes for a larger sample of taxa.

The relationship between group size and neocortical size implies that evolutionary changes in primate brain size have occurred as a consequence of social rather than ecological selection pressures. This is the burden of the analyses presented in Dunbar (1992a), where I sought to test between the competing hypotheses for the variation in brain (principally neocortex) size within the Order Primates. I was therefore surprised that some commentators should continue to insist that brain size in primates relates only to ecological variables such as diet, as originally suggested by Clutton-Brock and Harvey (1980) and Sawaguchi (1988) (**Deacon, Foley, Glezer & Kinzey, Harcourt**).

There are two problems here. First, none of these earlier analyses scaled their ecological variables for body size: a $1 km^2$ range is something very different when seen through the eyes of a 200g lemurid or a 20kg baboon. Partialling out the effect of body size removes any correlation between these ecological variables and neocortical size. Because group size, brain size, body size, and ranging behaviour all covary, it is necessary to be especially careful in partialling out their respective effects. Second, as both Willner (1989) and Deacon (1990) have pointed out (and Dunbar [1992a] has shown), body size is more labile than brain size and can increase or decrease well in advance of compensating changes in brain size. Some measure that is more consistent internally is needed to control for scaling effects when considering the brain. As it happens, it is the neocortex that has (mainly) undergone significant evolutionary change within the primates, with the other structures (and especially the hindbrain and midbrain) remaining more constant in relative size. It was for this reason that I chose to scale neocortical size against the volume of the rest of the brain.

This does not (as **Deacon** suggests) lead to scaling neocortex against itself: this would only be true if total brain size were limited and it were necessary to trade the size of the neocortex against the size of the rest of the brain. To my knowledge, no one has yet shown that such a constraint exists (except perhaps in birds, where the physics of flight makes a difference). In addition, the assumption that brain size has to be scaled to body size (or anything else) has been challenged: some neuropsychologists take the view that it is absolute size, not relative size, that is important. (I thank both Dick Byrne and Sue Parker for pointing this out to me.)

In any case, the issue is largely academic: Barton and Purvis (in press) have shown that although total brain volume (relative to body mass) correlates with both group size and range size (an ecological variable), only group size correlates with relative neocortical size (see also **Barton**). It seems likely that other structures within the brain correlate with ecological variables (as the hippocampus does with range size but not with group size, presumably reflecting the demands made on memory capacity by foraging strategies or mental maps; see Barton and Purvis, in press).

Finally, let me touch briefly on the question of what determines group size. Several commentators correctly noted that group size is determined by ecological selection pressures and therefore questioned the relevance of neocortical size (**Dugatkin & Wilson, Foley, Glezer & Kinzey, Wind**). It is important to be clear about the logic of the argument here. Seen from a historical (i.e., phylogenetic) perspective, the range of group sizes (and hence the mean size) typical of a species is a consequence of ecological selection pressures that reflect the habitats within which that species typically lives; the cognitive machinery designed to realise these group sizes is a consequence of the selection pressure exerted by the advantages of larger groups in those particular habitats. The causal sequence in evolutionary terms is: ecological factors determine group size, which in turn determines neocortical size. Seen from the point of view of the individual animal in the here-and-now, however, its cognitive machinery is not something that can be adjusted: instead, the cognitive elements act as a constraint by imposing an upper limit on the size of groups that the animal can maintain. Neocortical size thus determines group size (which is why the analyses are all carried out this way round). Therefore (to respond to **Harcourt**'s query concerning constraints on group size), the group in which we observe a *particular* individual primate is a trade-off between the conventional size- and habitat-dependent costs and benefits (Dunbar 1988; van Schaik 1982), subject to *at least* two sets of constraints on maximum size that are due, respectively, to (1) habitat-specific time-budgetting problems (Dunbar 1992b) and (2) species-specific cognitive limits on the processing of social knowledge (Dunbar 1992a), as well as a habitat-specific constraint on *minimum* size due to the local predation risk (Dunbar 1988; 1992b). This is a simple linear programming problem in which the area contained within the intersection of these lines represents the range of realisable group sizes. Animals will presumably opt for the minimum group size they can get away with in a given habitat, but that group size will be *habitat*-specific. This means that ecology *is* the ultimate factor determining neocortical size, but it is not itself the factor that dictates a species' neocortical size: it is group size (and in particular, the way the groups are organised in primates) that, in proximate terms, drives neocortex evolution.

