Multidimensional scaling

Multidimensional scaling was done using MATLAB (The Mathworks, Natick, MA) to allow simultaneous display of variation in all 11 F components (principal brain divisions and telencephalic components) of the cerebrotype. The quantity $\Sigma\Sigma(o_{ij}-d_{ij})^2/o_{ij}^2$ was minimized where o_{ij} is the cerebrotype distance and d_{ij} is the displayed distance in the plane. Minimizations were done using a bootstrapping procedure. The plot was initially seeded using three points chosen by a trial run to lie near the outskirts of the final plot. We added subsequent points one at a time in a random order. After each point was added, a round of error minimization was performed in which only the new point was allowed to vary, followed by a round of minimization in which all points were varied. Each minimization was performed at least ten times and the solution with the least error was accepted. In the 76-point minimization of all species (Fig. 3b), new points were added four at a time. This overall procedure resembles the Fitch–Margoliash algorithm for phylogeny reconstruction but yields a mapping in a plane rather than a connected tree.

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An evolutionary scaling law for the primate visual system and its basis in cortical function

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A hallmark of mammalian brain evolution is the disproportionate increase in neocortical size as compared with subcortical structures[1]. Because primary visual cortex (V1) is the most thoroughly understood cortical region, the visual system provides an excellent model in which to investigate the evolutionary expansion of neocortex. I have compared the numbers of neurons in the visual thalamus (lateral geniculate nucleus; LGN) and area V1 across primate species. Here I find that the number of V1 neurons increases as the 3/2 power of the number of LGN neurons. As a consequence of this scaling law, the human, for example, uses four times as many V1 neurons per LGN neuron (356) to process visual information as does a tarsier (87). I argue that the 3/2 power relationship is a natural consequence of the organization of V1, together with the requirement that spatial resolution in V1 should parallel the maximum resolution provided by the LGN. The additional observation that thalamus/neocortex follows the same evolutionary scaling law as LGN/V1 may suggest that neocortex generally conforms to the same organizational principle as V1.

Any study of evolutionary scaling relations—the allometric laws that relate the size of one structure to another—must deal with species that are homogeneous in their scaling properties. Various taxonomic orders or suborders can conform to scaling laws with the same power but different scale factors[2]. The data presented here are for haplorhine primates, a suborder that appears to be homogeneous with respect to the brain areas that I consider.

Figure 1 plots the number of neurons in V1 as a function of number of LGN neurons for 23 haplorhines whose average brain volumes range from 3.4 cm^3 (tarsier) to 1,252 cm^3 (human). This figure is derived from data presented by various authors as indicated in the Methods. A nonlinear fit reveals that these data are well described by a power law with an exponent of 3/2 (1.54 ± 0.07). That is, across the haplorhines the number of V1 neurons N varies

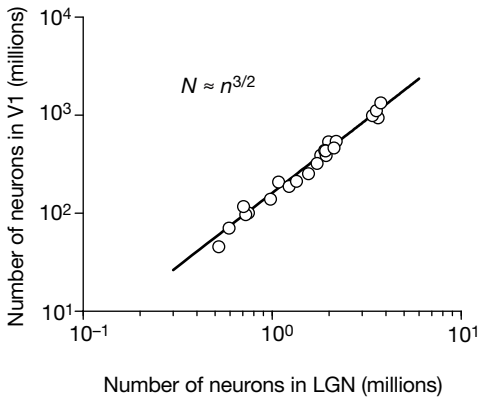

Figure 1 Number of neurons in VI (N) as a function of number of LGN neurons (n) for 23 haplorhine primates. The smooth lines are power functions with exponents of 3/2 and 1.54 (the best fit to the data). For this graph, the tarsier has the smallest LGN/VI ratio, and the human the largest.

with the number of LGN neurons n according to,

$$N = 161n^{3/2}$$

where numbers of neurons are measured in millions. For V1 and LGN, then, the number of neurons in neocortex increases with brain size more rapidly than the number of thalamic neurons, as has been observed[1]; this increase follows an allometric relation with a power of 3/2.

The 3/2 scaling relation applies not only across species but, as shown in Fig. 2 (here represented as the volumes of V1 and LGN), within a single species (humans) for which the sizes of LGN and V1 co-vary between individuals by several fold[3]. The 23 haplorhines in Fig. 2 are the same as those appearing in Fig. 1, and the data were obtained from refs 3 and 4. The human data from ref. 3 were scaled so that the mean V1 and LGN volumes coincide with the human data point from ref. 4; this normalization was necessary to compensate for different measuring procedures used in the two studies.

