

## *Review Articles*

# **Lateralisation, Hubs and Cognition in the Mammalian and Avian Brain**

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This article concerns an analysis of the frequently uttered statement that due to similarities in avian and mammalian brain connectivity and development comparable cognitive capacities are present. Two citations are given: “It is in the circuitry of mammalian and avian brains, rather than in their cytoarchitecture, that a marked degree of similarity exists”; “Cognitive functions are similar in birds and mammals”. Subjects treated are physiognomy and phrenology, both exponents of form asymmetry, causing the awakening of functional asymmetry. Dax, Broca and their speech localisation in the human brain are dealt with. Lateralisation in mammals and birds, the importance of the corpus callosum, differences between cortex of mammals and pallium of birds are described. Claustrum’s relation with cognition involves claustrum connections, split brain in humans is compared to avian hemisphere structure together with development of the avian and mammalian claustrum. Avian neuroanatomy contradicts the claim of similarity of mammalian and avian cognition.

*Keywords:* mammalian & avian cognition, lateralisation, Claustrum, physiognomy, phrenology

## **Introduction**

Physiognomy, a person’s facial features or expression, especially when regarded as indicative of character, came into vogue when portraits became realistic representations of body or face. A tribute to Bulgaria in this respect is the work of Zograf Vasilie [41]. Vasilie belongs to the first painters that produced Pre-Renaissance natural portraying and started off even earlier than Cimabue (1240-1302; first work, crucifix, 1268).

Vasilie's decorations of the Saint Nicola temple of 1259, Boyana, Bulgaria, are legendary (**Fig. 1**).

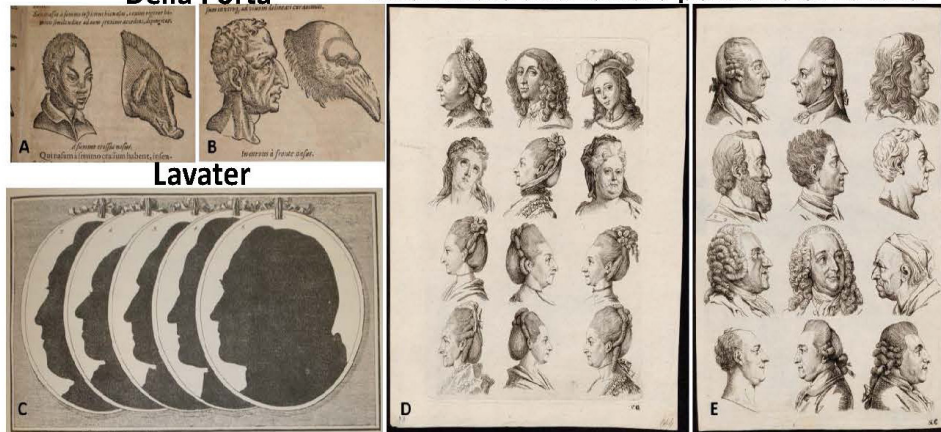
Giambattista Della Porta (1535–1615) wrote “De humana physiognomonia libri III” (on human physiognomy in three parts) in 1586 [42]. Although the Greek and Roman works already indicated the resemblance between human faces and animal ones, Della Porta's book stressed the similarity. Since characteristic properties are given to animals (e.g., the lion symbolizing force), the resemblance also indicated that these animal properties are present in the nature of man (**Fig. 1**). Johann Casper Lavater (1741–1801) claimed physiognomy to be a science. His four volumes called “Physiognomische Fragmente zur Beförderung der Menschenkenntnis und Menschenliebe” [27] (Essays on physiognomy designed to promote the knowledge and the love of mankind, 1775–1778) produced serious controversies in literary and scientific circles, e.g. Johan Wolfgang Goethe (1749–1832) and Friedrich Schiller (1759–1805), and later on Duchenne de Boulogne (1806–1875), due to his electrophysiological studies of human facial muscles. Nevertheless, the success of Lavater's physiognomy books was based on his claim that physiognomy scientifically studied the inner and outer selves. Arguments are a semiotic one “The relations of facial signs contain a meaning”, the other, instinctively we all think at the first appearance of a person that we can deduce his nature: unconscious judgements or snap judgements (**Fig. 1**). Thus, founded on Renaissance ideas, form of the head and/or face was related to (psychological) functions, which created the ambiance for Franz Joseph Gall (1758–1828). His ideas were “based on his early observations about the skull sizes and facial features of his classmates” by “making a connection between one classmate's odd shaped skull and advanced language abilities” [56]. In 1818 Gall introduced phrenology, changes of the skull cap due to the underlying brain differences. You could define it as physiognomy by the skull cap alone (**Fig. 1**). Gall supposed that parts of the brain were specialized in steering special human functions. He proposed that in particular cases (e.g. musicians or scientists) these cortical areas could grow larger than other areas and as a consequence the skull at these places protruded. **Form** asymmetry of the brain was phrenology's base, but was grounded on conjectures. Physiognomy and phrenology failed gravely, e.g. Lombroso (1835–1909); (see 31 for an extended description). Nevertheless, Gall produced the base for modern neuroscience by distributing and popularizing the idea of functional localizations within the brain that was accepted and/or discussed by the scientific circles of the 19<sup>th</sup> century.

