

Pigeons as a model species for cognitive neuroscience

Introduction

(Rock-) pigeons and men share several 1000 years of common history [7]. Pigeons were arguably the first domesticated birds and were originally bred because of their tasty breast muscles. However, already 4000 years ago, another unique trait of this species was discovered: homing, i.e., the ability to return to the home flock from an arbitrarily chosen unfamiliar starting point located up to some hundreds of kilometers away. This innate capacity was used for message transmission already in ancient Greece, e.g., for nation-wide announcement of the winners of the Olympic Games. Homing pigeons were employed for mail delivery well into the 20th century. For example, thousands of homing pigeons served in the military during World War II, and many of them were decorated for bravery.

Regarding basic science, pigeons were used as experimental animals in the 19th century already. Josef Breuer, a mentor of Sigmund Freud and one of the founding fathers of psychoanalytic theory, used pigeons to investigate semicircular canal function. Charles Darwin himself was a pigeon fancier, and the variability in pigeons brought about through selective breeding constituted an important argument in favor of natural selection as the central mechanism of evolution.

In the 1930s, US psychologist B.F. Skinner introduced pigeons into experimental psychology. Skinner, who originally studied mechanisms of operant conditioning with rats, switched to pigeons mainly because of their extended life span. However, pigeons offer a whole range of other favorable traits which together render them su-

perb experimental subjects, which include the following.

Longevity

Pigeons grow considerably older than, for example, rats, which live up to 2 or 3 years and start showing signs of aging after around 18 months. Pigeons, on the other hand, may live up to 20 years in captivity. For psychologists working with elaborate behavioral study designs, the short life expectancy of rats constitutes an important limit on the complexity and duration of possible experimental paradigms. Pigeons, however, can be trained and tested for an extended period of time, including the possibility of re-training them on different experimental tasks.

Impressive cognitive capacities

Pigeons can acquire a wide range of skills and master cognitively demanding tasks. Their visual long-term memory encompasses hundreds of pictures, and they retain memory for these pictures over several years [18]. They form complex perceptual categories and are, e.g., able to discriminate unfamiliar paintings from distinguished artists such as Monet and Picasso solely on the basis of previous experience with different pictures from these artists [2, 20].

Highly developed visual system

Like most birds, pigeons possess a highly developed visual system. The pigeon retina contains five types of cones, and each of them houses one of various types of oil droplet within their inner segment; these

droplets are thought to serve as cut-off filters and co-determine the spectral sensitivity of their associated cone [11]. Each retina sends its information via roughly 2.3 million nerve fibers to higher brain centers (a human retina contains about 1 million fibers). Accordingly, a major portion of the pigeon endbrain is concerned with the processing of visual information. Such a well-developed visual system is highly advantageous for behavioral research, and this may be one reason why the avian visual system might be a better model to study visual cognition than those of rats or mice.

Excellent work ethic

Behavioral researchers appreciate cooperative animal subjects. Pigeons are highly focused on the task at hand and are willing to work for several hours in a row. Importantly, pigeons are quite resistant to frustration: even when rewarded only occasionally, they work reliably and steadily. Skinner claimed to have trained a pigeon to peck 35,000 times on a pecking key—for merely half an ounce of grain.

Gentleness

In contrast to other bird species, adult pigeons quickly adapt to human handling. They rarely exhibit aggressive behavior and tolerate handling from both familiar and unfamiliar human experimenters. Magpies and crows, on the other hand, have to be hand-raised to tolerate human handling as adults.

We will illustrate the utility of some of the abovementioned traits with a study conducted in our laboratory. In each of

