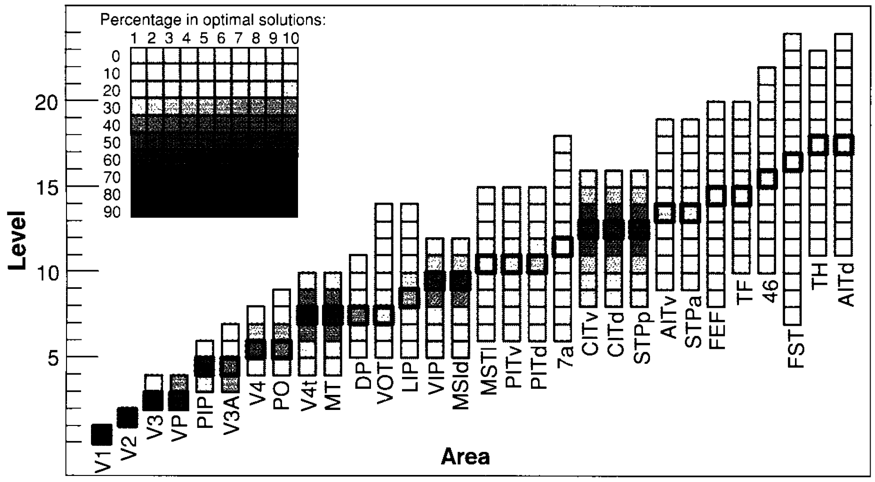

Wiring the brain. Area frequency distribution for 150,000 different optimal hierarchical orderings of brain areas. The boxes are shaded according to the relative occurrence of an area at a particular level across all the computed hierarchies. The main peaks are denoted by frames in thicker lines, and the ordering of the peaks also represents an optimal hierarchy. The number of levels in the optimal hierarchies ranged between 13 (for 21 hierarchies) and 24 (for 3 hierarchies), with the peak of the distribution of levels around 18 levels (39,636 hierarchies) and 19 levels (40,131 hierarchies). The variability in the positions of the areas is due to the indeterminacy of the relations between areas, which allows both different positions relative to one another in different hierarchies and hierarchies with different total numbers of levels. The cortical area abbreviations are explained in (*2*).

reported absent. The sparsity of connectivity, particularly between parietal and inferotemporal areas, leaves many degrees of freedom for arrangements of the areas that fit the constraints equally well. Hence, further data, if classified by the presently understood criteria, would still not specify the exact ordering of cortical stations in the visual system.

Some visual areas had fixed relative positions (see figure). These were the uniquely placed V1 and V2, V4t and MT (same level in all hierarchies), MSTd and VIP (same level), and CITv, CITd, and STPp (same level). FST (fundus of the superior temporal sulcus) gave rise to most of the violations, yet the anatomical information on the relations of FST to other areas is quite reliable (*2*, *7*). FST was also the only area whose frequency distribution over the hierarchical levels exhibited two peaks (see figure), one on level 12 (for 6779 hierarchies), and the main one on level 17 (29,550 hierarchies). We used the processor to test the hypothesis that area FST in the macaque consists of two components that differ in their connections to other areas. Subdividing FST, coupled with the exclusion of the 36 less reliable constraints (or just MSTd < PITv and its counterpart), permitted hierarchies that violated none of the constraints. These two assumptions allowed many hierarchies that fitted the pairwise relations perfectly.

Thus, the visual hierarchy is indeterminate. No single hierarchy can represent satisfactorily the number and variety of hierarchical orderings that are implied by the anatomical constraints. Nevertheless, the network processor derived new information about the visual system: It has more hierarchical levels than previously suspected, and there are fixed relations between some visual areas. FST may consist of two subcomponents whose connectivity we have predicted.

This computational approach further allows precise predictions about connectivity; these predictions suggest specific anatomical experiments that would be particularly informative (see <http://www.psychology.ncl.ac.uk/www/predictions.html> for our top ten predictions).

References and Notes

1. K. S. Rockland and D. N. Pandya, *Brain Res.* **179**, 3 (1979); J. H. R. Maunsell and D. C. Van Essen, *Annu. Rev. Neurosci.* **10**, 363 (1983); T. A. Coogan and A. Burkhalter, *J. Neurosci.* **13**, 3749 (1993).
2. D. J. Felleman and D. C. Van Essen, *Cereb. Cortex* **1**, 1 (1991).
3. Nodes in a conventional neural network have fixed connections with variable weights. Computation consists of numerical operation on an input vector to generate an output vector. The data in our case are not numbers but relational constraints. We generalized the properties of the simulated network so that each node could be associated with a variable position in the network and could have a relation with other nodes, or none at all, as defined by the input constraints. This organization allowed the structure of the simulated network itself to stand for the network in the real brain, rather than the representational states being patterns of numbers distributed over the nodes. These features might extend the processor's use to other relational problems, such as macromolecular conformation.
4. W. Metropolis *et al.*, *J. Chem. Phys.* **21**, 1087 (1953); P. J. M. Van Laarhoven and E. H. L. Aarts, *Simulated Annealing: Theory and Applications* (Kluwer, Dordrecht, 1987).
5. MDP and MIP were excluded from the analysis.
6. The relatively low number of violations in (*2*) suggests that this hierarchy may be in the top 100 million hierarchies.
7. D. Boussaoud, L. G. Ungerleider, R. Desimone, *J. Comp. Neurol.* **296**, 462 (1990).

8. Supported by the Medical Research Council, the McDonnell-Pew Foundation, Newcastle University and the Royal Society.

On Hierarchies:
Response to Hilgetag *et al.*

David C. Van Essen and
Daniel J. Felleman

By demonstrating vast numbers of hierarchical schemes that are equally good solutions to a set of anatomically based hierarchical constraints, Hilgetag *et al.* (*1*) have provided an interesting twist to the notion of hierarchical processing in the macaque visual cortex. A major reason why they found such a large number of solutions is that they elected not to apply an important constraint used in previous hierarchical analyses (*2*, *3*), namely that two areas should be placed at the same level whenever possible to minimize the total number of levels in the hierarchy. It would be interesting to know how many equivalent solutions their search strategy would identify if this constraint were reinstated. If that number remains large, further reduction might be attained by using more stringent anatomical criteria (relating, say, to the number of hierarchical levels between a pair of connected areas, not just whether the relation is higher, lower, or equal).

Clearly, there is more than one way to skin the hierarchical cat. It remains an open question whether the complete mosaic of visual areas in primates will ultimately be described as a "pure" hierarchy with one or many solutions with no constraint violations. Alternatively, the evidence may eventually point more toward visual cortex as a "quasi-hierarchy" (*3*) that includes inherent ambiguities and irregularities, not unlike hierarchical relations in other complex systems—such as human society.

References

1. C.-C. Hilgetag *et al.*, *Science* **271**, 776 (1996).
2. J. H. R. Maunsell and D. C. Van Essen, *J. Neurosci.* **3**, 2563 (1983).
3. D. J. Felleman and D. C. Van Essen, *Cereb. Cortex* **1**, 1 (1991).

D. C. Van Essen is at Washington University School of Medicine, St. Louis, MO 63110, USA. D. J. Felleman is at the University of Texas Medical School, Houston, TX 77030, USA.

Rejoinder: We have considered optimal hierarchies with as few levels as possible. A large number of hierarchies still emerge. But this approach requires preferring "=" to ">" or "<", when the constraint is "≥" or "≤", an arbitrary choice that is difficult to justify.

C.-C. Hilgetag
M. A. O'Neill
M. P. Young