Given this, what are we to make of specific examples that appear to contradict the relationship? **Cords** and **Harcourt** note that some species of primates occasionally occur in much larger groups than those predicted by the relationship in Figure 1 (e.g., *Macaca fuscata*, which occurs in groups of up to 1,000 animals in provisioned populations; Rwandan *Colobus* monkeys, which are reported to occur in groups of 200–300). Although the significance of the Rwandan colobus will have to await detailed reports on the structure and stability of their groups, it is clear that the unusually large groups of *M. fuscata* are anything but stable: Mori's (1977) analyses show quite uncontroversially that interindividual relationships begin to become unstable at group sizes well below 100. If anything, Mori's data support my argument rather than refute it. In this context, the gelada also conform to the pattern: this species is commonly found in much larger groups (herds) than would be predicted by its (estimated) neocortical size, but these groups have no temporal stability. Neocortical size would predict something closer to the observed size of one-male units (the only coherent stable form of grouping found among the gelada). The real issue here goes back to the relationship between mean group size (the index used in the present analysis) and maximum-ever-observed group size (see above).

Several people have noted that the large-brained orangutan appears to lead a solitary lifestyle and would thus seem to be an inconvenient exception. However, it cannot in any sense be said to refute the hypothesis in the way **Dean** suggests (if only because the hypothesis simply suggests that one may not have groups larger than the cognitively determined maximum). We should, however, be cautious before jumping to conclusions on the basis of apparent brain size: the gorilla, too, has a large brain (even for body size), but its neocortex is very small and close to what would be predicted by its (very small) typical group sizes (Dunbar 1992a). In any case, I am not entirely sure why Dean thinks I should worry about one or two exceptions: given the complexity of the real biological world, we can only ever test hypotheses at a statistical level, hoping that the effect is strong enough to overcome the error variance introduced by confounding variables we do not yet know about. In real life, theories can only have no exceptions when their discovery is based on omniscience (a claim that I am not yet prepared to make). Only under what philosophers of science conventionally refer to as "naive Popperianism" do single counterexamples imply that a hypothesis is incorrect; Popper himself rightly emphasised that when a test fails it can either be because the theory is wrong or because the data are not a "fair" test of the theory. Common sense (and conventional practice in science) dictates that the first thing we should do is check the data.

As I noted in my original analysis (Dunbar 1992a), apparent anomalies of this kind should prompt us to ask whether we really know what the species' social system is like. In fact, most of the orang fieldworkers have commented on the apparent existence of stable communities of individuals that appear to know each other well. The same is probably true of many of the supposedly solitary prosimians, as both **Hauser et al.** and I (Dunbar 1992a) point out. I chose to assume a group size of one in these cases because it would act conservatively by increasing the error variance in the data (thus reducing the significance of any regression line). (In this context, let me correct an error of misinterpretation by Hauser et al.: at no point do I suggest that fission-fusion societies have been excluded from this part of the analysis. They were excluded only from the analysis of grooming time, for the reasons given below.)

The final problem in this section concerns the statistical analysis. **Barton** and **Martins** both draw attention to the fact that my analysis of the relationship between group size and neocortical size appears to ignore the effects of phylogenetic inertia. However, as should be clear from my discussion of the problem in Dunbar (1992a), this is not strictly true: after consideration of the issues I opted for a genus-level analysis on the grounds that, in primates at least, generic differences tend to correlate with major adaptive grades in ecological or reproductive strategies: generic means should therefore tend to be statistically independent samples. I thank both commentators for their careful demonstration that my original analysis was in fact correct: there is indeed a significant relationship between neocortical size and group size. Barton's analysis is especially important here (and also as a reply to Deacon's comment on removing body size effects), because he partialled out the confounding effects of body and brain size using a method different from the one I used.

Martins is mistaken, however, in asserting that the slope of the relationship is shallower than I originally claimed (with the result that the predicted group size for humans is only about 65). She used least squares regression, which consistently tends to underestimate the slope in these kinds of analyses because it assumes no error variance on the X-axis (see Pagel & Harvey 1988a). Although not perfect, reduced major axis (RMA, which assumes equal error variance) is likely to give a more reliable estimate of the true slope, given that there is sure to be error variance on both variables. In fact, the least squares regression equation for a simple comparison across genera (as in my original analysis) is virtually identical to that obtained by Martins, suggesting that there is a negligible effect due to phylogenetic inertia in the dataset (as I originally suggested). Martins's estimate of the slope is close to the lower 95% confidence limit on the RMA slope (and is within the range yielded by the different indices of neocortical size; see Dunbar 1992a).

One important reason for opting for RMA rather than least squares regression is precisely because we want to be able to predict beyond the range of data on which the original analysis is based (though not *so* far beyond that we should be quite as nervous about doing so, as **Kincaid** would have us be). Contrary to **Janson**'s presupposition, least squares is appropriate only for making predictions *within* the observed range; RMA is likely to give a more reliable estimate elsewhere precisely because it makes less extreme assumptions about the distribution of error variances. It is worth reemphasising that the RMA line using neocortex ratio turns out to be the median value obtained from all possible analyses using different methods to compute the regression slope and different indices for neocortical size. (I thank Mark Pagel for advice on the various statistical points, but he bears no responsibility for any errors that remain.)

