

Neural maps versus salt-and-pepper organization in visual cortex

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Theoretical neuroscientists have long been intrigued by the spatial patterns of neuronal selectivities observed in the visual cortices of many mammals, including primates. While theoretical studies have contributed significantly to our understanding of how the brain learns to see, recent experimental discoveries of the spatial irregularity of visual response properties in the rodent visual cortex have prompted new questions about the origin and functional significance of cortical maps. Characterizing the marked differences of cortical design principles among species and comparing them may provide us with a deeper understanding of primate and non-primate vision.

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Introduction

Neural maps have traditionally raised significant attention among theoreticians. A prominent example is the orientation preference map (OPM) found in cat, ferret, tree shrew and several primates, describing the layout of neurons in the visual cortex selective for the orientation of visual edges. The OPM is almost continuous at the cellular scale [1,2] (Figure 1, upper scheme). Exceptions are pinwheels: points around which the neuronal preferences for stimulus orientation are circularly arranged (see Figure 2a for examples of OPMs). Over the past years, it has become evident that in at least three rodent species — mouse, rat and gray squirrel — cells in the visual cortex are orientation selective [3–6], but their spatial layout shows little order [7,4,8*,9,10,11*], termed interspersed or ‘salt-and-pepper’ organization (Figure 1, lower scheme). Across mammals, the only unifying organizational principle so far is a retinotopic organization [9,8*]. It appears plausible that such marked differences are accompanied by different processing strategies, which may become more apparent on the circuit level than on the neuronal level.

The focus of this review is to highlight from a computational/theoretical perspective recent advances in understanding OPMs versus salt-and-pepper organization of orientation preference in the visual cortex. The review is organized roughly by time scale, starting with evolution, then approaching the time scales of months to minutes, on which circuits develop, before zooming in on subsecond time scales, on which neural computations unfold.

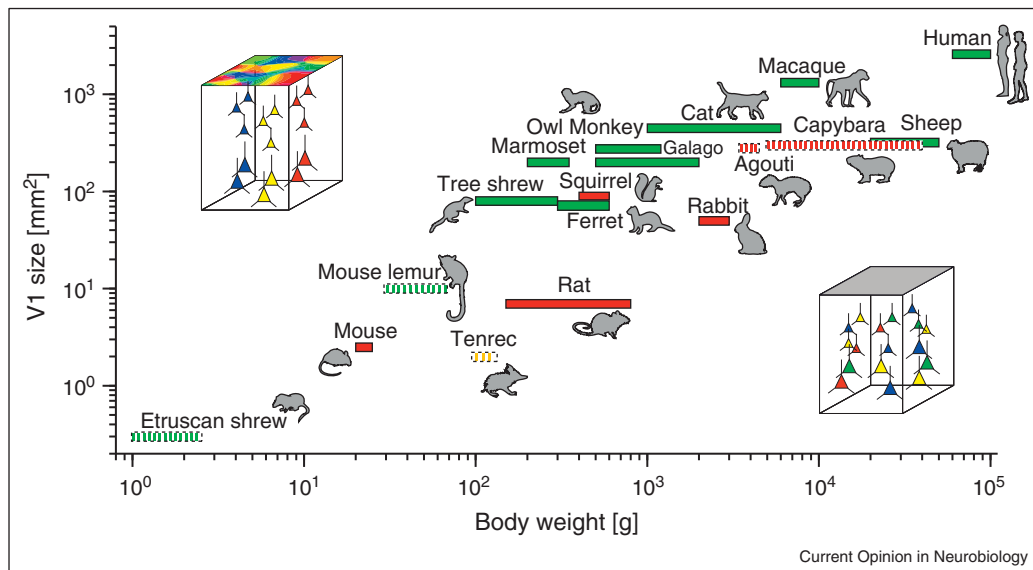
Evolution: does size matter?

Both types of organization, OPMs and salt-and-pepper, exist in species with relatively large visual cortices [4,9] (Figure 1). Salt-and-pepper seems to be common to the phylogenetically closely related rodent and lagomorph (rabbit) species [12**,13*], and may thus also be present in the largest living rodent, the capybara. Currently, it is unclear whether a relatively small cortex can support an OPM containing several pinwheels. This could be addressed by studying, for instance, the mouse lemur, which is a small primate, or the Etruscan shrew [14], a member of the clade Laurasiatheria, which also includes carnivores (Figure 1). Moreover, since the common ancestor of primates and carnivores was likely relatively small brained [15,16], this could shed light on the question whether in evolution pinwheels developed independently in these two orders or, alternatively, vanished in rodents and lagomorphs (see [17,12**] and discussions therein).

