



Owls, such as this Eurasian Eagle-Owl (*Bubo bubo*), as well as crows and pigeons have brain organization—and probably cognitive ability—that is similar to mammals.

NEUROSCIENCE

Birds do have a brain cortex—and think

Like mammals, birds have a pallium that sustains correlates of consciousness

By **Suzana Herculano-Houzel**

The term “birdbrain” used to be derogatory. But humans, with their limited brain size, should have known better than to use the meager proportions of the bird brain as an insult. Part of the cause for derision is that the mantle, or pallium, of the bird brain lacks the obvious layering that earned the mammalian pallium its “cerebral cortex” label. However, birds, and particularly corvids (such as ravens), are as cognitively capable as monkeys (1) and even great apes (2). Because their neurons are smaller, the pallium of songbirds and parrots actually comprises many more information-processing neuronal units than the equivalent-sized mammalian cortices (3). On page 1626 of this issue, Nieder *et al.* (4) show that the bird pallium has neurons that represent what it perceives—a hallmark of consciousness. And on page 1585 of this issue, Stacho *et al.* (5) establish that the bird pallium has similar organization to the mammalian cortex.

The studies of Nieder *et al.* and Stacho *et al.* are noteworthy in their own ways, but not because either is the first demonstration of

close parallels between mammalian and bird pallia. That neuroscientists still refer to how bird cognition happens “without a cerebral cortex” (6), as Nieder *et al.* have done themselves (4), is a testament to how neuroscience has grown so much that specialists in different subfields often are not familiar with each other’s findings, even when groundbreaking.

Stating that birds do not have a cerebral cortex has been doubly wrong for several years. Birds do have a cerebral cortex, in the sense that both their pallium and the mammalian counterpart are enormous neuronal populations derived from the same dorsal half of the second neuromere in neural tube development (7). The second neuromere is important: The pallium of birds and mammals lies posterior to the hypothalamus, the true front part of the brain, which is then saddled in development by the rapidly bulging pallium. Owing to the painstaking, systematic comparative analyses of expression patterns of multiple homeobox (Hox) genes that compartmentalize embryonic development, it is now understood that in both birds and mammals, the pallium rests on top of all the neuronal loops formed between spinal cord, hindbrain, midbrain, thalamus, and hypothalamus.

In both birds and mammals, the pallium is the population of neurons that are not a necessary part of the most fundamental cir-

cuits that operate the body. But because the pallium receives copies, through the thalamus, of all that goes on elsewhere, these pallial neurons create new associations that endow animal behavior with flexibility and complexity. So far, it appears that the more neurons there are in the pallium as a whole, regardless of pallial, brain, or body size, the more cognitive capacity is exhibited by the animal (8). Humans remain satisfyingly on top: Despite having only half the mass of an elephant pallium, the human version still has three times its number of neurons, averaging 16 billion (9). Corvids and parrots have upwards of half a billion neurons in their pallia and can have as many as 1 or 2 billion—like monkeys (3).

Additionally, it has been known since 2013 that the circuits formed by the pallial neurons are functionally organized in a similar manner in birds as they are in mammals (10). Using resting-state neuroimaging to infer functional connectivity, the pigeon pallium was shown to be functionally organized and internally connected just like a mouse, monkey, or human pallium, with sensory areas, effector areas, richly interconnected hubs, and highly associative areas in the hippocampus and nidopallium caudolaterale. The nidopallium caudolaterale is the equivalent of the monkey prefrontal cortex (10), the portion of the pallium that is the seat of

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the ability to act on thoughts, feelings, and decisions, according to the current reality informed by the senses.

Now, adding to their resting-state neuroimaging tool set the power and high resolution of polarized light microscopy to examine anatomical connectivity, Stacho *et al.* show that the pallia of pigeons and owls, like that of mice, monkeys, and humans, is criss-crossed by fibers that run in orthogonal planes. Repeated imaging of the brain with light shone at different orientations revealed that fibers within and across bird pallial areas are mostly (although not exclusively) organized at right angles, reminiscent of the orthogonal tangential and radial organization of cortical fibers in mammals (11). The broad-minded neuroscientist with some knowledge of developmental biology might not find this surprising; what would be the alternative, a spaghetti-like disorganized jumble of fibers? But then again, the mantra that “birds do not have a cortex” even though they share pallial development and organization with mammals has been repeated so exhaustively that recognizing that columns and layers are actually observed—visible under polarized light if not to the naked eye—brings new hope that this mantra will join the ranks of myth.

