

resources for the sea urchin can be found at http://www.ncbi.nlm.nih.gov/genome/guide/sea_urchin/ and at <http://hgsc.bcm.tmc.edu/projects/seaurchin/>.

Where can I find out more?

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Primer

Evolution of the avian brain and intelligence

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In Western society, the term 'bird brain' is often used as a derogatory term for a person of diminished intellect, partly because many people tend to think of birds as pecking machines, responding reflexively to stimuli in their environment, and partly because birds seem so different from us, with their beady eyes and small heads. But over 40 years ago William Thorpe, who was the leading authority on bird learning at that time, pointed out: "The poor development in birds of any brain structures clearly corresponding to the cerebral cortex of mammals led to the assumption among neurologists not only that birds are primarily creatures of instinct, but also that they are very little endowed with the ability to learn...this misconceived view of brain mechanisms, hindered the development of experimental studies on bird learning".

In the 1960s little was known about the cognitive capacities of birds, but recent studies lend support for Thorpe's view: we now know that some bird species make and use tools, can count, remember specific past events and reason about the mental states of individuals, behaviours that some have considered to be unique to humans. Despite the apparent cognitive similarity between humans and some birds, neuroscientists have tended to view bird brains as interesting curiosities with little relevance to the workings of the human brain. Recently, however, the Avian Brain Nomenclature Consortium published a series of papers attempting to re-address the issue of the importance of the bird brain to neuroscience by investigating how the avian brain evolved, how

the structure of the avian brain relates to that of the mammalian brain, and how names have had a negative influence on how birds are perceived.

Negativity surrounding the avian brain began in the late nineteenth century, when Ludwig Edinger provided names for the various parts of the vertebrate brain. His form of nomenclature was based on the naïve view that evolution occurs in a linear progression, so that each new species is an elaboration of an older species. This *scala naturae* is often represented as a ladder. With respect to intelligence, Arthur Jensen, one of the key figures in studies of human intelligence argued that "single-cell protozoans, such as amoeba, rank at the bottom of the scale, followed in order by the invertebrates, the lower vertebrates, the lower mammals... and finally the primates, in order: New World monkeys, Old World monkeys, the apes, and at the pinnacle, humans".

With respect to brain evolution, Edinger applied this *scala naturae* suggesting that the brains of living vertebrates retained ancestral structures, but that new brain areas were added onto older ones, or older areas increased in size and complexity to form new areas (Figure 1A). According to this view, evolutionarily older brains are simple, and so produce simple instinctive behaviour, and evolutionarily newer brains are complex, and therefore can control learned and intelligent behaviour. The oldest brain regions — those present in all vertebrates — were prefixed with the term 'paleo-', the next oldest brain regions were given the prefix 'archi-', whereas the new brain regions — those present in the species closest to the top of the 'ladder' — were assigned the prefix 'neo-'.

We now know that, as with other parts of the body, the brains of distantly related species tend to be derived from the same basic elements found in the common ancestor — they exhibit homology (Figure 1B). So although the common ancestor of birds and mammals lived approximately 300

million years ago, studies of extant reptiles have revealed that the reptilian (therapsid and sauropsid) forebrain is pallial in origin and so the common ancestor should also have shared this trait. If so, then the forebrain of modern birds and mammals will also be pallial. This seems to be the case.

Edinger mistakenly thought that the majority of the avian brain was derived from the striatum or basal ganglia, which tends to be involved in species-specific instinctual behaviours, such as feeding and sexual and parental behaviour, as well as responses to rewards and motor coordination. In mammals, the basal ganglia has a striated appearance due to the fibre bundles running through it. Areas in the avian forebrain tended to resemble the mammalian striatum and so most areas (paleo-, archi- or neo-) were named with the root word 'striatum'. For example, the avian cerebrum was originally separated into neostriatum, hyperstriatum, archistriatum, paleostriatum and ectostriatum (Figure 2). Note that very few structures were thought to be derived from the pallium, and named with the root words 'cortex' or 'pallium'. By contrast, much of the mammalian forebrain was known to be derived from the pallium, which resulted in a six-layered neocortex, the area of the brain which is involved in thinking, reasoning and planning.

