Cortical computation in mammals and birds

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We humans are particularly proud of our cortices. Our brains are bigger than they should be, given our body size; furthermore, our neocortices constitute a larger fraction of the brain than in all other mammals, and our cortices probably contain more neurons than those of any other species on the planet (1). This cortical expansion is thought to give us our cognitive edge over the rest of the animal kingdom. However, even though our cortices may be bigger, their fine structure appears quite similar to that of other mammals. The human cortex appears to contain the same cell types, and their patterns of wiring and gene expression appear basically similar to well-studied model systems, such as the mouse. This finding suggests that, as mammals evolved, a common "canonical cortical microcircuit" has been repurposed to implement the different types of information processing required by different species, including, in our case, language and abstract reasoning (2, 3). In PNAS, Calabrese and Woolley (4) present data that suggest that computations akin to those performed by the mammalian cortex occur also in birds.

It is often assumed that mammals are more cognitively advanced than other vertebrates. Subcortical structures have been termed the "reptilian brain" and assumed to implement only primitive instincts (5), whereas "bird brain" remains a schoolyard insult. Nevertheless, recent research has removed any doubt that birds, at least, can be very smart. In particular, members of the corvid (crow) family are capable of cognitive tasks once thought exclusive to primates: tool use, impressive spatiotemporal memory, and apparent causal reasoning (6). In the age of YouTube, feats of bird intelligence are going viral: for example, the remarkable way Japanese Carrion Crows crack nuts by dropping them on a pedestrian crossing, letting cars drive over them, then waiting to collect the kernels once the lights turn red and the traffic stops (https://www.youtube.com/watch?v=BGPGknpq3e0).

Birds don't have a neocortex; at least, they don't have a brain structure with six layers that match those of the mammalian neocortex. However, a long-standing theory holds that the avian pallium contains circuits homologous to those of the mammalian neocortex. Even though the avian pallium has a nucleated rather than laminated architecture, patterns of afferent connectivity and neurotransmitter distribution led Karten to hypothesize that distinct nuclei in the bird's pallium are homologous to the different layers of the mammalian cortex (7). Although this

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hypothesis was first formulated over 45 y ago, it has received strong experimental support very recently. Anatomical analysis has shown that the connectivity patterns of the avian auditory pallium are remarkably similar to those of mammalian neocortex (8). Furthermore, gene-expression analysis shows that avian pallial nuclei can express many of the same molecular markers as their hypothesized mammalian homologs (9).

To show that avian and mammalian cortices really work the same in way, however, requires functional evidence. Anatomical data suggest that within the avian auditory pallium, fields L1 and lateral caudal mesopallium (CML) are homologous to the superficial layers of the auditory cortex, fields L2a and L2b to the middle layers, and field L3 to the deep layers. (Somewhat confusingly, L does not here stand for "layer" but refers to subnuclei of the auditory region, named "field L.") In PNAS, Calabrese and Woolley (4), by performing population recordings in these regions with silicon microelectrodes, discover a stunning series of similarities between the firing patterns of neuronal populations in the zebra finch pallium, and the corresponding layers of mammalian auditory cortex (Table 1).

The first similarity occurs at the level of timing. In the mammalian cortex, sensory inputs from the thalamus terminate strongly in layer 4. Consistent with this pattern, recordings in multiple sensory regions have shown that sensory-evoked activity occurs earliest in layer 4 (often together with a secondary thalamic input site at the boundary of layers 5 and 6) (10, 11). In birds, auditory thalamic input terminates most strongly in L2; correspondingly, this is where the earliest firing is seen. In the mammalian auditory cortex, the representation of acoustic stimuli in the nongranular layers is not just more delayed, but also more complex and nonlinear than that in layer 4 (12). Calabrese and Woolley (4) find the same in the zebra finch, with stimulus representations in L1 and L3 showing greater nonlinearity and nonseparability than those in L2.

The cortex contains a great variety of excitatory and inhibitory neuronal classes (3). Whereas most of these cannot be distinguished in electrophysiological recordings, one class of cells—the fast-spiking interneurons—can be putatively distinguished by their narrow action potential waveforms (13). Recordings in multiple sensory cortices suggest that these cells fire at higher rates and are more broadly tuned than their pyramidal neighbors (10, 14, 15). Calabrese and Woolley (4) find that the same holds in the avian pallium.

Cortical neurons do not operate alone, but as part of large, correlated assemblies, the activity of which is only partly controlled by sensory stimuli. Understanding the structure of their activity therefore requires recording from many neurons simultaneously. Recent recordings from primate visual cortex indicate that "noise correlations," which indicate that population activity shows coordination beyond that imposed by sensory stimuli, are weakest in layer 4, and stronger in sub- and supragranular layers (16, 17). Consistently, Calabrese and Woolley (4) find that correlations are weakest in field L2. Even more remarkably, the precise spatial structure of correlations in the avian auditory pallium matches that of mammals. In the rat auditory cortex, correlations fall rapidly with distance in superficial layers, but slowly with distance in the deep layers (9); the same holds in the bird's equivalent nuclei.