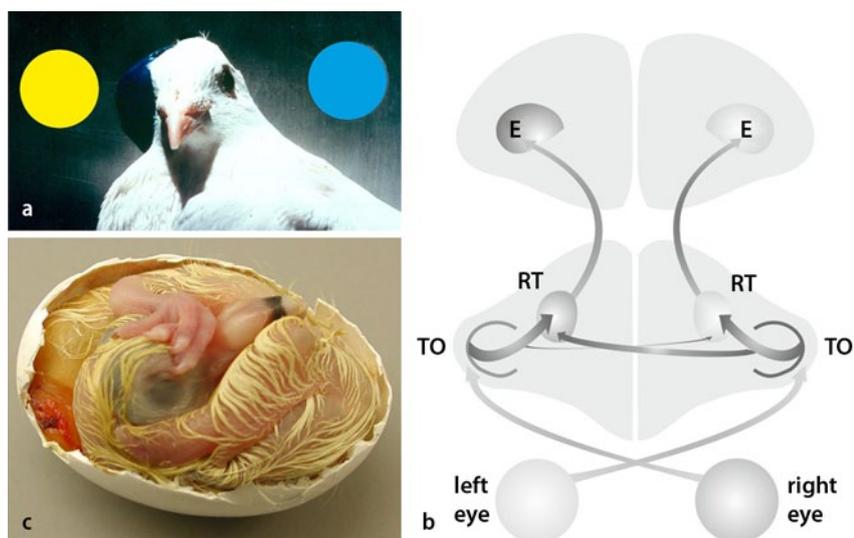


Fig. 1 **a** Pigeon with eye caps used for testing hemisphere-specific performance. **b** The pigeon's tectofugal visual system. Retinal fibers terminate in the contralateral optic tectum (*TO* corresponds to the mammalian superior colliculus). Efferences of the *TO* project bilaterally into the thalamic nucleus rotundus (*RT* corresponds to mammalian pulvinar), which innervates the ipsilateral telencephalic entopallium (*E*). The projection arising from the right *TO* to the left *RT* is roughly twice as strong as the projection from left *TO* to right *RT*. **c** Asymmetrical positioning of a pigeon embryo within the egg shell. The right eye faces the shell and, thus, receives visual stimulation

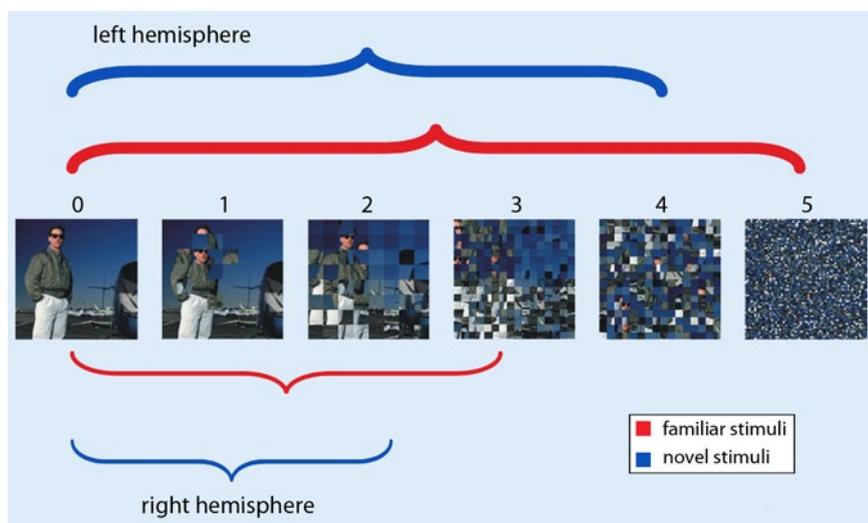


Fig. 2 **a** Hemisphere-specific analysis for visual categorization. Panels show an example visual stimulus, scrambled over six different degrees of fragmentation. Scrambling level 5 contains 4096 equally-sized shuffled fragments of the original picture (scrambling level 0). Still, the left hemisphere reliably categorizes familiar pictures scrambled to this level. Even unfamiliar pictures can be categorized well up to scrambling level 4. However, the right hemisphere achieves satisfactory categorization performance for familiar stimuli only up to level 3, for unfamiliar stimuli up to level 2

many experimental sessions, pigeons learn to peck at one of two different choice keys following presentation of a novel visual stimulus A, and to peck at the other choice key following presentation of a novel visual stimulus B. Each correct response yields a small food reward (*acquisition of an operantly conditioned response*).