R2. Can we predict a group size for humans? The second proposition is that we can predict the size of groups that humans live in on the basis of their neocortical size. Three main issues arise under this heading.

Hauser et al. suggest that the group size of one used for the prosimians is inappropriate; they suggest that if sleeping group size is used instead, the predicted value for humans is much lower (58–72). Unfortunately, they have used *maximum* sleeping group size for small-brained solitary prosimians (presumably because these are the only figures available in the literature), while continuing to use *mean* group size for everyone else (with their large brains). Not surprisingly, this significantly reduces the slope of the regression equation. It would have been more sensible to drop the solitary prosimians altogether. It is also not clear which regression method they used to estimate the slope (see above).

This does raise an interesting point, however. A more careful examination of the data reveals what appear to be striking grade differences between the prosimians, the nonape simians, and the apes. The RMA equations for these three grades are given in Table R1. For present purposes, I excluded large-brained "solitary" prosimians from the analysis for the reason given by **Hauser et al.** The ape equation is based on just three points. These equations differ in their intercepts but not in their slopes. One obvious interpretation of this is that the computing power required to handle social decisions at a given group size increases as the sophistication of the decisions (i.e., achievable levels of intensionality?) increases (see **Byrne**). The predicted group size for humans is 207.3 using the ape equation, 205.5 for the simian equation, and 1,903.2 using the prosimian equation. Considering the quality of the data and the exploratory nature of this exercise, I am happy to settle for the fact that the value predicted by the ape equation is within the 95% confidence limits on the original estimate. (Recomputing the ape equation by forcing it to have the same average slope as the other two grades gives a predicted value for modern humans of 146.0). The fact that the New and Old World monkeys appear to lie on the same grade, whereas the apes lie on a lower grade, is intriguing, and the matter clearly merits further investigation.

The second issue is the question of what should count as the appropriate group in humans (**Donald, Freeman, Glezer & Kinzey, Graber, Hyland, Jarvenpa, Kincaid**). There seems to be some misunderstanding of the argument here. Let me reiterate its logic. The regression equation predicts a specific group size for humans. I ask simply: Is there any evidence that such a group size exists in humans? I make no presumptions about what form that grouping should take (Donald, Graber), nor do I assume that hunter-gatherers live in pristine "natural" human societies (Graber, Jarvenpa). It seems obvious that the form of such a grouping will depend on the needs or dictates of the local ecology (*including* government intervention) and the cultural milieu. The point is that, in most (if not all) hunter-gatherer societies, ethnographers have identified a number of social groupings: the distribution of group sizes is trimodal (at least – it might even have four modes, if megabands at about 500 are distinguished from tribes at about 1,500), and one of these groupings invariably turns out to consist of about 150 individuals. Having found that numbers in the statistically acceptable region of 150 keep turning up, I then ask whether these groups meet the cognitive requirements on which the primate relationship seems to be founded. I suggest the evidence indicates they do: these groups do seem to be different from the many other kinds of grouping found in all human societies (which include other cognitively bound groups such as "empathy" groups of 11–12, ecologically determined groups such as bands, and sociolinguistically determined groups such as tribes). The definition of this level of grouping is very specific: the primate data (and the whole thrust of the social intelligence theory for the evolution of primate brain size) suggest that it should be defined as the number of individuals with whom you can maintain a coherent relationship (i.e., one that can be picked up again on meeting after an absence without any need to reestablish where you stand). One possible informal definition might be the number of people you would not feel uncomfortable about joining *uninvited* at a chance meeting in a bar.

Deacon doubts the validity of extrapolating from nonhuman primate groups to human groups in this context. I suspect that he speaks for many nonprimatologists in underestimating the intrinsic structural complexity of

Table R1. *Reduced major axis equations for mean group size plotted against neocortex ratio for separate grades for the data shown in Figure 1*

Grade	Equation	r^2	p	N
Prosimians	$\mathrm{Log}_{10}(N) = 0.419 + 4.688\ \mathrm{Log}_{10}(C_R)$	0.91	<0.001	7
NWM + OWM[a]	$\mathrm{Log}_{10}(N) = -0.221 + 4.135\ \mathrm{Log}_{10}(C_R)$	0.53	<0.001	23
Apes	$\mathrm{Log}_{10}(N) = -1.683 + 6.527\ \mathrm{Log}_{10}(C_R)$	0.89	—	3

Source: Data from Dunbar (1992a, Table 1).

[a] New World monkeys and Old World monkeys.

primate social systems. Contrary to his presupposition, primate social systems do not consist of simple, structurally homogeneous groups; rather, they consist of networks of relationships that are hierarchically structured, just as they are in human societies (see Dunbar 1988). This kind of nesting of social layers (each subserving a different function in the animal's life) may even be characteristic of the societies of all birds and mammals (Dunbar 1989a).

