UMIACS-TR-2007-14 CS-TR-4861

Global Layout Optimization of Olfactory Cortex and of Amygdala of Rat

Raul Rodriguez-Esteban and Christopher Cherniak*

June 2005

Committee for Philosophy and the Sciences, Department of Philosophy, University of Maryland, College Park, MD 20742

Principles of connection minimization in the nervous system apply not only to complete neural systems but also to smaller subsystems such as rat olfactory cortex and rat amygdala. These subsystems have a three-dimensional organization, rather than previously-studied two-dimensional and one-dimensional schemes. Nonetheless, wire-cost savings show optimality at similar levels, suggesting neural optimization principles are widespread, followed at multiple scales of the nervous system.

1 Introduction

"Save wire" principles of optimization in neural layout design have been shown in structures like the gangion system of the nematode *C. elegans* (Cherniak, 1994) and mammalian cortex (Cherniak et al., 2004). These wire-minimizing mechanisms have been suggested to come "for free" from basic physical laws, similar to the formation of neuron arbors (Cherniak et al., 1999), rather than from detailed coded instructions in the DNA information bottleneck (Cherniak, 2005).

Some questions arise about limitations of these analyses, whether more confined structures than entire cerebral cortex regions or all ganglia of the nematode nervous system follow the same wire-saving network principles. If that is the case, smaller-scale optimized organization could be embedded in larger, optimized superstructures forming a multi-level system, with a fractal-like property of increasingly smaller structures following similar arrangement laws.

It is also unknown whether essentially three-dimensional neural organizations can be analyzed in the same fashion as the *C. elegans* ganglia system or the mammalian cortical areas, which can be roughly modeled as, respectively, one-dimensional and two-dimensional in their layout composition. In order to start addressing these questions, we have analyzed two anatomically and physiologically well-understood neural formations: the rat olfactory cortex and the rat amygdala.

2 Methods

We followed the procedure Cherniak et al. (2004) outlined, gathering anatomical topology and connectivity data for areas of rat olfactory cortex and of rat amygdala. Strength of connection was not included: each connected area pair was assigned a value of 1 in the connectivity matrix regardless of their connection magnitude, while disconnected pairs were assigned a value of 0. Area pairs situated alongside each other were assigned an adjacency matrix value of 1, while area pairs that were not next to each other (or only touched tangentially) were assigned an adjacency matrix value of 0.

The wirelength cost-measure used is a surrogate "all or nothing" distance metric, which consists of counting all area pairs that are connected but not adjacent. To generate alternative layouts from the actual one, the areas were randomly scrambled, exhausting all combinatorial possibilities (for a set of 14 areas, $n = 14! = 8.7 * 10^{10}$). For each combinatorial layout-possibility, the wirelength measure was computed and compared to the wirelength measure of the actual layout. The optimality rank of the actual layout was computed by comparing the wirelength cost of that layout with the cost of all other alternative layouts of that size.

To assess optimality rank changes in relation to sub-system size, we computed the optimality rank for increasingly larger subset sizes. For every subset size, we included the areas immediately surrounding the subset (“the edge-ring”) for wire length cost computation, but we only scrambled the areas belonging to the subset (“the core”). See Figure 1 for the sequence of areas added to the core in rat olfactory cortex, and the ring areas for size 15.

2.1 Rat olfactory cortex

The rat olfactory cortex extends over the ventral part of the telencephalon, folding like a section of a conical surface with the tip of the cone in the olfactory tubercle. The areas near the tip, such as the olfactory tubercle, the ventral tenia tecta or the anterior olfactory nucleus, wrap around the full circumference. (This cannot be seen in the two-dimensional projection of Figure 1, just as, in a Mercator projection centered on London, it cannot be appreciated that Alaska is very close to Russia.)

The primary olfactory cortex receives stimuli from the olfactory bulb and processes information through associational connections across cortically differentiated structures. The rat olfactory system includes both the primary olfactory cortex and other not strictly cortical parts like amygdaloid nuclei (Price, 1987). We collected connectivity data from Haberly (2001), Luskin and Price (1983), and Price (1987); and topological mapping from Price (1987), including the subdivision suggested by Ekstrand et al. (2001). See Table 1.