It takes a pigeon roughly 100–500 trials to achieve criterion performance of 80% correct responses. Following successful acquisition, one of the two responses is randomly chosen to undergo *extinction*, i.e., reward ceases to follow correct responding, so the animal is less and less likely to emit that specific response. Finally, the

correct response is again reinforced, until the animal again reliably emits that response (*reacquisition*). In parallel, the pigeon is working on a visual discrimination control task with familiar stimuli throughout the entire experimental session.

In this paradigm, pigeons work up to 1500 trials per day (work ethic) and manage to acquire, extinguish, and reacquire an operant response (cognitive capacity). However, it takes many months of training before animals are performing at a level that allows implantation of intracranial electrodes for tracking action potential firing of individual neurons while the pigeons are performing the task (longevity). This newly developed paradigm, thus, allows registration of single-neuron activity over three different stages of learning: acquisition, extinction, and reacquisition of a conditioned response [5].

Neuroscientific studies on pigeons have yielded central insights into the mechanisms of goal-directed behavior and its neural underpinnings. In the following, we will illustrate this by focusing on two areas of research: (1) the functional relevance of brain asymmetries, and (2) the neural basis of executive functions. Moreover, we will show that these findings facilitate an understanding of the phylogeny of cognitive abilities and the neural networks which support them, as we will argue in a third section on comparative neuroanatomy.

The neural basis of cerebral asymmetries: the right and the left side of the bird brain

Lateralization, the functional and structural asymmetry of the cerebral hemispheres, is a fundamental principle of brain organization. While handedness is probably the most obvious example, a whole range of abilities is lateralized, e.g. the production and comprehension of natural language, and spatial cognition. For a long time, it was assumed that cerebral asymmetries are unique to the human brain and constituted a crucial step in the evolution of cognition. Meanwhile, however, it is widely accepted that neural lateralization is widespread in the animal kingdom. For example, monkeys, mice, and kangaroos exhibit clear paw preferences, and

toads tend to remove an object from their snout consistently using the same forelimb [16]. Even insects can show structural and functional asymmetries: honeybees are better at associating an odor with a food reward when they perceive the odor with the right rather than the left antenna [8, 9]. The widespread distribution of brain asymmetries suggests that neural lateralization somehow provides a selective advantage. Indeed, more strongly lateralized individuals exhibit superior performance in several perceptual and cognitive tasks. One possible explanation is that cerebral asymmetries serve to avoid computational redundancy.

The visual system of birds such as pigeons and chicks provides an excellent model to study lateralized information processing at both neurobiological and cognitive levels [6, 13]. A crucial advantage of birds over mammals is that the visual input into either cerebral hemisphere can be easily obstructed by simply occluding the contralateral eye (■ Fig. 1a), because the optic nerves decussate nearly completely in birds (but not in mammals). Accordingly, visual information reaching the eye is primarily routed to the contralateral hemisphere. Through the comparison of monocular left- and right-eye performance, one can then pinpoint lateralization of function. For example, both pigeons and chicks exhibit left-hemispheric dominance for visuomotor control, while the right hemisphere is dominant for spatial attention.

Functional asymmetries correlate with morphological and neurophysiological hemispheric differences in the tectofugal visual system, which corresponds to the extrageniculostriatal system of mammals, and which dominates visually-guided behavior in pigeons (■ Fig. 1b) [13]. Due to an asymmetric projection from the midbrain, the left hemisphere (i.e., the thalamic nucleus rotundus and the entopallium) receives stronger bilateral input than the right hemisphere. Accordingly, more left-hemispheric neurons respond to both contra- and ipsilateral visual inputs [17]. Additionally, entopallial neurons in the left hemisphere discriminate better between rewarded and non-rewarded conditioned stimuli than neurons in the right entopallium. In a similar vein,

the left hemisphere excels in the bilateral recall of memory contents [19].

Asymmetries in the visual system are determined through asymmetrical light stimulation during embryonic development—an instance of ontogenetic plasticity. Pigeons, like other birds, lie asymmetrically in the egg shell. Their head is positioned such that the right eye faces the egg shell, while the left eye faces the body (■ Fig. 1c). Therefore, any light shining on the egg can trigger neural responses in the right but not the left eye. Resulting activity differences between the left and the right hemisphere lead to asymmetric neural differentiation, which then determines structural and functional asymmetries in adult animals. Importantly, pigeons incubated in total darkness do not exhibit lateralization of function.

