lower latitudes, this lack of stability is well documented in the case of large tidewater glaciers, which advance down their fjords slowly, pushing a stabilizing terminal moraine shoal ahead of them, and retreat catastrophically if they thin and pull back off of that shoal into deeper water (*7*).

One possible consequence is a rise in sea level. The disintegration of the northern Larsen Ice Shelf did not directly influence sea level, however, as the ice was already floating. An ice sheet that was grounded on a bed below sea level might be susceptible to disintegration if the ice shelf in front of it were lost (*8*), but the glaciers and ice caps on the Antarctic Peninsula, which are in large part resting on beds above sea level, should not respond radically to the loss. Thus, the loss of the northern Larsen Ice Shelf is not an immediate threat to coastal communities, but rather a signal of changing conditions on the peninsula.

The meaning of the disintegration, in climatic terms, is problematic. As Rott *et al.* point out (*1*), measurements of temperature on the peninsula have indicated a warming trend over the last 40 years, and recent measurements show a warm period in the late 1980s. Was one of the recent warm periods responsible for the event, or was it caused by a much longer trend? This difficulty should not severely limit interpretation, however, as the retreat of ice shelves on both sides of the peninsula clearly indicates that the change is regional.

The complete disintegration raises a question about the origin of ice shelves: Can these ice shelves re-form under climatic conditions similar to today's, perhaps with a slight drop in temperature, or were they able to form only under the colder conditions of the last glacial period, and so represent a remnant of that climatic regime (or an artifact of the retreat from those conditions)? The answer will determine just what significance we can read into the climatic signal presented to us in the form of progressive ice shelf disintegration along the Antarctic Peninsula. If the ice shelves can re-form in a few centuries, then the signal we are seeing is possibly a small perturbation with a few-hundred-year cycle; if the ice shelves cannot re-form, even with a slight drop in temperature, then we may be witnessing an event that is unique for this area in the Holocene.

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Indeterminate Organization of the Visual System

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How is the visual system organized? The data on the anatomical subdivisions of the primate visual cortex and on the many connections among them are now so complex that it is difficult to draw conclusions about overall organization without systematic analysis. Hierarchical analysis (*1, 2*), one method for accomplishing this task, classifies connections as ascending, descending, or lateral according to their patterns of origin and termination in the cortical layers (some layers send information out and some receive information). This classification now includes connections among at least 30 areas in the monkey visual cortex and 318 pairwise hierarchical relations for these areas (*2*). In a familiar hierarchical scheme by Felleman and Van Essen (*2*), the visual areas are arranged so as to obey most of the pairwise anatomical constraints. Visual scientists make wide use of this scheme to choose cortical areas for investigation.

The number of possible orderings for 30 areas in a hierarchical ladder is large—about 10^{37}. We were interested in whether the anatomical constraints are sufficient to specify one ordering of the hierarchy out of the large number of possible orderings.

Previous attempts to construct a hierarchy that fits these data as well as possible have relied on manual sorting. We have now developed a computer algorithm that uses evolutionary optimization to find hierarchies that have the fewest departures from a perfect hierarchy in which all the anatomical constraints are satisfied. A computational network generalizes the properties of the nodes of conventional neural nets (*3*), so that the arrangement of the nodes itself can represent the anatomical network in the real brain. Starting from randomly chosen structures, the algorithm proceeds by cumulative modification and cost evaluation of candidate hierarchies, in a process analogous to simulated annealing. The cost of any hierarchy is the number of anatomical constraints it violates (*4*).

With the most recent collation of hierarchical constraints (*2, 5*), the processor computed more than 150,000 different hierarchical structures, each with a cost of six violations (see figure). Only the limitations of the computer prevented the calculation of an even larger set of optimal hierarchies. The generation of so many optimal hierarchies answered our question: The information in the anatomical constraints cannot be expressed satisfactorily by any single hierarchical ordering. Further, conclusions drawn from considering only a single hierarchy will be misleading.

All the computed optimal hierarchies contain fewer violations than any previous hierarchy. The Felleman and Van Essen scheme (*2*), for comparison, has eight violations (*6*) and three fewer levels of visual cortical areas than any of the computed optimal hierarchies. The number of violations of the computed hierarchies—six—is remarkably low when compared with the number of violations obtained for random orderings of the areas (mean, 167 violations) and to optimized structures from shuffled constraint sets (mean, 124 violations). Only two constraint violations (FST to MSTd and MSTd to FST) remained for optimal hierarchies computed from a constraint set that excluded the 36 less reliable constraints (*2*). The primate cortical visual system is therefore surprisingly strictly hierarchical, but it is nonetheless not possible to determine the exact hierarchy.

Would further experimental data constrain a unique hierarchical arrangement of the visual areas? We considered all possible ways of filling in the 240 possible connections whose laminar direction is presently unknown. We assumed that all unknown connections exist, have laminar direction, and that these artificial data would not give rise to further constraint violations. These assumptions all aid determination of a unique ordering, but we found multiple hierarchies in all cases, even for constraint sets without any undetermined connections whatsoever. The reason for this result is that about half of the known connections (312 of 630) have been

An expanded version of this Perspective is available on the World Wide Web at <http://www.psychology.ncl.ac.uk/www/hierarchy.html>.

Further response from Felleman and Van Essen is at <http://science-mag.aaas.org/science>.

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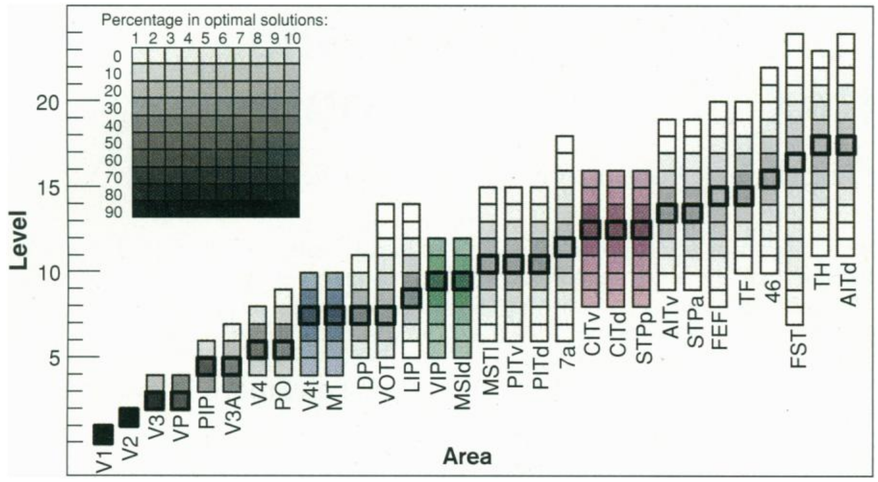

Wiring the brain. Area frequency distribution for 150,000 different optimal hierarchical orderings of brain areas. The boxes are shaded according to the relative occurrence of an area at a particular level across all the computed hierarchies. The main peaks are denoted by frames in thicker lines, and 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).

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On Hierarchies:
Response to Hilgetag *et al.*

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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.

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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.

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