Still, inconsequentially form asymmetry has been used a fifty years ago. Just the reverse argumentation has been employed in e.g. dyslexia. Absence of asymmetry in the left and right planum temporale supports dyslexia [12, 13]. The more general Geschwind-Behan-Galaburda (GBG) model of cerebral lateralization (caused by testosterone) provides a “complex but testable theory of cerebral lateralization”. “Evaluation of the model suggests that it is not well supported by empirical evidence and that in the case of several key theoretical areas, the evidence that does exist is inconsistent with the theory” [5]. Structural brain asymmetries are nowadays found in various species e.g. great apes and rat. One should note that anatomical asymmetries need not to be directly coupled to actual asymmetries in function and vice versa.



**Della Porta**

**Twelf male and female portraits of Lavater**

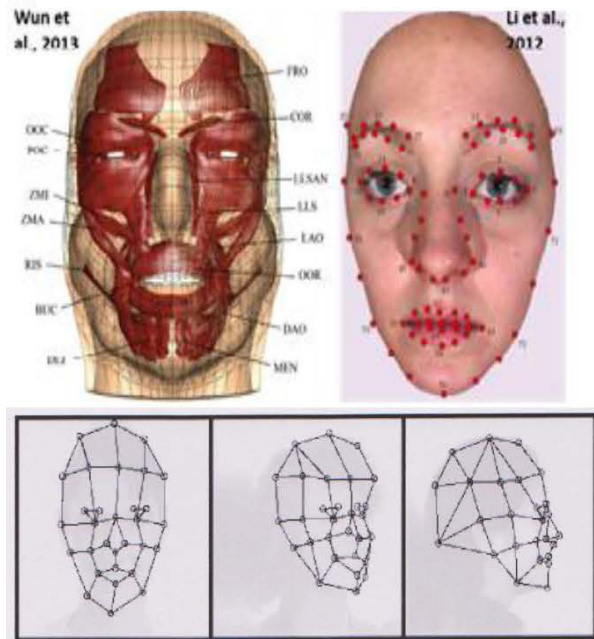


**Lavater**

**Fig. 1.** Left upper part: Parts of the frescoes of the Boyana Church to demonstrate the Pre-Renaissance picturing of 1259. Left upper fresco is the Holy Mandylion (cloth upon which a miraculous image of Jesus’s face is present); left lower figure contains the faces of the Holy Virgin and Child; upper right figure shows the face of St. Nicholas of Myra, and the lower right is the face of St. Ekaterina. Note the realistic portraying and facial expressions (oral permission Boyana church). Phrenology. Skull with extended bone areas related to specific brain areas and functions. Round game with all types of skulls for comparison and caricature of the phrenology application (courtesy Leiden Anatomical Museum) A to E: A and B are figures from Della Porta’s work on physiognomy, indicating comparable face structures between man and animal. C, contains the silhouettes of faces made by Johann Casper Lavater: from left to right, 1 is the silhouette of Johan Martin Miller (poet, 1750–1814) described as: forehead and eye of a soft-feeling poet, weak lower lip and weak chin; 2, Asmus, pseudonym of Matthias Claudius (poet, 1740–1815): not weak, nor clever, honourable, credulous and direct, truth, man of feeling, modesty and tranquillity; 3, Friedrich Heinrich Jacobi: sharp angle of the forehead and the characteristic upper lip to chin indicates searching, wisdom and by its bent face weakness or poetry; 4 and 5 are compared: 4, critical mind, nose and forehead indicate poetic forces; 5, more active brain, nose indicates wisdom and is more beautiful, and mouth and chin relate to wisdom and tranquillity, modesty. D, Twelfth heads of unknown famous wives (men in E) of different nationalities and ages for Lavater. (Figures Della Porta and Lavater, courtesy Leiden University Library with permission)