However, lateralization can be induced even after hatching through manipulation of visual experience. Occlusion of the (usually dominant) right eye for 1 week reverses the normal pattern of lateralization, and the right hemisphere achieves stronger control over visuomotor performance [13].

Pigeons are one of only a handful of species in which lateralization of higher cognitive functions has been investigated. In the following, we will present two studies on (1) hemispheric specialization and (2) hemispheric cooperation.

Hemispheric specialization: analysis and categorization of visual stimuli

In humans, the left hemisphere is specialized for the analysis of local features of the visual scenery, while the right hemisphere focuses more on global and configural features. Taking face recognition as an example, this implies that the left hemisphere encodes the form and the color of the eyes, while the right hemisphere registers interocular distance in relation to the width of the face. Importantly, this fundamental dichotomy of hemisphere-specific strategies seems to have a long evolutionary history.

In a seminal study, Herrnstein and Loveland [2] confronted pigeon subjects with hundreds of pictures with and without a human. Pigeons were reinforced for pecking on pictures depicting humans

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O. Güntürkün · M.C. Stüttgen · M. Manns Pigeons as a model species for cognitive neuroscience

Abstract

Deeper understanding of the neuronal basis of behavior and its evolution requires investigation of model organisms taken from different taxonomic groups. The merits of this comparative approach are highlighted by research on birds: while their cognitive capacities have long been underestimated, research on avian model systems more recently has begun to provide central insights into the functional organization of the brain. In particular, domesticated homing pigeons (*Columba livia*) have been used as a model for the study of the psychological processes underlying learning, memory, and choice behavior, and much of current animal learning theory is based on findings with pigeons. Moreover, the vast amount of available behavioral and anatomical data has rendered the pigeon one of the key model species of behavioral and comparative neuroscience. This article illustrates some insights gained from research with pigeons with applicability beyond the class of *aves*.

Keywords

Cerebral asymmetry · Executive function · Prefrontal cortex · Nidopallium caudolaterale · Bird

only. Animals quickly learned to discriminate between positive and negative stimuli and, more importantly, were able to transfer this knowledge to novel pictures. This transfer of knowledge shows that the animals extracted a complex visual concept—“presence of a human being”—from the pictures in the training set. To answer the question whether the left and the right hemisphere differ in terms of their mode of picture analysis, we trained pigeons on the same task—discriminating pictures with and without humans—and then confronted them with novel pictures under monocular conditions [21]. As an additional experimental manipulation, we modified the pictures through scrambling (■ Fig. 2). When pictures were scrambled into smaller fragments, animals were still able to perform the discrimination when tested with the right eye (left hemisphere), but showed severe impairments

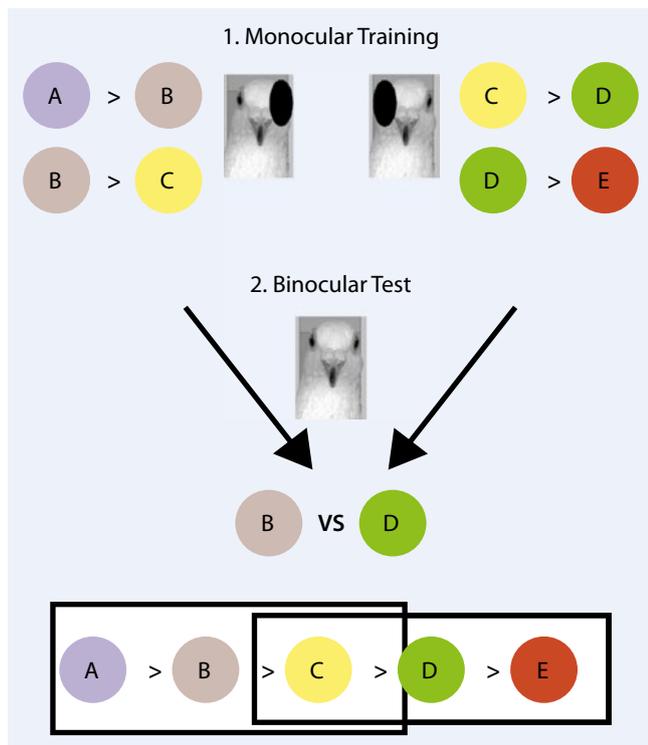


Fig. 3 ◀ Hemispheric cooperation for transitive inference. Pigeons were trained monocularly to perform a color discrimination task and were required to peck on a specific color or of grit. However, whether pecking on a specific color was reinforced depended on which differently-colored type of grit was concurrently presented. See text for further details