Research in the last 30 years on neural connectivity, gene expression and lesions has caused a revision in our thinking about the avian forebrain and the naming of its parts. We now know that the greatest expanse of the bird telencephalon is derived, not from the striatum as Edinger and others previously thought, but from the pallium. Indeed, the large area of forebrain that lies above the basal ganglia in birds is now recognised to be functionally and developmentally akin to the mammalian neocortex, derived in the same way from the pallial sector of the embryonic forebrain. But rather than producing a layered cortex as in mammals, in birds the result was a nucleated structure with pockets of grey

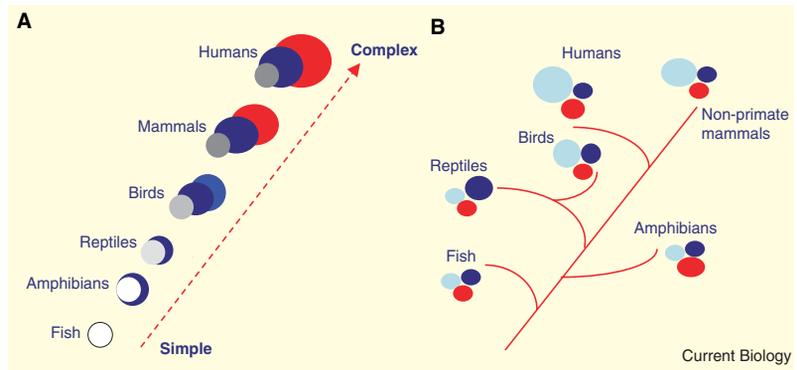


Figure 1. Schematic representation of two theories of brain evolution.

(A) The outdated '*scala naturae*' theory, where evolution occurs in a linear, progressive fashion up a ladder in which 'lower' (simple) species evolve into 'higher' (complex) species; going from fish and amphibians at the bottom through reptiles and birds to primates and humans at the top. With respect to brain evolution, the increasing complexity resulting from climbing the ladder leads to the appearance of completely new areas which are then added onto old ones. Each colour represents a different hypothetical brain region, either old or new. (B) The modern theory, where evolution is tree-like and new species evolve from older ancestral forms. With respect to brain evolution, complexity is derived from refining neural structures which are already present in ancestral forms, such that brain regions increase in size. There are no truly new brain areas, only elaborations of established regions. The colours represent different brain regions, but rather than new areas being added, evolutionarily old areas are increased or decreased in size (or complexity).

matter. The analogy would be to compare a club sandwich (mammalian) to a pepperoni pizza (avian).

The accumulation of new data led a consortium of avian neuroscientists to propose a new nomenclature for the avian brain, where the forebrain was renamed in the light of this modern understanding of its evolution and the relative contributions of the striatum and pallium (Figure 2). The proportion of the forebrain that is known to be cortical-like (pallial) in structure has increased significantly (Figure 2). These name changes reflect our current understanding of how these brain regions evolved (Table 1), but they have had a wider impact on our thinking about the intellectual abilities of birds. As stated so eloquently by William Thorpe over 40 years ago, this misunderstanding about the evolution of the avian brain has led to an extreme bias against the capabilities of birds in learning and cognition. Of course, we should not be carried away with the idea that, because the avian brain is structurally more similar to the mammalian brain than previously thought, all birds are intelligent, any more than we might think that all mammals are

intelligent. The names have changed, but not necessarily the abilities associated with them.

There are over 9,000 species of birds, however many of those studied by comparative psychologists are not well endowed with the cognitive skills associated with primates and dolphins. The humble pigeon, for example, is a master at visual discrimination and memory: it can remember hundreds of different objects for long periods, discriminate between different painting styles that would stump art history undergraduates, and navigate hundreds of miles by following the trajectory of major roads. But pigeons seem unable to perform accurately on tasks that require them to abstract a general rule to solve a suite of similar problems. For example, when presented with a choice between two colours, A and B, they cannot apply the following rule; 'If pecking A is rewarded, then continue to peck at A; if pecking A is not rewarded, peck at B'. This rule is called 'win-stay-lose-shift', and is easily learned by crows, monkeys and apes.