2.2 Rat amygdala

The rat amygdaloid complex is formed by several nuclei and other cell masses in the medial part of the temporal lobe. Its almond-shaped structure has a three-dimensional organization (see Figure 2), and nuclei are adjacent across different spatial dimensions rather than only through edge contiguity. We collected connectivity data from Pitkanen (2000), and anatomical mapping of divisions and subdivisions from Kemppainen and Pitkanen (2000), Pitkanen et al. (1997), and Pitkanen (2000). See Table 2.

3 Results

As shown in Figure 3, rank optimality for complete rat olfactory cortex and for amygdala is $2 * 10^{-6}$ and $3.9 * 10^{-6}$, respectively; that is, the actual layout of each complete system falls in the top one-millionth of all possible alternative layouts. This is comparable to cat and macaque visual cortex (Cherniak et al., 2004) and *C. elegans* ganglia (Cherniak, 1994). In addition, a Size Law appears as subset size increases, pointing to an increasing optimization across each neural system. The fact that more specialized, confined, and geometrically more complex neural systems display optimization patterns similar to other, more overarching systems suggests optimization mechanisms might work in a fractal-like fashion, where local, smaller systems are optimized within larger, globally-optimized organizations.

The results also suggest feasibility of optimization analyses in geometrically complex systems that go beyond simple two-dimensional or one-dimensional approximation.

*Corresponding author: Christopher Cherniak, cherniak@umd.edu

References

Cherniak, C. (1994). Component placement optimization in the brain. J Neurosci, 14(4): 2418–27.

Cherniak,C. (2005). Innateness and brain-wiring optimization: Non-genomic nativism. In Zilhao, A., ed, Evolution, Rationality and Cognition, 103–112. Routledge, London.

Cherniak, C., Changizi, M., and Kang, D. (1999). Large-scale optimization of neuron arbors. Phys Rev E, 59: 6001–9.

Cherniak, C., Mokhtarzada, Z., Rodriguez-Esteban, R., and Changizi, K. (2004). Global optimization of cerebral cortex layout. Proc Natl Acad Sci USA, 101(4): 1081–6.

Ekstrand, J.J., Domroese, M.E., Johnson, D.M., Feig, S.L., Knodel, S.M., Behan, M., and Haberly, L. B. (2001). A new subdivision of anterior piriform cortex and associated deep nucleus with novel features of interest for olfaction and epilepsy. J Comp Neurol, 434(3): 289–307.

Haberly, L. (2001). Parallel-distributed processing in olfactory cortex: new insights from morphological and physiological analysis of neuronal circuitry. Chem Senses, 26(5): 551–576.

Kemppainen, S. and Pitkanen, A. (2000).Distribution of parvalbumin, calretinin, and calbindin-d(28k) immunoreactivity in the rat amygdaloid complex and colocalization with gamma-aminobutyric acid. J Comp Neurol, 426(3): 441–67.

Luskin, M. and Price,J. (1983). The topographic organization of associational fibers of the olfactory system in the rat, including centrifugal fibers to the olfactory bulb. J Comp Neurol, 216(3): 264–291.

Pitkanen, A. (2000). Connectivity of the rat amygdaloid complex. In Aggleton, J. P., ed, The Amygdala: A Functional Analysis, 31-115. Oxford University Press, Oxford.

Pitkanen, A., Savander, V., and LeDoux, J. E. (1997). Organization of intra-amygdaloid circuitries in the rat: an emerging framework for understanding functions of the amygdala. Trends Neurosci, 20(11): 517–23.

Price, J. (1987). The central olfactory and accessory olfactory systems. In Finger, T. E. and Silver, W. L., eds, Neurobiology of Taste and Smell. Wiley Interscience, NewYork.

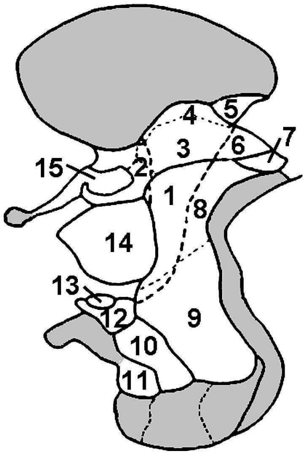

Figure 1. Rat olfactory cortex, layout from Luskin and Price (1983). Core areas for subset sizes 1 - 15 are shown in white, and edge areas for subset size 15 are in gray. Numbers indicate the order in which areas were added to the core subset. See Table 1.