when tested with the left eye (right hemisphere). These performance differences demonstrate that the left hemisphere relies on local features for categorization, but to some extent disregards their configuration; as a result, it recognizes relevant aspects of stimuli even when they are rearranged. The right hemisphere, on the other hand, uses the configuration of local features for categorization and, therefore, does not correctly classify pictures in which arms and legs of the depicted humans were detached from the body as belonging to the positive stimulus category.

These and other studies show that the dichotomy of hemisphere-specific analysis is similar in pigeons and humans, and therefore suggests that this pattern is conserved across different classes of vertebrates and may have a long evolutionary history.

Interhemispheric cooperation

In a lateralized brain, the two hemispheres need to exchange information to arrive at a unitary decision about how to act. While the bird brain is devoid of a corpus callosum, interhemispheric fiber tracts such as the anterior commissure enable the two hemispheres to communicate. However,

can the two hemispheres combine hemisphere-specific knowledge to master complex cognitive tasks?

Chicks and pigeons are capable of relational learning. They can infer that, if A is larger than B and B is larger than C, A must be larger than C as well. To investigate relational learning, animals are trained to discriminate pairs of stimuli ($A+B-$, $B+C-$, $C+D-$, $D+E-$, where + designates the positive and - designates the negative stimulus), which together form a transitive line ($A > B > C > D > E$; **Fig. 3**). Thus, the reinforcement contingency of stimuli B, C, and D depends on which other stimulus is concurrently visible.

We trained pigeons on a two-alternative forced choice color-discrimination task to study interhemispheric integration (**Fig. 3**) [4]. To induce hemisphere-specific knowledge, pigeons were trained on the first two stimulus pairs ($A+B-$, $B+C-$) with one eye and on the last two stimulus pairs ($C+D-$, $D+E-$) with the other eye. Following successful training, animals were confronted binocularly with novel stimulus combinations, which could only be classified correctly if hemisphere-specific knowledge was integrated across hemispheres. Indeed, normally hatched

(lateralized) pigeons were able to correctly classify the stimuli, while non-lateralized pigeons (incubated in darkness) could not solve the task [4]. This work demonstrates that environmental factors (here, light experience) not only determine the pattern of hemispheric specialization, but also the efficiency of interhemispheric integration.

The neural basis of executive functions

The term “executive functions” denotes a loosely defined group of cognitive processes entailing the planning and implementation of goal-directed behaviors, such as the allocation of attentional resources, decision making, and manipulation of working memory contents. In mammals, neural substrates of executive functions are primarily found in the prefrontal cortex (PFC). Pigeons—like other birds—do not have a cerebral cortex, but instead feature homologous (pallial) structures (see the next section: Comparison of mammalian and bird brains). The hypothesized functional analogue of the mammalian PFC is the nidopallium caudolaterale (NCL). Just as the PFC, the NCL receives afferents from all secondary sensory areas, directs projections to premotor structures, and is massively innervated by dopaminergic midbrain fibers, whose action is mediated primarily by D1 receptors. Lesions of the NCL do not result in obvious sensory or motor deficits, but instead impair performance in a range of cognitive tasks [3].