The third point concerns the historical record. **Hyland** notes that the archaeological evidence from campsites suggests groups of 25–50 in prehistoric communities during the critical period when language is likely to have evolved. This does not, however, tell us anything about whether or not these peoples' social systems *also* involved larger scale groupings. After all, modern hunter-gatherers typically live in camps of this size, but in addition they also exhibit at least two (and perhaps more) higher levels of social organisation that are no more likely to leave physical traces for the ethno-archaeologist to find than those from the fossil record. That it may prove difficult to test such predictions from the archaeological record (**Graber**) is bad luck for the archaeologists, but is neither here nor there for my argument. At best, it affects one element in the story (and one that, from an evolutionary point of view, is the least interesting: the timing of a phenotypic change is only interesting in determining who might and who might not have inherited a particular character from a common ancestor). Cosmologists face the same problem in studying the evolution of stars and we need to take a leaf out of their book and use theory to generate predictions about those aspects of behaviour that *do* leave traces in the record. The key lies in forcing competing hypotheses to generate contradictory predictions, and then identifying the kinds of evidence that might be relevant. Mithen's (1990) use of optimal foraging theory to predict neolithic midden compositions under different foraging strategies is an encouraging start in the right direction.

Four subsidiary comments: (1) Memory is not the limiting constraint here (**Freeman, Hauser et al.**): it is the computing power to manipulate knowledge about sets of relationships within the mental/social hyperspace that imposes the cognitive constraint. Setting names to faces is a much less demanding task than knowing how you relate to another individual, and using that knowledge in future interactions. In humans, the upper limit on memory for faces seems to be around 2,000 individuals (as Freeman indirectly notes) and the constraint may well be hippocampus size. I doubt whether either Freeman or I could seriously claim to have equally detailed social knowledge about all 2,000 members of our respective outer networks of acquaintances.

(2) **Dean**'s suggestion that electronic communications have greatly increased the size of human networks is, regrettably, unlikely to be true. Initial attempts to design the hardware for computer networks encountered just this problem when it was discovered that the chips then available would limit network sizes to around 250 nodes; however, extensive research suggested that people's networks were in fact typically in the order of 150 individuals, and thus safely within the limitations imposed by the hardware (D. Leevers, personal communication). (I was not aware of this at the time I wrote the target article.) Even if electronic mail has made it possible for Dean to communicate with more individuals, only a handful of those additional relationships are likely to meet the requirements imposed by the definition of a relationship given above. Counting entries in address books (but excluding business and other impersonal relationships) might be more informative: for two instances in which this was done, the figures were 144 (Glendinning 1993) and 135 (personal observation).

(3) I do not know where **Kincaid** obtained his figures, but only one estimate of *mean* group size (that for the Mae Enga of New Guinea) falls outside the 95% confidence intervals around the predicted value. It would be easy, but equally pointless, to observe that most (all?) primate species are occasionally found in groups that far exceed the species' mean group size (see above).

(4) **Janson** is right to point out that my estimates of the 95% confidence limits around the predicted value are technically incorrect. In fact, I was more interested in determining the range within which estimates of the slope would occur. I should not, however, have used these as a basis for evaluating the statistical significance of the difference between observed and predicted values. I am, of course, very happy to use Janson's corrected estimates for this purpose: their wider range simply increases the statistical significance of the fit between observed and predicted values (at worst, the estimates of mean group size for intermediate level groups given in Table 1 differ from the predicted value by no more than 0.19 standard deviations: $p > 0.85$ 2-tailed). Although it means that a wide range of possible values falls within the limits around the mean, this does not mean that the hypothesis is unfalsifiable (**Holloway, Janson**). We are interested not in testing the theory per se (the primate data do that), but in identifying possible equivalences in another taxon (i.e., humans). We can use Bayes' Theorem to ask which of the four possible groupings suggested by the distributions in Figure 2 is most likely to be the one predicted by the neocortex equation. Assuming equal prior likelihoods of $p_{Prior} = 0.25$ and using the probabilities associated with the appropriate z-values (based on Janson's 95% confidence intervals) to estimate the conditional likelihoods, a rough calculation yields posterior likelihoods of $p_{Post} = 0.106$ for bands (mean = 35), $p_{Post} = 0.894$ for intermediate groups ("clans"; mean = 150), $p_{Post} < 0.00001$ for megabands (mean = 500) and $p_{Post} < 0.00001$ for tribes (mean = 1,500). By any criterion, the intermediate grouping comes out as much the most likely candidate (likelihood ratio test on the two most likely candidates: $G = 4.265$, $df = 1$, $p < 0.05$).

R3. Function of social grooming. The third proposition is that there is a simple linear relationship between group size and grooming time in catarrhine primates (reflecting the fact that social grooming is the primary mechanism used in social bonding). This relationship applies both within and between species among the catarrhines (**McCune**: for examples of the former, see Dunbar 1992b; Iwamoto & Dunbar 1983). A number of queries were raised about these claims (**Harcourt, Hauser et al., Jacobs & Raleigh, Janson, Jerison, Whiten**), but I think most of the reservations expressed are based on misinterpretation.