As with all other taxonomic groups, there are the Dumbos and the Einsteins, and a species' level of intelligence tends to be

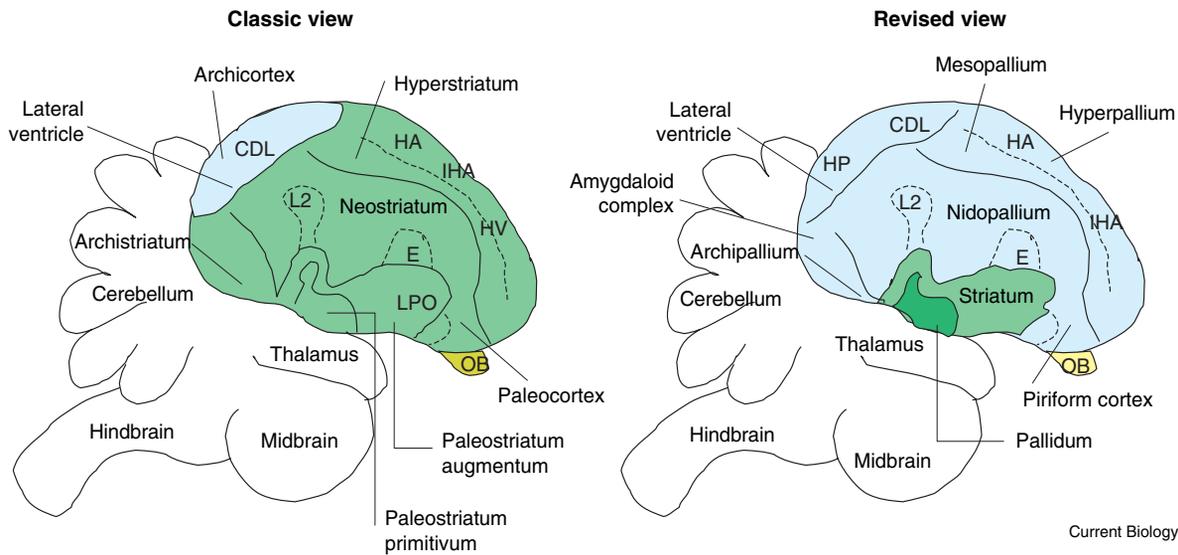


Figure 2. Comparison of the classic and revised views of the avian forebrain. Left: classic view of the avian forebrain, in which the greatest expanse of the cerebrum was classified as *striatal* in origin (light green), compared to the smaller extent of the *pallium* (light blue). Right: revised view of the avian forebrain, in which the majority of the cerebrum has been re-classified as *pallial* in origin (light blue) compared to the smaller *striatum* (light green). The *pallidum* is coloured dark green, and the olfactory bulb is coloured yellow. Adapted from Avian Brain Nomenclature Consortium (2005). CDL, area corticoidea dorsolateralis; E, ectostriatum (classic) or entopallium (revised); HA, hyperstriatum accessorium (classic) or hyperpallium apicale (revised); HP, hippocampal complex; IHA, interstitial nucleus of the hyperpallium intercalatum; L2, field L2; LPO, parolfactory lobe; OB, olfactory bulb.

reflected in brain size (relative and absolute). Within fish, for example, the sharks and rays have large brains for their body size, and although they have not been tested for their cognitive skills in the laboratory, they are adaptable, flexible and opportunistic, all hallmarks of intelligence. Compare this with lampreys, which have a very small brain for their body size, and although biologically successful in terms of reproductive success, do not display any particularly striking psychological adaptations. Similarly within the mammals: dolphins, monkeys and apes are the intellectual champions, compared to say, rabbits, sheep or wild boar. The same holds true for birds. Recently, we have suggested that corvids (crows, ravens and jays) and parrots compare favourably with the apes in terms of both relative brain size and intelligence, but pigeons, chickens and quail are more comparable to rats and mice.

Avian and mammalian brains compared

How can corvids, parrots and possibly other birds rival apes in their intellectual capacities, when

they do not have the traditional six-layered prefrontal cortex of mammals? Although corvids and parrot brains are relatively the same size as those of chimpanzees, gorillas and orangutans, bird and mammal brains are structured very differently. We have suggested that corvids and apes may represent a case of convergent mental evolution — similar cognitive processes, with the same outcome — but with divergent brains — very different brain structures. But there are clues from modern neuroanatomy suggesting that avian and mammalian brains may have come up with similar solutions to the same problems, thus demonstrating both mental and neural convergent evolution. Although the *gross* structures of avian and mammalian brains are radically different, there is evidence that there are *connectional* similarities in the brains which may go some way in explaining their cognitive similarities. Although these similarities are found in perceptual systems, it is not implausible that similar principles may also apply to cognitive systems.