If the bird pallium as a whole is organized just like the mammalian pallium, then it follows that the part of the bird pallium that is demonstrably functionally connected like the mammalian prefrontal pallium (the nidopallium caudolaterale) should also function like it. Nieder *et al.*, who established previously that corvids, like macaques, have sensory neurons that represent numeric quantities (12), now move on to this associative part of the bird pallium. They find that, like the macaque prefrontal cortex, the associative pallium of crows is rich in neurons that represent what the animals next report to have seen—whether or not that is what they were shown.

This representation develops over the time lapse of 1 to 2 s between the stimulus disappearing and the animal reporting what it perceived by pecking at a screen either for “yes, there was a stimulus” or for “no, there was no stimulus,” depending on a variable contingency rule. The early activity of these neurons still reflects the physical stimulus presented to the animal, which indicates that they receive secondhand sensory signals. However, as time elapses and (presumably) recurrent, associative cortical circuits progressively shape neuronal activity, the later component of the responses of the same neurons predicts instead what the animal then reports: Did it see a stimulus that indeed was there, or did it think the stimulus was there enough to report it—even if it was not? Future studies will certainly delve into more

complex mental content than simply “Was it there or not?”; but concluding that birds do have what it takes to display consciousness—patterns of neuronal activity that represent mental content that drives behavior—now appears inevitable.

Because the common ancestor to birds (and non-avian reptiles) and mammals lived 320 million years ago, Nieder *et al.* infer that consciousness might already have been present then—or might have appeared independently in birds and mammals through convergent evolution. Those hypotheses miss an important point: how fundamental properties of life present themselves at different scales. The widespread occurrence of large mammalian bodies today does not mean that ancestral mammals were large (they were not), nor do the nearly ubiquitous folded cortices of most large mammals today imply that the ancestral cortex was folded [it was not (13)]. The physical properties that make self-avoiding surfaces buckle and fold as they expand under unequal forces apply equally to tiny and enormous cortices, but folds only present themselves past a certain size (14). Expansion of the cortical surface relative to its thickness is required for folds to appear. But that does not imply that folding evolved, because the physical principles that cause it to emerge were always there.

Perhaps the same is true of consciousness: The underpinnings are there whenever there is a pallium, or something connected like a pallium, with associative orthogonal short- and long-range loops on top of the rest of the brain that add flexibility and complexity to behavior. But the level of that complexity, and the extent to which new meanings and possibilities arise, should still scale with the number of units in the system. This would be analogous to the combined achievements of the human species when it consisted of just a few thousand individuals, versus the considerable achievements of 7 billion today. ■

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SPECTROSCOPY

Intense x-rays can be (slightly) exciting

Imaging of neutral “survivor” atoms excited by x-ray blasts fights radiation damage

By Thomas Pfeifer

Since their discovery by Röntgen (1) in 1895, x-ray imaging and spectroscopy have revolutionized disciplines as diverse as astrophysics, materials science, chemistry, and the life sciences. However, in the medical context, x-rays are also known for their darker side: They damage tissue. Although even that destructive nature is turned into a benefit in radiation therapy, on a fundamental level, x-rays damage atoms from the inside out: They typically kick out deeply bound electrons, punching a “core hole” into the atom. This unstable situation unleashes a cascade of electronic relaxation events that turn neutral atoms into ions, thus breaking chemical bonds in molecules or creating defects in solids. On page 1630 of this issue, Eichmann *et al.* (2) show how to outpace the radiation damage of x-rays on the fundamental, single-atom level. They detect neutral neon atoms that are just slightly excited, not damaged. Counterintuitively at first, this process benefits from the extremely intense x-rays supplied by a free-electron laser (FEL).

The proof-of-principle setup used by the authors is a simple, elegant realization of a light-matter interaction experiment (see the figure). After a beam of atoms collides with the intense x-ray flashes of the FEL, all of the ions are deflected away, but the remaining neutral atoms hit a position-sensitive detector that is set such that only excited atoms trigger a signal. A characteristic shape on the detector (an “I” marking the spot instead of an “X”) identifies all of the atoms undergoing stimulated x-ray Raman scattering.

Absorbing one x-ray photon creates an unstable core hole (the seed of atomic dam-

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