How might this 3/2 power law arise? The number of neurons in LGN is roughly the same as the number of retinal ganglion cells[5,6]. This means that for larger animals with larger eyes and larger brains linear resolution of distances in the visual world increase as the $n^{1/2}$, where n is the number LGN neurons (close to the number of retinal ganglion cells and proportional to the number of visual pixels). To maintain the same spatial resolution in cortex, the number of cortical pixels must also increase in proportion to the number of LGN neurons. Cortical pixels are reasonably measured by the number of V1 hypercolumns[7] or "pinwheels"[8], with each pinwheel being responsible for reporting on a small region of visual space; the orientation of a line in that part of the visual scene is specified by a 'location code', in other words, by which neurons in the pinwheel are responding. The pinwheel number should thus be proportional to the number of LGN neurons for visual scenes to be represented, at the cortical level, with the same resolution as provided by the eye. If the number of neurons per pixel were constant, then the number of V1 neurons would increase in proportion to the number of LGN neurons; but it does not.

How should the number of neurons per pixel (that is, per pinwheel) vary with retinal and LGN size, as measured by the number of LGN neurons? To answer this question, I must consider the uncertainty with which angles (θ) made by lines and edges (relative to the vertical) are known from a sample of the visual scene provided by the retina. A little thought shows that the angular resolution (which determines the uncertainty in angles) is proportional to the linear resolution. To see this, note that an angle is defined for a unit radius vector by the length of arc swept out by the vector, and that the resolution for this length is the linear resolution. Each pinwheel should, then, contain a number of neurons sufficient to maintain this angular resolution.

Pinwheels use a location code in which line (edge) orientation is represented by the identity of neurons in the pinwheel that are firing[7]. The angular resolution available in V1 is set by the number of neurons per pinwheel, and this must be proportional to $n^{1/2}$ for the angular resolution available from the retina to be preserved. A way to appreciate why this is so is to picture V1 as a three-dimensional space with dimensions representing x, y and θ. To have the same resolution in all directions, the number of neurons in each direction must be proportional to $n^{1/2}$. Altogether, the number of neurons in V1 should vary as the number of pixels (proportional to n) times the number of neurons per pixel (proportional to $n^{1/2}$): cortical neurons should increase as $n^{3/2}$, as is found experimentally.

This same argument can be made in a more abstract way. The two-dimensional visual representation in the retina and LGN (up/down–right/left) is mapped onto (and fills) a three-dimensional cortical space (up/down–right/left–line orientation). The volume of the three-dimensional cortical space must increase as the 3/2 power of the area of two-dimensional retinal space as this 'input' space increases in size.

Of course V1 represents characteristics of the visual scene other than line orientation at each point in the visual world[9]. Characteristics such as ocular dominance and direction of movement appear, at least at the V1 level, to be represented by two populations of neurons (right eye/left eye, and opposite directions of edge movement) and these characteristics can be encoded by populations of neurons that are a constant fraction of the orientation-sensitive cells without loosing information provided by the retinal ganglion cells. The population of neurons that represent colour can also increase in proportion to the number of orientation-sensitive cells without loss of information provided by the retina. Although the map of spatial frequencies may be continuous[10], the argument used here would apply to this variable only if its resolution varied with brain size, which it probably does not. In general, the population of neurons that must increase like the $n^{1/2}$ are ones that make use of a location code to represent some continuous map characteristic (like line slope) whose precision must also be proportional to the resolution available in the map.

Does the argument given above apply to other areas of cortex and to other taxa? Unfortunately, similar data relating the number of thalamic neurons to number of cortical neurons (which that region of thalamus supplies) are not available for other cortical regions or for other taxa. Data are available, however, that relate thalamic volume to the volume of the entire neocortex[4,11], and these data are compared, for haplorhines, with the LGN/V1 volume data in Fig. 3. The slope on a double logarithmic plot of the overall thalamus/neocortex volumes is not significantly different from that of the LGN/V1 data, although the intercepts are different. This difference in intercepts presumably reflects the fact that primate V1 is 'two

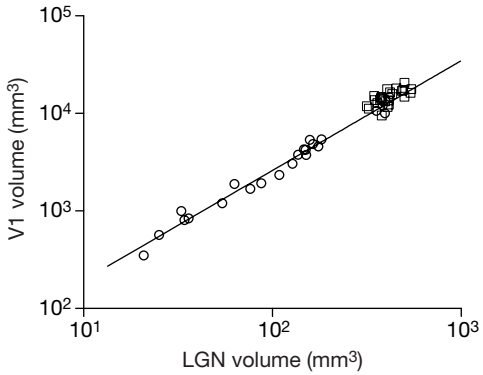

Figure 2 The volume of VI as a function of LGN volume for 23 haplorhines (circles), together with data from 24 different human specimens (squares). The relation between cell number (Fig. 1) and the volumes of structures (this figure) is discussed in the Methods.