Table 1. Functional similarities between activity patterns in avian and mammalian pallium

Neocortical layer	Avian nucleus	Latency	Noise correlations	Coding strategy (mammalian)	Coding strategy (avian)
2/3	L1/CML	Late	Strong, local	Sparse, nonlinear	Sparse, nonlinear
4	L2a/L2b	Early	Weak	Dense, linear	Dense, linear
5	L3	Late	Strong, widespread	Dense, nonlinear	Sparse, nonlinear

This list of similarities is so striking that one might ask whether there are actually any differences between the functional organization of the avian and mammalian pallia. Calabrese and Woolley (4) identify one. In mammals (or at least in rodents), cortical activity in the superficial layers is sparse: neurons fire at low rates and are only driven by very precise stimuli, whereas activity in the deep layers is denser, with high firing rates and lower selectivity (10, 15, 18). In the avian auditory cortex, activity is dense in L2 [similar to the dense firing reported in layer 4 of the rodent barrel cortex (18)], but firing in L3 is sparser than firing in L1.

Taken together, these results make a very strong case that the bird's cortex not only shares anatomical features with its mammalian counterpart, but that the circuits function along fundamentally similar lines. When two species share a set of traits, this may indicate a true homology—meaning that the traits are inherited from a single common ancestor— or simply an analogy resulting from independent evolution. The sheer number of coincidences between the avian and mammalian brain makes an analogy seem rather unlikely; to be sure, however, it requires studying a larger number of species. In this regard, it is interesting that the turtle's pallium also contains cell classes molecularly similar to those of mammalian cortical layers (9).

If there is a canonical cortical microcircuit, and if this circuit is indeed homologous

between birds and mammals, it means that this circuit was operating in the last common ancestor of mammals and birds over 300 million y ago. Perhaps the secret of the cortex is in fact even older: the fish brain contains a pallium (19), and deep homologies between the organization of vertebrate and invertebrate brains have also been proposed (20). Cephalopods can be pretty smart too (21). Perhaps intelligence isn't such a hard trick after all: a basic circuit capable in principle

of supporting advanced cognition might have evolved hundreds of millions of years ago, but only adapted to this purpose when the benefits actually outweighed the costs of increased head size, development time, and energy use. Tool-use wouldn't do much for a sheep; those few times intelligence was favored by evolution, it may have appeared with remarkably little effort, by repurposing an ancient circuit most animals use for other things.

1 Herculano-Houzel S (2012) The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost. *Proc Natl Acad Sci USA* 109(Suppl 1):10661–10668.
2 Douglas RJ, Martin KA (2004) Neuronal circuits of the neocortex. *Annu Rev Neurosci* 27:419–451.
3 Harris KD, Shepherd GM (2015) The neocortical circuit: Themes and variations. *Nat Neurosci* 18(2):170–181.
4 Calabrese A, Woolley SMN (2015) Coding principles of the canonical cortical microcircuit in the avian brain. *Proc Natl Acad Sci USA* 112:3517–3522.
5 MacLean PD (1990) *The Triune Brain in Evolution: Role in Paleocerebral Functions* (Plenum, New York), p xxiv, 672 pp.
6 Emery NJ, Clayton NS (2004) The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science* 306(5703):1903–1907.
7 Karten HJ (2013) Neocortical evolution: Neuronal circuits arise independently of lamination. *Curr Biol* 23(1):R12–R15.
8 Wang Y, Brzozowska-Prechtl A, Karten HJ (2010) Laminar and columnar auditory cortex in avian brain. *Proc Natl Acad Sci USA* 107(28):12676–12681.
9 Dugas-Ford J, Rowell JJ, Ragsdale CW (2012) Cell-type homologies and the origins of the neocortex. *Proc Natl Acad Sci USA* 109(42):16974–16979.
10 Sakata S, Harris KD (2009) Laminar structure of spontaneous and sensory-evoked population activity in auditory cortex. *Neuron* 64(3):404–418.
11 Armstrong-James M, Fox K, Das-Gupta A (1992) Flow of excitation within rat barrel cortex on striking a single vibrissa. *J Neurophysiol* 68(4):1345–1358.

12 Atencio CA, Sharpee TO, Schreiner CE (2009) Hierarchical computation in the canonical auditory cortical circuit. *Proc Natl Acad Sci USA* 106(51):21894–21899.
13 Barthó P, et al. (2004) Characterization of neocortical principal cells and interneurons by network interactions and extracellular features. *J Neurophysiol* 92(1):600–608.
14 Swadlow HA (1989) Efferent neurons and suspected interneurons in S-1 vibrissa cortex of the awake rabbit: Receptive fields and axonal properties. *J Neurophysiol* 62(1):288–308.
15 Niell CM, Stryker MP (2008) Highly selective receptive fields in mouse visual cortex. *J Neurosci* 28(30):7520–7536.
16 Hansen BJ, Chelaru MI, Dragoi V (2012) Correlated variability in laminar cortical circuits. *Neuron* 76(3):590–602.
17 Smith MA, Jia X, Zandvakili A, Kohn A (2013) Laminar dependence of neuronal correlations in visual cortex. *J Neurophysiol* 109(4):940–947.
18 O'Connor DH, Peron SP, Huber D, Svoboda K (2010) Neural activity in barrel cortex underlying vibrissa-based object localization in mice. *Neuron* 67(6):1048–1061.
19 Northcutt RG (2008) Forebrain evolution in bony fishes. *Brain Res Bull* 75(2-4):191–205.
20 Strausfeld NJ, Hirth F (2013) Deep homology of arthropod central complex and vertebrate basal ganglia. *Science* 340(6129):157–161.
21 Darmaillacq A-S, Dickel L, Mather JA, eds (2012) *Cephalopod Cognition* (Cambridge Univ Press, Cambridge, UK), p xviii.