Similar visual processing pathways

The mammalian neocortex is highly laminated, with six layers, from the superficial layers on the surface to the deeper layers underneath. Each layer has its own cell types, connectional patterns and neurochemical composition. By contrast, the avian telencephalon is nucleated, with little or no laminar organization. There is one striking exception: the Wulst or hyperpallium, on the dorsal surface of the forebrain, which consists of three to four layers, depending on its size. Each layer has its own connectional and neurochemical patterns, and visual information appears to be processed by similar pathways to the mammalian forebrain. Similar connectivity patterns have been found in the somatosensory and motor systems of birds and mammals. It is not yet certain which aspects of these anatomical traits have evolved from a common ancestor and which have evolved independently.

Similar vocal learning pathways

The song control system of songbirds (oscines), such as

zebra finches and canaries, has been the focus of neurobiological study for almost 40 years. Song birds learn their song from a tutor, often their father. Recent studies in two other orders of birds that also learn their vocalizations, the parrots and hummingbirds, have revealed similar connectivity patterns to songbirds in their vocal control pathways. In non-vocal learners, such as pigeons and doves, neural activation during vocalizing is restricted to the brainstem and midbrain, suggesting that vocalizations are relatively reflexive and innate. Indeed, non-vocal learners, perceive and produce vocalizations only using this neural system. By comparison, in vocal learners, neural activation when perceiving calls and vocalizing occurs in the brainstem, midbrain and additionally distinct song control nuclei in the forebrain. Very specific regions in the forebrain are involved in perceiving song or vocalizations, and separate regions are involved in producing song (often imitating songs produced by a tutor). Vocal learning has been suggested to have only evolved six times: within birds, in the oscines, parrots and hummingbirds; and within mammals, in the cetaceans (dolphins and whales), pinnipeds (seals and sealions) and humans. The neural pathways involved in vocal learning in cetaceans and pinnipeds are not known. In humans, however, functionally similar neural networks to birds have been implicated in language learning.

An avian 'prefrontal cortex'?

One final example of convergence in the neural systems of birds and mammals relevant to the issue of intelligence is the suggestion that birds may have a functionally equivalent structure to the mammalian prefrontal cortex. In mammals, the prefrontal cortex contributes to the organization, planning and flexibility of behaviour based on previously acquired information. As there is good evidence that some birds display these complex cognitive

Table 1. Old and new nomenclature of the avian telencephalon, with nomenclature of analogous structures in the mammalian telencephalon.

Avian old nomenclature	Avian new nomenclature	Mammalian nomenclature
Ectostriatum	Entopallium	Neocortex (sensory)
Hyperstriatum accessorium	Hyperpallium apicale	Neocortex (sensory)
Hyperstriatum dorsale	Hyperpallium dorsocellulare	Neocortex (sensory)
Hyperstriatum ventrale	Mesopallium	Neocortex (association)
Wulst (Hyperstriatum)	Wulst (Hyperpallium)	Neocortex (sensory)
Neostriatum	Nidopallium	Neocortex (prefrontal)
Paleostriatum augmentatum	Lateral striatum	Striatum
Paleostriatum primitivum	Globus pallidus	Globus pallidus
Parolfactory lobe	Medial striatum	Caudate and putamen

traits, these birds may also have functionally equivalent areas located in the telencephalon. The strongest candidate is the caudolateral nidopallium (CDLN). Neurobiological studies focused on the CDLN of pigeons have revealed similarities in connectivity, neurochemistry, neurophysiology and function to the mammalian dorsolateral prefrontal cortex. For example, lesions of the CDLN affect the performance of birds on traditional tasks used to gauge prefrontal cortex function in mammals: delayed alternation, reversal learning and other working memory tasks, such as Go/No Go. Neurons within the CDLN respond during the delay period of Go/No Go tasks similar to neurons in the primate dorsolateral prefrontal cortex.

There are also similarities between the avian CDLN and mammalian prefrontal cortex in the distribution of dopamine fibres, and the concentration of dopamine D1 receptors, but not D2 receptors. Indeed, blocking D1 receptors in the CDLN disrupts performance on similar tasks to those affected by permanent lesions. Finally, the CDLN is connected reciprocally with secondary sensory areas of all modalities, and projects to somatomotor and limbic areas of the basal ganglia which allow it to influence behavioural and affective responses similar to primate prefrontal cortex.