Face recognition started with facial recognizable points, in which Anatomy was leading. From 1800 onwards, Anatomy and Physical Anthropology collected the measures of the skull and its parts, face, teeth, nose, ears and eyes. The quantitative results have been summarized in anatomical overviews (e.g. 3, 32, 51). These measures have been studied during development into adulthood and ageing. However, “Elastic bunch graph matching” uses Gabor wavelets that are marked here by circles on the face images (Fig. 2) and has been applied in geometric and photometric face recognition. Other methods are principal component analysis and linear discriminant analysis. The conclusion is that face recognition does not need any anatomical qualitative or quantitative information using these mathematical methods. You need, e.g., a series of Gabor nodes, simple reference points (tip of the nose, eyes), and you can place them anywhere on the face. Moreover, to get emotions present on the human face subtle changes have to be detected by finite element meshes or best feature detection [28, 55]. However, realistic contraction of facial muscles can also be studied with the VICON movement capture system (Oxford Metrics, UK). Using the VICON system, normal patterns for the movements of wrinkling the forehead and frowning, smiling and opening and closing the eyes are described [22]. Even facial emotions can be detected by a movement capture system: another view of physiognomy due to biometric artificial intelligence that recognizes instant emotions?

**Fig. 2.** During smiling subtle changes are also noted around the eyes, mouth, face edges and nose. Wearing spectacles disturbs even more the recognition of facial emotions. Therefore, a series of subtle changes has to be detected that needs registration of facial changes around eyes, mouth nose and circumference of the face. Techniques in producing a finite element mesh with the realistic face muscles projected in it (Wu et al. 2013, with permission) are studied [55]. The basic research on circumferential information versus local changes in the face is shown by Li et al. (2012, with permission)[28]. Lower figure: Facial recognizable points based on Anatomy and Gabor wavelets that placed over the face (figure is taken from the National Science and Technology Council (NSTC) subcommittee of Biometrics; [31].