In a now-classic study on working memory [1], pigeons were confronted with one of two stimuli on each trial (interval “S” in **Fig. 4a**). After a brief delay “D”, in which no stimulus was present, the pigeons were required to emit a response (beak movements) following the presentation of one of the two stimuli ($S+$) and withhold responding after presentation of the other stimulus ($S-$; interval “response”). Since the operant response had to be emitted several seconds after presentation of the stimulus, the pigeon had to retain either the stimulus itself or the to-be-generated response in working memory. Importantly, similar to neurons in the PFC, single neurons in the NCL (called “delay neurons”) maintain vigorous firing

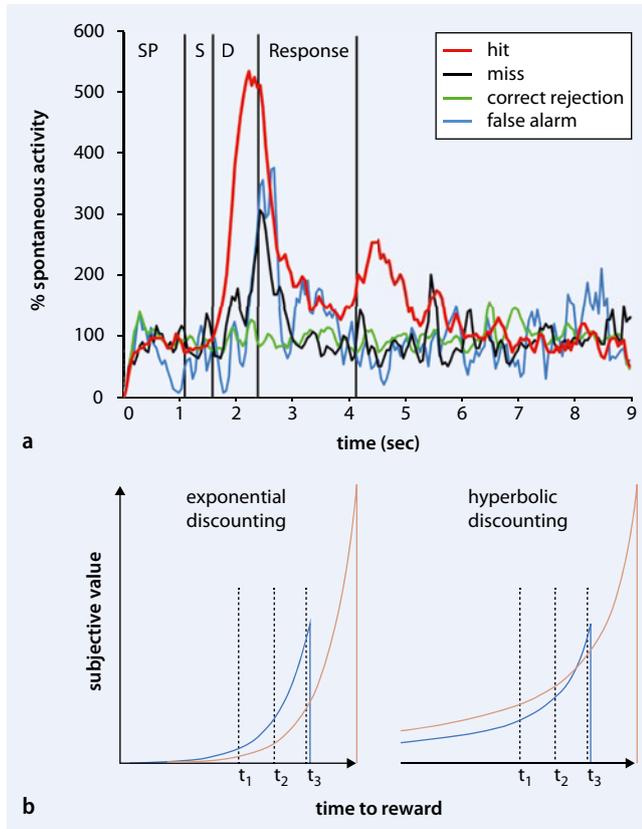


Fig. 4 **a** Activity of delay neurons in the pigeon NCL during the execution of a delayed go/no-go task. Each colored line represents the averaged firing rate of neurons in a specific condition: *red*, correct S+ trial (response, hit), *black*, incorrect S+ trial (no response, miss), *green*, correct S− trial (no response, correct rejection), *blue*, incorrect S− trial (response, false alarm). *SP* spontaneous activity, *S* stimulus presentation phase, *D* delay phase, *Response*, response phase. **b** Schematic depiction of a preference shift occurring under hyperbolic but not exponential discounting models (*right* and *left* panels, respectively). Both panels show the discounting of subjective value as a function of time for two differently attractive goods. In the *left panel* illustrating exponential discounting, a decision-maker choosing between two goods (*blue* and *red*) at time points t_1 , t_2 , or t_3 will always choose the good which is more attractive when delivered immediately (*blue*). In the *right panel* illustrating hyperbolic discounting, the decision-maker will choose differently on time points t_1 and t_2 compared to t_3 —she shifts her preference as the time to the smaller reward grows shorter

during this delay period and, thus, constitute a neural correlate of working memory (also see legend to **Fig. 4a**).

Another important type of executive function is impulse control, i.e., the ability to reject immediate gratification through a small reward in favor of obtaining a large reward at a later point in time. Classic economic theory posits that the subjective value (SV) of a good (such as a bar of chocolate, A) is discounted exponentially as a function of time (D): $SV = A \cdot \exp(-kD)$, where k differs from subject to subject. Put differently, the bar of chocolate is

more attractive when one has to wait for a few minutes only (e.g., $D=10$) compared to several hours (e.g., $D=1000$). Exponential discounting is “rational” in the sense that the value reduction of a good within a certain period of time is constant (e.g., 30% loss per hour), regardless of the value at the beginning of the time interval. However, behavioral research with pigeons has shown that the decrease of subjective value is better described by a hyperbolic function: $SV = A/(1+kD)$. Importantly, the superiority of the hyperbolic formula is not specific for pigeons, but also