The issue here is not grooming per se, but the opportunity for contact between individuals that grooming creates. Primates have only one source of information about other individuals' characters and foibles (the fundamental bases for any coalitions), namely, direct observation. My suspicion (and this is certainly the burden of the analyses of both grooming time [Dunbar 1991] and grooming networks [Kudo et al., in preparation]) is that primates rely much more heavily on ensuring that their intense primary networks (serviced by grooming) function effectively as coalitions than on attempting to acquire knowledge about every single individual in the group. It is conspicuous that in the gelada, for example, primary networks *decrease* in size (but are invested in more heavily) as group size (and hence the strains of coexistence, and thus the importance of alliances) increases (Dunbar 1984). In this context, grooming might serve either as a declaration of interest ("I would rather be here grooming with you than over there grooming with Fred") or as a mechanism for acquiring direct knowledge of how reliable another individual is as a social partner (or both); but other mechanisms are also possible. Enquist and Leimar (1993), for example, suggest that it may function as a test of the "sincerity" or honesty of an ally: the fact that alliances are more important and that "free riding" is easier in large groups would explain why grooming is linearly related to group size.

Janson, **Snowden**, and **Glezer & Kinzey** are right to point out that this argument totally ignores noncatarrhine primates. The evidence is quite clear, I think, that grooming subserves a largely hygienic function in platyrrhine primates (and prosimians; Barton 1985; Dunbar 1991). This is why I specifically limited the analysis of grooming time and group size to catarrhine primates: platyrrhines are, unfortunately, irrelevant to the story at this point.

Cords noted that by excluding fission-fusion species I necessarily generated a steeper relationship between group size and grooming time than would otherwise be the case. I did so for three very good reasons. (1) I did not know what group size to use for either the gelada, the hamadryas, or the Guinea baboons (three substantively fission-fusion societies with unusually large groups that would heavily weight any regression equation); I therefore thought it safer to exclude all fission-fusion social systems. (2) The point was, in any case, to establish a relationship that related to group cohesion, a property that is manifestly conspicuous by its absence in most fission-fusion societies (e.g., *Papio papio*, gelada). (3) It seems reasonable to assume that animals do not, in general, have an infinitely flexible time budget, and that the demands of foraging impose an upper limit on the amount of time they can afford to devote to social interaction: this, of course, represents a trade-off between the advantages of group size, the demands of foraging, and the time costs of grooming (Dunbar 1992b).

That such a limit exists is not the issue, however. The substantive question here is how much time they *ought* to devote to social interaction to maintain the cohesion of the group. We know that when baboons fail to devote as much time to grooming as they ought to (given the relationship indicated by Fig. 3), their groups are more likely to become socially fragmented and to undergo fission (Dunbar 1992b). By including species with super-large groups that already seem to have hit that upper limit, we learn only about the compromises the animals use to cope with reality, not what they ought to do when all other things are equal. This is a common problem in reverse optimality modelling (see Dunbar 1984); it requires us to be a little more sensitive to the biology of an animal so as to be able to identify just what it is *trying* to do and what constraints it has to cope with in doing so. In this respect, **Cords**'s revised estimate of the functional relationship between group size and grooming time cannot be right, because it consistently underestimates the amount of time spent grooming by all primates that live in very large groups (e.g., gelada, *P. papio*).

Finally, **Deacon**'s assertion that language is so unique that it cannot be seen as part of an evolutionary trend with its origins in the primates misses the point of the exercise. The issue is not whether language is part of some allometric trend but what upper limits within those trends that *are* a part of primate biology might have been responsible for jolting the ancestral humans (not hominids, as **Wind** assumes!) onto an entirely new plane of communication. This question requires a reverse optimality approach to identify the boundary conditions that impose constraints on the preexisting system. Assuming that Deacon is willing to agree that humans did evolve from some kind of conventional primate rather than arriving by fiery chariot from a prehistoric cloud, I see no other way in which he can possibly answer this question. The only plausible alternative (dismissing the question as trivial) is merely a declaration of lack of interest. But we cannot dismiss such questions by fiat: they are an intrinsic part of biology. **Cords**'s worries notwithstanding, attempting to reconstruct the time budgets of extinct species under different foraging regimes is one of the few ways we can genuinely explore the issues involved (see Dunbar 1992c; 1993).