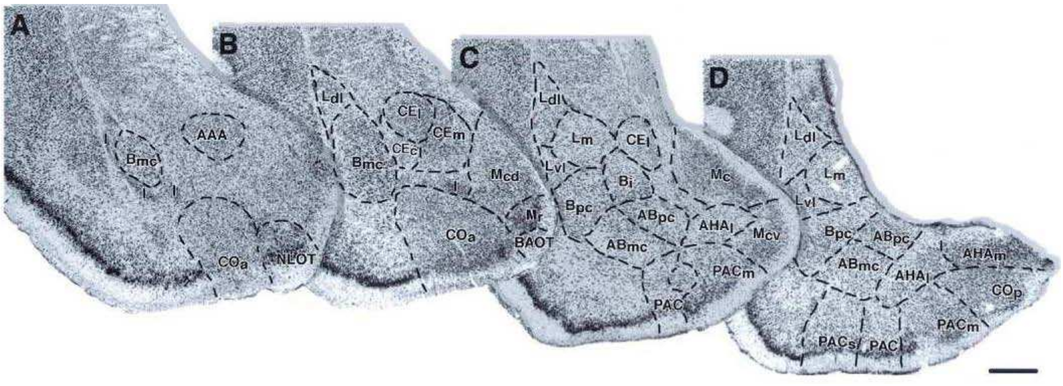

Figure 2. Rat amygdala sections with different functional areas outlined (Pitkanen et al., 1997). Scale bar: 0.5 mm. See Table 2.

	PC$_{av}$	AON$_{m/vp}$	AON$_{l}$	AON$_{e}$	AOB	DPC	AON$_{d}$	PC$_{ad}$	PC$_{p}$	PAC	Co$_{p}$	Co$_{a}$	NLOT	OT	TT$_{v}$
PC$_{av}$															
AON$_{m/vp}$	**1**														
AON$_{l}$	**2**	**1**													
AON$_{e}$	0	0	**1**												
AOB	0	0	0	**1**											
DPC	0	0	0	0	0										
AON$_{d}$	0	0	**0**	1	0	**1**									
PC$_{ad}$	**1**	0	0	0	0	**0**	**2**								
PC$_{p}$	**0**	1	0	0	0	0	1	**2**							
PAC	0	0	0	0	0	1	0	0	**2**						
Co$_{p}$	0	0	0	0	1	0	0	0	0	**0**					
Co$_{a}$	1	0	0	0	0	0	0	0	**2**	**0**	0				
NLOT	0	0	0	0	0	0	0	0	0	0	0	**0**			
OT	**1**	**0**	0	0	0	0	0	0	1	1	0	0	1		
TT$_{v}$	1	**1**	1	0	0	**0**	0	0	0	1	0	0	0	0	
OB	2	**2**	2	**2**	**0**	2	**2**	2	2	2	0	1	2	1	2
TT$_{d}$	0	**0**	0	0	0	0	1	0	1	1	0	0	0	0	**0**
Me	0	0	0	0	1	0	0	0	0	**0**	**2**	**0**	0	0	0
VMEA	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0
VLEA	0	1	0	0	0	0	0	0	**1**	**2**	**0**	0	0	1	0
DLEA	0	0	0	0	0	2	0	0	**2**	0	0	0	0	0	0
AI$_{v}$	1	0	0	0	0	**0**	0	**1**	1	0	0	0	0	0	0
AI$_{p}$	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0
Pr	0	0	0	0	0	0	0	0	**1**	0	0	0	0	0	0
LO	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VLO	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IL	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1. The series of 15 core rat olfactory areas are listed (PC$_{av}$ − TT$_{v}$), in the order they were successively added to the analyzed subset. Below are listed the 12 edge-ring areas (OB − IL) for a size 15 core. Connections of an area to itself are excluded. 0 indicates no known connection between an area pair; 1 indicates connection in one direction; 2 indicates two-way connection. **Bold** values designate topological contiguity of a pair of areas. (Adjacencies do not include tangential contiguity, where only corners of two areas touch.)