applies to humans, monkeys, and other species as well. Note that hyperbolic discounting is not rational in the above sense: subjective value decreases more rapidly in the initial phase of the delay period. This distinction does not just constitute mathematical sophistry, but entails an important prediction: when asking to decide between two differently valued goods, both delivered after a certain amount of waiting time, subjects might change their mind on which item is to be preferred (“preference reversal”; **Fig. 4b**). Such a preference reversal is not predicted by the exponential discounting formulation and is not “rational” [10]. Notably, the phenomenon of preference reversal has now been demonstrated in several different species of vertebrates, demonstrating that behavioral findings obtained in pigeons can be translated to different species such as humans or monkeys. Above and beyond this important insight, single neurons in the NCL (as well as in mammalian PFC) represent the subjective value of a good through modulations of firing rate [12]. The similarity between pigeons and mammals in decision making in intertemporal choice tasks is, thus, not limited to behavioral observations, but holds at the neural level as well, a finding that carries important implications for our understanding of the evolution of cognitive abilities. These neurophysiological and behavioral similarities of bird and mammalian species are paralleled by similarities of structural brain organization, as has been documented in the past decades.

Comparison of mammalian and bird brains

For the major part of the 20th century, our views on the evolution and organization of the brains of vertebrates were heavily influenced by German neuroanatomist Ludwig Edinger (1855–1918). Edinger posited that the different classes of vertebrates—fish, amphibians, reptiles, birds, mammals—developed one after the other and form a strict hierarchy. In addition, he suggested that the appearance of each new class was accompanied by a new brain component, while earlier brain components were retained in a largely conserved fashion. In this scheme,

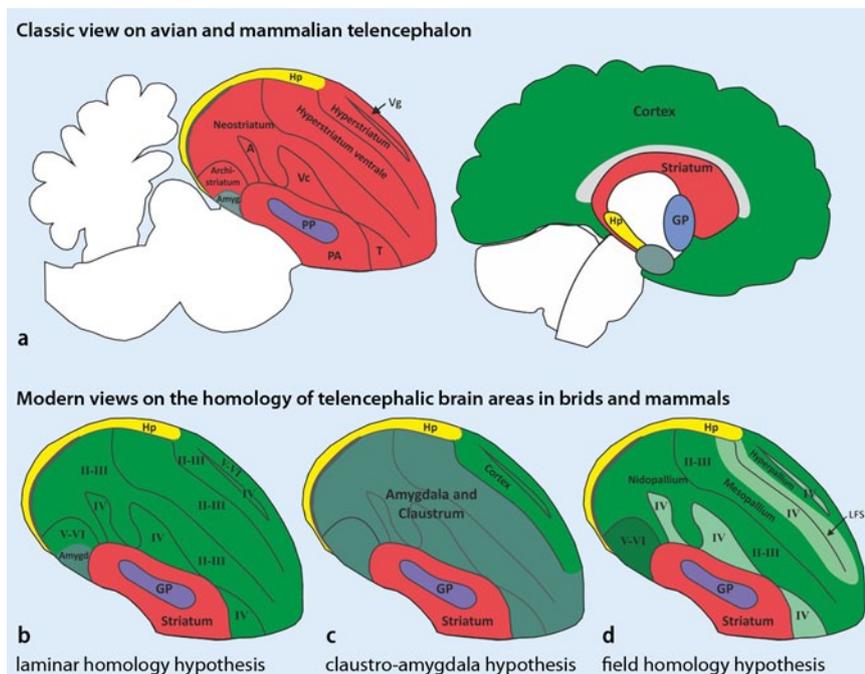


Fig. 5 ▲ Comparative theories on the avian endbrain. Identical colors imply homology between areas of the bird and the mammalian brain (schematic brains represent pigeon and human brains). **a** The top panel depicts the theory of Ludwig Edinger from 1902. The bottom panel illustrates three of four competing models

the cerebral cortex constitutes the most recent development and is accordingly only found in mammals (ergo, “neo-cortex”). Since higher cognitive abilities are assumed to depend on cortical processing, and since birds do not have a cerebral cortex, this implies that birds are incapable of higher cognition [3, 14].