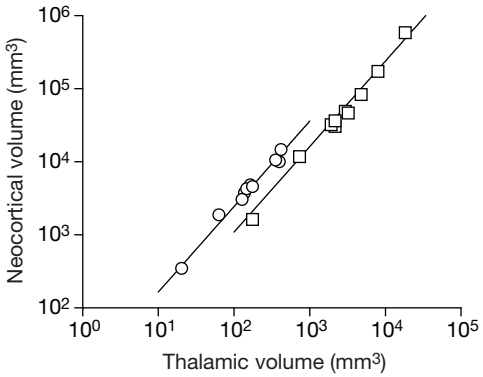

Figure 3 Volume of VI (circles) and all of neocortex (squares) as a function of LGN and total thalamus volume. The data here are a subset, for which volume data are available, of the same 23 haplorhines as in Figs 1 and 2.

cortices in one', with twice the number of neurons underneath a square millimetre of surface than the remainder of neocortex[12]. The density of neurons in the rest of neocortex scales similarly as in V1 (ref. 12), and all of the hominoid thalamic nuclei also have neuronal densities that vary in about the same was as in LGN[13–15]; altogether, then, the relations between number of thalamic neurons and number of neocortical neurons is about the same as the 3/2 power scaling law described above for the primary visual cortex.

The conservation of these scaling relations raises the possibility that a similar basis for the scaling laws exists for all cortical areas. In this view, each cortical area would be provided with a map of some sort—perhaps one with very abstract quantities—and the job of the cortex would be to extract some characteristic of the map at each point that would be represented as a location code by the neurons in each map 'pixel'. Note that the information in the map need not be supplied by thalamus; this structure would only have to determine the number of pixels in the map. If n pixels are present in a cortical region, then the number of neurons per pixel needed to maintain the same resolution within a pixel as across pixels would vary as $n^{1/2}$. A 3/2 power relation would result. □

Methods

To obtain the relation between the number of LGN and V1 neurons, I must make use of three separately determined scaling relations. First, for haplorhines, the volume V of the grey matter in V1 is related to the LGN volume v by a power law[4,16] (see Fig. 2),

$$V = Av^{\alpha}$$

where $A = 14.61 \pm 4.78$ and $\alpha = 1.125 \pm 0.057$; volumes are measured in cubic millimetres and refer to both hemispheres.

These volumes can be converted to numbers of neurons, if the neuronal densities in LGN and V1 are known. The numbers of neurons n in the LGN, as a function of LGN volume v, conform to a power law[17] for 23 haplorhines and 17 strepsirhines,

$$n = Bv^{\beta}$$

with $\beta = 0.659 \pm 0.06$ for haplorhines and $\beta = 0.683 \pm 0.22$ for the strepsirhines, values that are not significantly different. The scale factor B, however, is different with a value of 0.071 ± 0.025 for haplorhines and 0.046 ± 0.029 for strepsirhines. This power law is based on data from ref. 17 combined with data from ref. 4.

The relation between V1 volume V and the number of V1 neurons N also follows the power law,

$$N = DV^{\delta}$$

where $D = 0.232$ and $\delta = 0.902$. This relation is obtained by using the observation[12] that 0.195 million neurons are found beneath a square millimetre of V1 surface in primates (the value is corrected for 18% shrinkage), and the weak power law dependence of V1 thickness t on cortical surface area S described[12,18] by;

$$t = 0.825S^{0.108}$$

When V and v are converted to N and n with the equations above, a power law results (Fig. 1) with an exponent λ:

$$\lambda = \alpha\delta/\beta = 1.54 \pm 0.072$$

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Interocular rivalry revealed in the human cortical blind-spot representation

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To understand conscious vision, scientists must elucidate how the brain selects specific visual signals for awareness. When different monocular patterns are presented to the two eyes, they rival for conscious expression such that only one monocular image is perceived at a time[1,2]. Controversy surrounds whether this binocular rivalry reflects neural competition among pattern representations or monocular channels[3,4]. Here we show that rivalry arises from interocular competition, using functional magnetic resonance imaging of activity in a monocular region of primary visual cortex corresponding to the blind spot. This cortical region greatly prefers stimulation of the ipsilateral eye to that of the blind-spot eye. Subjects reported their dominant percept while viewing rivalrous orthogonal gratings in the visual location corresponding to the blind spot and its surround. As predicted by interocular rivalry, the monocular blind-spot representation was activated when the ipsilateral grating became perceptually dominant and suppressed when the blind-spot grating became dominant. These responses were as large as those observed during actual alternations between the gratings, indicating that rivalry may be fully resolved in monocular visual cortex. Our findings provide the first physiological evidence, to our knowledge, that interocular competition mediates binocular rivalry, and indicate that V1 may be important in the selection and expression of conscious visual information.

Despite extensive research, the neural basis of binocular rivalry has remained highly controversial. Specifically, it is debated whether discrepant monocular patterns rival because of interocular competition or pattern competition. Human psychophysical studies have provided evidence that rivalry results from interocular competition among monocular neurons in primary visual cortex (V1)[3]. However, single-unit recordings in awake, behaving monkeys have