

(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

Ralph L. Holloway

Department of Anthropology, Columbia University, New York, NY 10027  
Electronic mail: rh2@columbia.edu

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 (Klemp et al. 1987), should be expected to have a more difficult time in substituting language as a "cheap" form of social grooming.