A simplified (and outdated) version of Edinger’s theory on the homology of avian and mammalian brains is depicted in **Fig. 5a**. Edinger assumed that birds feature a hypertrophied striatum consisting of different clusters, and he accordingly labeled these clusters archistriatum, neostriatum, hyperstriatum, and paleostriatum augmentatum (PA). The paleostriatum primitivum (PP; lilac) and the hippocampus (Hp, yellow) correspond to the globus pallidus (GP) and the hippocampus of mammals. However, Edinger assumed that the avian brain is largely devoid of neocortex (green).

In the decades following Edinger’s seminal writings, however, it became clear that the so-called striatal structures of the bird brain contain auditory (A), trigeminal (T), visual-colliculothalamic (Vc) and visual-geniculate (Vg) sensory areas. The discovery of these areas

raised skepticism against Edinger’s original conception, because the connectivities of the ascending sensory systems were highly similar to those of the mammalian brain. Neurochemical and neurogenetic findings provided additional support that the so-called striatal areas of the avian brain are in fact equivalent to mammalian cortex. At the same time, behavioral research with birds showed that several avian species, most notably corvids and parrots, exhibit an impressive array of cognitive functions that compare favorably with those of primates. In 2002, cumulative evidence against Edinger’s theory led to a workshop being held at Duke University which summoned most of the leading comparative neuroanatomists working on the avian brain (The Avian Brain Nomenclature Consortium). The consortium not only developed an updated nomenclature for the avian endbrain, but also formulated different concepts for the homologies of the avian and mammalian telencephalons [3, 14]. Most importantly, avian brain areas whose name ended with the suffix “striatum” were relabeled with the suffix “pallium” to highlight the homology of the avian pallium and the mammalian cortex. Thus, birds indeed do have a cerebral

“cortex”; the pallium, but this structure is not layered and does not form a small sheath of tissue covering the endbrain, but exhibits a nuclear structure.

Still, there is currently no consensus on the correspondence of specific subparts of the telencephalons of birds and mammals. There exist four competing theories:

- The *laminar homology hypothesis* draws primarily on hodological data and states that the subfields of the avian telencephalon correspond to the supragranular cortical layers II–III, granular layer IV, and infragranular layer V–VI. In this view, the avian amygdala corresponds to the mammalian amygdala.
- The *claustrum-to-amygdala hypothesis* draws on neurogenetic data and states that these two structures have undergone massive expansion in birds and now make up most of the telencephalic volume, while cortex-equivalent parts are minor in comparison. Part of the ascending sensory systems thus corresponds to the sensory-thalamic projections to the amygdala, other parts (including the visual-geniculate as well as the somatosensory system) are homologous to the corresponding projections in mammals.
- The *field homology hypothesis* integrates neurogenetic and ontogenetic data as well as molecular imaging results. It states that the avian endbrain is mirrored along the Lamina frontalis superior (LFS). The field homology hypothesis resembles the laminar homology hypothesis in the sense that some clusters of the avian telencephalon are homologous to the cortical layers.
- A fourth hypothesis (*new design*; not illustrated) states that, although the telencephalons of birds and mammals are homologous, they have strongly diverged over 300 million years of evolution, such that it will be impossible to define equivalent fields.

Concluding remarks

Pigeons are exquisite model organisms for the study of learning, categorization, and cerebral lateralization, and as a refer-

ence species for the investigation of convergent evolution of cognition and comparative neuroanatomy [15]. There exists a comprehensive database on the behavior of this species, as well as on the neuroanatomy of the endbrain. However, there are relatively few studies in which behavior is assessed in combination with neurophysiological and neuropharmacological manipulations. To date, existing evidence supports the assumption that the neural mechanisms of learning and executive functions are highly similar in avian and mammalian brains. These similarities could result either from common ancestry—the last common ancestor of birds and mammals is believed to have lived about 300 million years ago—or alternatively from convergent evolution. If the latter turned out to be correct, this would imply limited degrees of freedom in the construction of brains tuned to the orchestration of complex and adaptive behavior.

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Compliance with ethical guidelines

Conflict of interest. O. Güntürkün, M.C. Stüttgen, and M. Manns state that there are no conflicts of interest.

The accompanying manuscript does not include studies on humans or animals.

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