The relative thickness of cortical layers seems to be a better predictor for the type of cortical organization than their lateral extent. An anatomical study [18] comparing somatosensory cortices in six rodent species, five primates and three carnivores found that while layers II/III occupied on average 44% and 35% of the total cortical thickness in primates and carnivores, respectively, in rodents only 26% were devoted on average to these layers. In contrast, layers V and VI together occupied only 34% of the total cortical thickness in primates and 39% in carnivores, but a total of 54% in rodents. Importantly, the distributions of these quantities did not overlap between rodent and non-rodent species. These findings indicate that certain aspects of intralaminar and cross-laminar networks have evolved to be different in rodents versus primates/carnivores, perhaps also affecting the visual cortex and its functional organization.

A recent study [19**] identified systematic differences between primates and rodents in cortical expansion in evolution, which previously was considered universal across mammalian species [20,21]. Whereas in 10

Figure 1



Both orientation preference maps (OPMs) and salt-and-pepper layouts of orientation preference appear over wide and overlapping ranges of primary visual cortex (V1) surface area and body weight. The two types of cortical organization are indicated by schemes: upper scheme, OPM; lower scheme, salt-and-pepper. Green color indicates species of the Laurasiatheria clade, which includes carnivores, and of the Euarchonta clade, which primates belong to. Red color indicates Glires, which consist of rodent and lagomorph species. Yellow color indicates Afrotheria. Filled/hatched bars indicate known/unknown spatial organization of orientation preference. Green filled bars indicate OPM; red filled bars indicate salt-and-pepper organization. For body weight, the extent of each bar marks the observed range (for V1 size the range is suppressed for clarity). Data from [4,89,14,90,91]. Figure reproduced from [12**].

examined primate species plus tree shrew white matter volume increased roughly linearly with the number of added cortical neurons, it scaled approximately quadratically in six rodent species with comparable distribution of brain sizes. Most of this volume gain was attributed to an increase in cable length. Intriguingly, the estimated fraction of cortical neurons connected through the white matter did not change much over two orders of magnitude, but was about four times larger in rodents than in primates. Consequently, the addition of cortical neurons required less brain volume in primates than in rodents. While primate brains resemble in their scaling small world networks [22], rodent brain circuits expanded in evolution more like dense networks [19**]. These observations indicate that systematic differences between the two mammalian orders are not only found in individual sensory cortical areas, but are manifest at the level of the whole brain.

Dynamical factors shaping the layout of visual response properties

OPMs in widely different species share many of their basic features (Figure 2a). A recent study [17,12**] found that several statistics of the spatial organization of pin-wheels differed only by a few percent in species separated by more than 64 million years [16] of evolution (Figure 2b). This is in stark contrast to the organization of ocular dominance, which varies substantially among

species, sometimes even within an individual cortical area [23]. Whereas for ocular dominance columns this has been interpreted as evidence against a crucial functional role [24], the common design [17] of OPMs could point to a, yet unknown, functional benefit, strong enough to generate sufficient selective pressure during mammalian evolution. However, species with similar OPMs can occupy widely different ecological niches. For instance, galagos are nocturnal, arboreal frugivores from the African rainforest; tree shrews are diurnal, semiarboreal insectivores from deciduous tropical forests of Southeast Asia. On the other hand, gray squirrels, who lack OPMs, are highly visual animals and similar to tree shrews in terms of life rhythm, visual acuity and eye position [9]. Thus, at least on first sight, relating OPM layout to fitness appears difficult.

Moreover, physicists have long been aware of the fact that highly similar spatial structures can arise via very different mechanisms. Prominent examples are hexagonal patterns, which can form in a broad range of systems in both the animate and inanimate world [25,26], and appear repeatedly in models of OPM development [27–33]. While the degree of hexagonal organization in OPMs is, at best, small (Figure 2a) [17,30], more complex patterns appear better suited to model OPM layouts [17,34]. A family of quasi-periodic patterns [28] that was found to match several

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