R4. The function of language. The final proposition is that language removed a critical constraint present in grooming by allowing humans (1) to interact with a wider set of individuals at any one time and (2) to exchange socially relevant information. The first point is surely critical, not just for the extended network that one can reach through indirect contacts but also in terms of the interactants' ability to exchange information about themselves (something that had not occurred to me when I was writing the target article). By talking to you, I learn a great deal about how you "tick," and this enables me to build a better relationship with you. (It also, of course, allows me to exploit you through the use of deception, as **Dean** notes, but this is only a small part of the benefit of being clever: all primate social systems are necessarily founded on trust, and counterselection against cheats will inevitably ensure that deception is the exception rather than the rule.) [See also Maynard Smith: "Game Theory and the Evolution of Behaviour" *BBS* 7(1) 1984; and Caporael et al.: "Selfishness Examined" *BBS* 12(4) 1989.] In addition, of course, relationships are two-way processes (a fact that almost everyone seems to have forgotten), and we can greatly speed up the process of acquiring the information on which to build a relationship by telling each other about ourselves, our likes and dislikes, and so on. It would take me months to acquire that information about a person by observation alone. The time saved can be put to much better use elsewhere.

The conventional wisdom has, until recently, been that language evolved to facilitate hunting (or, alternatively, to enable reference to be made to the environment). Any social function (if indeed such a thing exists) is presumably secondary, a kind of icing on the evolutionary cake. My argument turns the conventional wisdom on its head: I suggest that language evolved to facilitate social interaction, and that the ability to refer to objects in the environment, to coordinate hunting, and so on, arose as an evolutionary by-product of this capacity. (The latter step would, of course, have been under selection pressure from its obvious advantages, but the selection pressure here would have been for the insertion of a symbolic element into an existing – social – language, not selection for the evolution of language *per se*. I think we need to be more careful about unpacking the layers in the selection cake.) I would suggest that the hypothesis that language evolved first to handle social problems and only later acquired its symbolic content is more consistent with the evidence from developmental psychology (which suggests that children learn social functions long before they learn abstract or concrete operations) [See Gopnik: "How We Know our Minds" *BBS* 16(1) 1993], with our current understanding of primate social systems and their evolution, with the evidence for the Machiavellian Intelligence hypothesis [See Whiten & Byrne: "Tactical Deception in Primates" *BBS* 11(2) 1988], with the evidence from primate vocalisations, and with all the evidence I collated in the target article concerning the design features of language. [See also multiple review of Cheney & Seyfarth's *How Monkeys See*, *BBS* 15(1) 1992.]

For those who doubt the wider validity of conversations in refectories (**Cords**, **Donald**) or who remain unsure as to what people actually talk about (**Hyland**, **Whiten**), I can only invite them to listen. We have, I believe, been seduced by the capacities with which language has endowed us (the "Shakespeare-and-Einstein" theory of language), but neither we (as academics) nor ordinary members of society use language in this way very often in everyday life. It is quite clear, both from our own research and from that of others in less-structured environments, that most conversations revolve around gossip (that is, the exchange of social information) rather than matters of substantive cultural or technical import.

Cords worries about what null hypothesis to consider in this context. This would be a serious problem were social relationships and factual matters more equally balanced in their frequencies of occurrence in conversations. But the fact that we typically spend nearly all our time talking about social matters is surely good enough to make the point without having to resort to a statistical test. If it was of so little importance to them, why would people waste so much time discussing social experiences?[1]

The traditional hypothesis that language is related to hunting and tool use (**Donald**, **Glezer & Kinzey**, **Hyland**, **Kincaid**) now seems to be implausible. For one thing, it is refuted by the lack of correlation between the evidence for hunting and tool use and the changing pattern of brain size in the fossil record: the hominid brain does not begin to increase in size until long after the appearance of the first tools and scavenging forms of hunting, but long before the appearance of sophisticated tools and artwork (the Upper Palaeolithic revolution) and coordinated large-scale hunting (see Wynn 1988).

From this emerges an answer to the question posed by **Falk & Dudek**, **Graber**, **Harcourt**, **Holloway**, and **Wind**, namely, when did language evolve? If we use the equations relating grooming time, group size, and neocortical size in conjunction with allometric equations that allow us to estimate neocortex ratio from cranial capacity, we can determine the time at which the grooming time required to service groups of the size predicted by the neocortices of fossil hominids broke through the critical limit (somewhere between the maximum ever observed in living primates and that predicted for modern humans). We obtain the relatively early date (250,000 B.P.) favoured by the neuroanatomists (see Aiello & Dunbar 1993). But note that this is language-as-gossip, not language in its fully symbolic form (which is more likely to date from around 50,000 years ago, when the first evidence of symbolism appears in the archaeological record).

The last point raised in this context concerns the origins of human language within primate communication systems. Gestural theories for the origin of language are clearly in vogue in certain circles at the moment (**Corballis**). However, I find the arguments for these less convincing (see also Burling 1993), if only because they tend to rest on demonstrative uses of gestural "languages" (pointing, attention-attraction, etc.), and this merely replaces verbal commands with (semantically labelled) gestures. It is just as difficult to see how category terms like nouns might have arisen in the ancestral hominid by this route as it is to see how speech might have arisen fully formed.