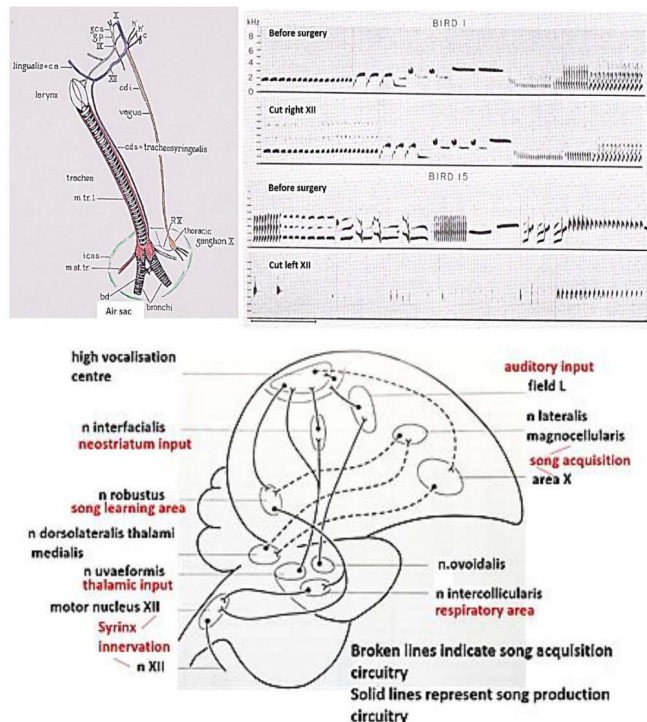


**Functional** asymmetry of the human brain was found due to the study of brain damage. Aphasia was presented during a discourse at the medical society of Montpellier in France by Marc Dax (1770-1837) in 1836. Disability of speech has already been well known and the lecture of Dax was not unique. However, Dax noted that aphasia was exclusively coupled to the left hemisphere. “His paper was an unqualified flop. It aroused virtually no interest and was soon forgotten” [11]. The son Gustave Dax (1815-1893) published and extended his father’s work. “*Observations tendant à prouver la coïncidence constante des dérangements de la parole avec une lésion de l’hémisphère gauche du cerveau*”, (*Observations performed to prove the constance coincidence of word disturbances with a lesion of the brain left hemisphere*) was published in April 1865. The functional asymmetry of the brain got its establishment by Paul Broca (1824-1880). He indicated a special area in the sole left hemisphere responsible for speech: posterior inferior frontal gyrus (pars triangularis) now called Broca’s area. Damage to this area produces aphasia. Broca himself did not recognize directly the importance of his findings in 1865 (“*Sur le siège de la faculté du langage articulé.*”), but in fact he established the significance of the frontal left hemisphere in speech and consequently the functional lateralisation of the brain for speech [4]. By the way, Broca was greatly influenced by Gall’s ideas, since Gall’s functional brain localizations retained a certain reputation among scientists. Paul Broca’s publication arrived one week after Gustave Dax’s publication, not mentioning the Dax’s works. Broca knew the work of Dax, because in 1863 he wrote: The hypotheses of Dax were valueless and without future in the eyes of history, because they were not published [15, 45]. Right hemisphere specialisations were also detected and concern orientation and awareness. Damages in the right hemisphere give hemispatial inattention, agnosias and also amusia, since e.g. singing is controlled by the right hemisphere. Although interest in cerebral dominance stayed present, its momentum occurred in 1960-1990. Mountcastle’s (1962) “Interhemispheric relations and cerebral dominance” (John Hopkins Press) was followed by “Lateralization in the nervous system” produced by Harnard et al. (1977, Academic Press) and Glick’s “Cerebral lateralisation in non-human species” (1985; Behavioral biology, Academic Press) to mention a few of the larger publications [18, 57, 58]. The popularization of the theme by “Left brain, right brain” of brought it to the attention of the layman [11].

## **Initial avian lateralisation studies**

Cutting the left or right branch of the hypoglossal nerve, the tracheosyringeal nerve of the canary (*Serinus canaria*) does produce different results. Surgery of the right tracheosyringeal nerve does not change the song of the male canary as studied by sound spectrograms. However, surgery of the left tracheosyringeal nerve destructs the main repertoire of the song (**Fig. 3**). The song is replaced by silent gaps, clicking sounds or distorted modulations. “Such birds sing vigorously, as judged by their posture and motion, yet look like actors in a silent cinema film” [38]. The conclusion of these surgical results of 49 male canaries is that the left tracheosyringealis nerve, is dominant for song

control. Extra results show that this dominance is not related to auditory processing but is a muscle motor phenomenon. We owe to Nottebohm the establishment of asymmetry in bird's brains [38]. In the canary the left hemisphere is the location for both song and song learning (Fig. 3). Small and large lesions targeted to the nuclei involved in song production showed that in the canary the left hemispheric lesions disturbed song production heavily, while analogous lesions to the right hemisphere had clearly less effect on song production. The Zebra finch (*Taeniopygia guttata*) shows the reverse. In this bird species the right hypoglossus nerve is dominant for song control. Moreover, there is a difference between male and female, the male sings and the female is mostly silent as in the canary. The Zebra female hypoglossal nucleus volume is 63% of the male, the female neuron somata within this nucleus are 86% of the male and the female syrinx musculature weight is 51% of the male [53]. Females masculinized by hormones do start singing. The part of the hyperstriatum that respond to sounds and normally induces song in the males, can be stimulated with the consequence of song of the males, but not of the females. Although the same stimulation has been applied no response passes over the right tracheosyringeal nerve of the female [54].



**Fig. 3.** Left upper part: topography of the left XII cranial nerve around trachea and syrinx: The sternotracheal muscle (m.st.tr) and the syrinx muscle mass (red). In green is the interclavicle air sac's position indicated (i.c.a.s.). Right: effects on song of the canary before and after surgery of the right and

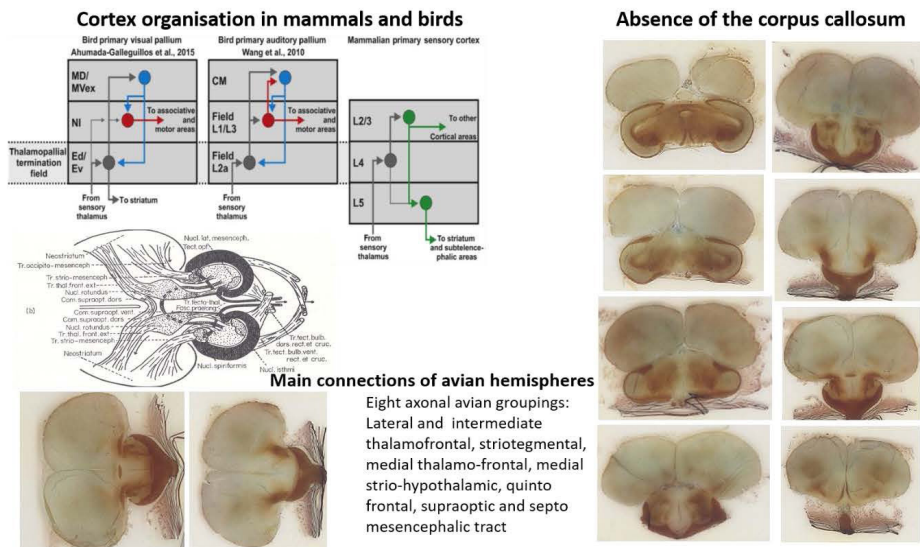
the left tracheosyringeal nerve (branch of the XII). Lower figure: Left hemisphere is dominant for song production and song learning in the canary adapted from [38]