	AB_{pc}	B_i	L_m	L_{vl}	B_{pc}	AB_{mc}	AHA_l	CE_l	CE_c	CE_m	CE_i	M_{cd}	M_{cv}	CO_p	AHA_m
AB_{pc}															
B_i	**2**														
L_m	2	2													
L_{vl}	2	**2**	**0**												
B_{pc}	**2**	**2**	**2**	**2**											
AB_{mc}	**2**	**2**	2	2	**2**										
AHA_l	**2**	2	2	1	2	**2**									
CE_l	1	**1**	0	1	**2**	1	1								
CE_c	1	1	1	1	2	1	1	**2**							
CE_m	1	**1**	0	1	2	1	1	**2**	**2**						
CE_i	0	0	0	0	0	0	0	**2**	2	**1**					
M_{cd}	2	1	2	2	2	2	**2**	0	1	**1**	0				
M_{cv}	2	1	2	2	1	**2**	**2**	0	1	1	0	**2**			
CO_p	1	1	1	1	1	2	**2**	0	0	0	0	2	2		
AHA_m	2	1	1	1	2	1	**1**	0	1	1	0	2	1	**1**	
L_{dl}	2	2	**1**	**1**	2	2	2	1	1	1	0	1	1	1	1
B_{mc}	1	**2**	1	**2**	2	2	1	1	**1**	**1**	0	1	0	1	1
NLOT	1	1	0	1	1	1	1	0	0	0	0	0	0	1	0
BAOT	1	0	0	0	0	1	1	0	0	0	0	1	1	1	2
CO_a	2	2	1	2	2	2	2	2	2	**2**	0	**2**	**2**	2	1
M_r	1	0	0	0	1	1	1	0	0	0	0	**1**	1	1	1
M_c	2	0	0	0	0	2	**2**	0	1	**1**	0	**2**	**2**	2	1
PAC	1	1	2	2	1	**1**	**1**	0	0	0	0	1	1	2	0
PAC_m	**1**	0	0	1	1	**1**	**1**	0	0	0	0	0	**0**	**1**	0
PAC_s	1	1	1	1	1	**1**	1	0	0	0	0	1	1	**1**	0
AAA	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1

Table 2. As in Table 1, the series of 15 core rat amygdala areas are listed (ABpc − AHA_m) in the order they were successively added to the analyzed subset. Below are listed the 11 ring areas (L_{dl} − AAA) for a size 15 core.

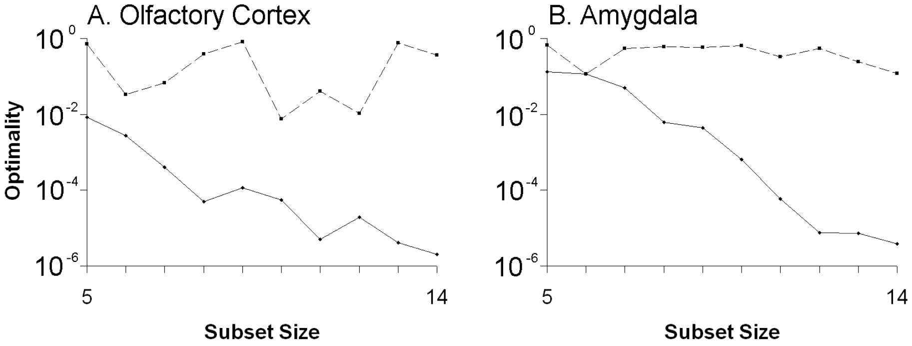

Figure 3. Rat olfactory (A) and amygdala (B) optimality ranks over a range of subset sizes (solid line), compared with randomly chosen scrambled layout (dashed line) of each set of areas. In each case, a Size Law -- increasing optimality with increasing subsystem size -- is apparent for the actual layout, but not for its scrambled version. Optimality ranking for complete systems: olfactory, $2 * 10^{-6}$; amygdala, $3.9 * 10^{-6}$. Exponential best-fit line for actual layouts: $r^2 = 0.90$ for olfactory cortex, $r^2 = 0.96$ for amygdala.