In contrast, the suggestion that language arose out of the vocally enriched conversational exchanges already present in higher primates makes for a more plausible transition. Primates never point, but they do use vocalisations to comment on (and refer to) both social and ecological phenomena (Cheney & Seyfarth 1990; Dunbar 1988). It is easy to see how, later on, that might both be supplemented by gesture and lead to the formation of words. **Hyland**'s observation that language may have first evolved to facilitate emotional synchronisation and the formation of affectionate bonds (citing Buck & Ginsburg 1991) is not in conflict with my argument concerning the use of language to exchange social information (indeed, it was the whole point of the discussion of conversational exchanges in the gelada). My point, rather, is that the earliest forms of true language were designed to facilitate the exchange of social information and that this was developed off a springboard already present in at least some nonhuman primates (namely, the ability to use vocalisations as a form of grooming-at-a-distance to service social relationships). This suggests a minimum three-stage sequence in the evolution of language: enhanced vocal "grooming," then gossip, and finally, fully fledged symbolic language (Aiello & Dunbar 1993). I suspect that most of the disagreements at this point reflect different conceptions of what is important about language.

Corballis's emphasis here on Pinker and Bloom's (1990) argument that language is designed to handle propositional communication is, of course, equally compatible with both the second and third stages: social commentary is as dependent on a propositional calculus as commentary on the environment (or anything else). The obvious test is whether a novel could be written without the use of propositional language. It would certainly be possible to write *something*, but I suggest that the product would have too much in common with poetry to be very informative (i.e., it would be too open to interpretation by the reader). My point is not about *how* language permits information to be transmitted, but *why*. The issue, once again, is: Did social language come before symbolic (perhaps metaphysical would be a better term) language (and, hence, the ability to describe the way the world is) or not?

Finally, there is indeed recent work on the conversational and languagelike properties of primate vocalisations I failed to cite (**Hauser et al.**, **Seyfarth & Cheney**, **Snowdon**). However, the fact that other primates exhibit the speechlike properties originally identified many years ago by Richman (1976; 1978; 1987) in a quite original study of gelada vocalisations simply reinforces the substantive point I was making (that the precursors of language are to be found in primate contact calls). I am, of course, delighted to discover that, with the benefit of nearly two decades of hindsight, Snowdon has been able to improve on Richman's seminal studies. However, these authors overstep the evidence by suggesting that vocalisations are a crucial mechanism for social bonding in primates. Primates simply do not acquire social knowledge about each other through vocal exchanges (except in the very crudest sense). Only face-to-face interaction provides that kind of information. Primate vocalisations are, however, relevant to identifying the precursors of language: on that we are all agreed.

R5. Some more general evolutionary issues. There remain a small number of more general points relating to evolutionary analyses that need to be clarified. A number of commentators argue that it is inappropriate to suggest specific functions for features like brain size (or language?) that are obviously used in many different aspects of daily life (**Brace**, **Donald**, **Falk & Dudek**, and **Kincaid**). The suggestion that evolutionary change can be a consequence of many selection factors acting simultaneously is a common misapprehension. It is perfectly possible for several selection pressures to be contributory, but it is implausible to suggest that they can be all *equally* important. The key test here is whether the removal of one of them would leave the other(s) unable to make sufficient headway to force a change in the character concerned. In other words, the crucial evolutionary question concerns which is the necessary and sufficient selection pressure and which is simply the icing on the cake?

The evolution of the computer provides us with an apposite example. The equivalent argument would be that computers evolved because they are all-purpose tools that can serve many functions: that, after all, is what we see now. In this case we happen to know that this is not what happened. Throughout the century after their initial invention by Charles Babbage, digital computers were solely designed to crunch numbers. Only after the space exploration programmes of the 1960s reduced their size to the point where they could be placed in offices and homes did novel (and hitherto unsuspected) uses emerge for them (controlling manned and unmanned flight, word processing, diary management, product assembly and quality control, video games, etc.) (Goldstine 1972; Moreau 1984). These additional benefits arose because of windows of opportunity created by developments in both computer hardware and software during the 1960s. In one sense, the possibility had always been there, but the uses to which they were later put depended on the machinery being developed first for another purpose. (This much is evident from the fact that we call them all "computers.")

I suggest that the origin of language is precisely analogous: it evolved first to handle social information, but once this facility had developed it contained within it the necessary capacity to be exploited in other dimensions. There is nothing unusual about this from a biological point of view: it has long been recognised that parts of an organism can be taken over (or "captured") by other motivational systems to be exploited for other functional purposes (social grooming itself appears to be a classic example; see Dunbar 1991). In contrast, the argument for multiple purposes is both biologically implausible and in principle unfalsifiable, because no data can ever contradict it. I offer a specific sequence of events: it is now up to us to set about identifying appropriate ways to force the hypothesis into conflict with the alternatives so as to effect a clear-cut test between them. I suggest that the concern expressed about the difficulty of falsifying my hypothesis (**Dean**, **Graber**, **Kincaid**) simply reflects our perennial unwillingness to sit down and think through the consequences of hypotheses in order to identify crucial tests. Thinking, not arm waving, is what is needed at this point.