Although this is striking evidence for functional and possibly anatomical convergence between the avian CDLN and primate prefrontal cortex, there are a number of outstanding questions. For one thing, the only tasks that have been affected by both prefrontal cortex and CDLN lesions are working memory tasks. Other more complex tasks, such as attentional set-shifting, have not yet been tested in birds. Secondly, the only avian species to be examined is the pigeon, which as stated earlier is not the brightest pupil in the flock, and certainly does not demonstrate the same forms of complex cognition displayed by birds with larger forebrains, and importantly, a larger nidopallium. Indeed, the nidopallium of crows is four times larger than that of quail, pheasants and partridges (the only species for which there are data). From absolute brain size, the nidopallium of crows is predicted to be significantly larger than that of pigeons. It remains to be seen what effect CDLN lesions will have on corvids and parrots. Finally, many aspects of complex cognition which have been demonstrated in corvids, such as episodic-like memory and theory of mind, are known to be dependent on other parts of the prefrontal cortex (ventromedial sector) in humans. If these abilities in corvids are functionally equivalent to humans, we might expect to find areas within the

corvid brain that are structurally, as well as functionally, analogous to the ventromedial prefrontal cortex of humans. This hypothesis remains to be tested.

Avian intelligence is not an oxymoron

Some birds are capable of cognitive feats which put most mammals to shame. In the rainforests of New Caledonia and Mare, New Caledonian crows use and construct a number of different tools which are used to gain access to large grubs found in the crevices of trees. These tools are crafted from raw materials (sticks and *Pandanus* leaves), and there is a suggestion that, like chimpanzees, crow tool use is a form of culture. In the laboratory, New Caledonian crows are equally impressive, demonstrating some understanding of 'folk physics' (the common sense view of how the world works). Perhaps the best demonstration of this is Betty the crow, who appeared to spontaneously bend a piece of wire into a hook to gain access to out-of-reach food.

Other corvids are equally impressive, providing evidence of cognitive abilities thought to be uniquely human. Western scrub-jays, for example, are the first non-human animals to demonstrate episodic-like memory — the ability to remember the 'what, where and when' of a specific past event. In these studies, jays cache different types of food which decay at different rates in specific locations. In order to recover food that is still fresh and edible, the jays had to remember 'what' type of food they cached, 'where' they cached and 'when' they cached it. Scrub-jays are also extremely wary of the presence of conspecifics during caching. If an observer is watching when scrub-jays cache, the storers come back later when alone and move their caches to new places that the observer does not know. Interestingly, storers only do this if they have been thieves themselves in the past. This suggests that experienced scrub-jays may

attribute others with the intention of pilfering, and so implement strategies to reduce this possibility in the future. Scrub-jays also protect their caches by reducing the amount of information available to an observer at the time of caching, by hiding caches behind barriers, in the shade or as far from an observer as possible. All this suggests that western scrub-jays may demonstrate another supposedly unique form of human cognition: theory of mind. Parrots, such as Alex the African grey, have also demonstrated intellectual abilities which rival primates, such as understanding whether objects are the same or different, their number (including zero), their colour and shape.

Our new appreciation of the complexity of the avian brain is closely tied with a new appreciation of the complexity of the avian mind, particularly with respect to corvids and parrots. It is now the job of behavioural biologists, comparative psychologists and neuroscientists to determine how one translates into the other.

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Multidimensional scaling reveals a color dimension unique to 'color-deficient' observers

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Normal color vision depends on the relative rates at which photons are absorbed in three types of retinal cone: short-wave (S), middle-wave (M) and long-wave (L) cones, maximally sensitive near 430, 530 and 560 nm, respectively. But 6% of men exhibit an X-linked variant form of color vision called deuteranomaly [1]. Their color vision is thought to depend on S cones and two forms of long-wave cone (L, L') [2,3]. The two types of L cone contain photopigments that are maximally sensitive near 560 nm, but their spectral sensitivities are different enough that the ratio of their activations gives a useful chromatic signal. Like color-normal observers, deuteranomalous observers are formally trichromatic, in that they need three primary lights if they are to match all possible spectral power distributions, but the matches they make are different from those of the normal. Here we use multidimensional scaling (MDS) [4,5] to reveal the color dimension that is private to the deuteranomalous observer.

For both normal and anomalous observers, MDS has previously been used to reconstruct subjective color spaces (for example [6,7]). The input to the scaling program is a matrix of the judged similarities of all possible pairs in a set of stimuli; and the output is a map of the stimuli that minimizes the differences between the input proximities and the corresponding proximities in the derived space. The length of the vector between any two stimuli in the output space indicates how