Dean and **Holloway** are, of course, quite right to emphasise the problem of disentangling causes from correlations in this context. However, *all* correlations necessarily have explanations (or causes) – even if it is only that they are statistical accidents. Those explanations (including the null hypothesis that the correlation is an artefact) require testing: simply asserting the possibility of the null hypothesis is not an adequate alternative. I have endeavoured to do that here by following up the implications of the hypothesis at each step in the argument, but I am happy to concede that further tests are required.

Hauser et al. raise another relevant problem in this context, namely, that of assuming that current function is the same as the original function. I am as aware of that as anyone else (see, for example, the discussion in van Schaik & Dunbar 1990). But, it seems that this is precisely what most discussions of language have always done: they have assumed that the ways in which we can use language now is the way it always has been used. One consequence of this has been the (biologically implausible) necessity to assume that language, speech, and all the rest appeared as the product of a single simultaneous set of mutations. Hauser et al. would apparently prefer to duck the issue by declaring that we cannot specify the original function. This is not especially helpful. A more constructive approach to historical problems is to take a leaf out of the cosmologists' book and ask what kinds of information we *can* obtain and how we might use that to test between competing hypotheses. Our problem hitherto has been precisely that we could not *test* the conventional hypothesis for the evolution of language, because we did not have any alternative hypotheses (or even a *null* hypothesis!) to test it against. We now have two competing hypotheses that make contradictory predictions; our job should be to try to work out crucial tests that will allow us to decide between them.

The final point that needs emphasis is the common mistake of confounding different senses of Tinbergen's "four why's." Whole organism biologists have learned the hard way that fatal errors arise from failing to keep explanations about mechanism, function, ontogeny, and phylogeny clearly separate (see Huxley 1942; Tinbergen 1963). I therefore value the developmental hypotheses advanced by **McCune** and others, and the mechanismic explanations offered by **Corballis** (in relation to language) and **Glezer & Kinzey** (in relation to group size): these add important dimensions to the whole story. But they do not in any sense constitute an alternative to the functional explanations I offer here. In the end, we have to answer all four senses of "Why?"

Martins runs into the same problem when she asserts that no explanation (other than phylogenetic inertia, presumably) is required to account for both the large neocortical size and the large group sizes of humans. This is a biologically indefensible claim, if only because humans in fact have (1) a neocortex larger for body/brain size than any other species, and (2) group sizes larger than all other primates (at least as far as the intermediate and large groupings identified in Table 1 are concerned). These cannot be made to go away merely by vague arm-waving references to phylogenetic inertia. Large neocortices come at an enormous cost (60% of total energy consumption for neonates and 20% of total daily energy consumption for adult humans), and evolution simply does not produce (or even retain) costly structures merely because it happens to be possible. In the absence of a selective advantage for a larger neocortex, there is no reason for humans to have a neocortex any different from that of chimpanzees. The same is true for group size, which is under intense counterselection pressure from stress and resource competition (Dunbar 1988; van Schaik 1982). The fact that allometric relationships exist is not an alternative explanation to selection: it simply states that constraints exist in the real world and that only certain values are possible. We still have to explain why a species has come to adopt the particular value it has rather than settling for a lower one. In other words, this is yet another example of ontogenetic and functional explanations being confounded.

Allometrists are sometimes tempted to argue at this point that a large brain is simply a convenient consequence of having a large body (and so being able to bear the costs of a large brain). But this claim rests on hidden assumptions about the direction of causation. The causal sequence can equally well be interpreted in reverse: a species becomes large bodied to allow the development of a large brain. We cannot simply assume that large body size (a much less costly "organ" than the brain) is the most fundamental factor in an organism's biology. Evidence that life history variables correlate with brain size rather than body size (e.g., Harvey et al. 1987) supports the view that it is brain size that drives the system.

NOTE

1. I am conscious here of the two senses in which the word *gossip* is used: some people clearly regard the pejorative sense as its only legitimate definition, but I suggest this says more about what *these* individuals talk about than anything else. In fact, malicious gossip occupies only a small fraction of total conversation time. It is worth reminding ourselves that the word derives from a corruption of the Old English *god-sib* – meaning someone with whom you had a special, usually spiritual, relationship, in other words, the peer-group equivalent of a godparent. It came to be used in the fourteenth century to mean a familiar acquaintance: literally, someone with whom you "gossiped" (see Hoad 1986).

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Letters *a* and *r* appearing before authors' initials refer to target article and response respectively.

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