## Differences between mammalian and avian brain

Brain structure of birds differs from mammalian brain structure. A few examples are: The cortex structure is different. The avian pallium is based on nucleated clusters, while the mammalian cortex is known by its laminated neuron organisation (**Fig. 6**) [21, 25]. The storage of neurons in the avian forebrain is different, resulting in more neurons/volume [39]. The density of the avian neuron storage in the forebrain gives e.g. starling (483 million neurons) compared to rat (200 million), rook (1509 million) and marmoset (636 million neurons), all with the same brain mass. Birds contain on average twice more neurons per brain mass. The avian brain halves are restrictedly interrelated by its *commissura anterior* and a *commissura supraoptica* (**Fig. 4**), while the mammalian brain has an enormous interhemispheric connection, the corpus callosum. Specific areas of the bird pallium, e.g., nidopallium *caudolaterale*, have no connection with the hippocampus while several avian cortical areas do contain this memory construction inherently. Episodic memory, conscious memory of a previous experience, is more limited and processed in a different manner in birds when compared to mammals. “Food hoarding birds can remember what food they hide, where and when. Neuroanatomical and neurophysiological studies suggest that there may be a fundamental difference between episodic-like memory in birds and mammals. In contrast to the mammalian hippocampus, the avian hippocampus only receives visual and olfactory input; most high-order association areas in the avian brain involved in performing functions similar to those performed by neocortical association areas do not project to the hippocampus or structures providing it with direct input.” [44].

All placental mammals do contain the corpus callosum, which constitutes the mutual functional hemispherical connections. Although the mammalian cortex is constructed layered, a module-like organization is present [50]. The modules are 200-300  $\mu\text{m}$  sectioned, explaining that corresponding cortical areas can be connected. The human corpus callosum contains over 200 million fibres (160 million [1]; 180 million [52]). Growth during childhood and adolescence shows callosal increase in thickness over the whole corpus, except the rostrum in women [29]. The rhesus monkey contains 56 million myelinated callosal fibres [26]. The diameter of the myelinated fibres counted can vary. In the rat brain diameters between 1 and 3  $\mu\text{m}$  are noted [2]. One should note that beside myelinated fibres also unmyelinated ones are present, but hardly counted. Total commissurotomy of the human corpus callosum, known as split brain, has been studied by Sperry (1974). He concluded: “We can now demonstrate with appropriate tests a whole of distinct impairments that are most simply summarized by saying that the left and right hemispheres, following their disconnection, function independently in most conscious mental activities [48]. Each hemisphere, that is, has its own private sensations, perceptions, thoughts, and ideas all of which are cut off from the corresponding experiences in the opposite hemisphere. Each left and right hemisphere has its own private chain of memories and learning experiences that are inaccessible to recall by the other hemisphere. In many respects each disconnected hemisphere appears to have a separate “mind of its own”.

The corpus callosum is absent in the avian brain (**Fig. 4**), meaning that interaction between both hemispheres is strongly reduced and is not comparable to the hemispherical interaction of mammals. Information towards avian hemispheres asks for relay groupings, of which 8 are discerned: Lateral and intermediate thalamofrontal, striotegmental, medial thalamo-frontal, medial strio-hypothalamic, quinto frontal, supraoptic and septo mesencephalic tract (**Fig. 4**) [10, 24, 40]. The functional lateralisation as common in the human brain is also present in the avian brain, but in its own hemispherical separated way. Lateralisation comprises several of the functional asymmetries in the avian brain, which clearly can differ in various bird species. Generally, the left hemisphere is dominant for mate recognition, category distinction, vocalisation, olfactory cues, while the right hemisphere knows dominance for spatial abilities, predator recognition, fear expression and aggression.



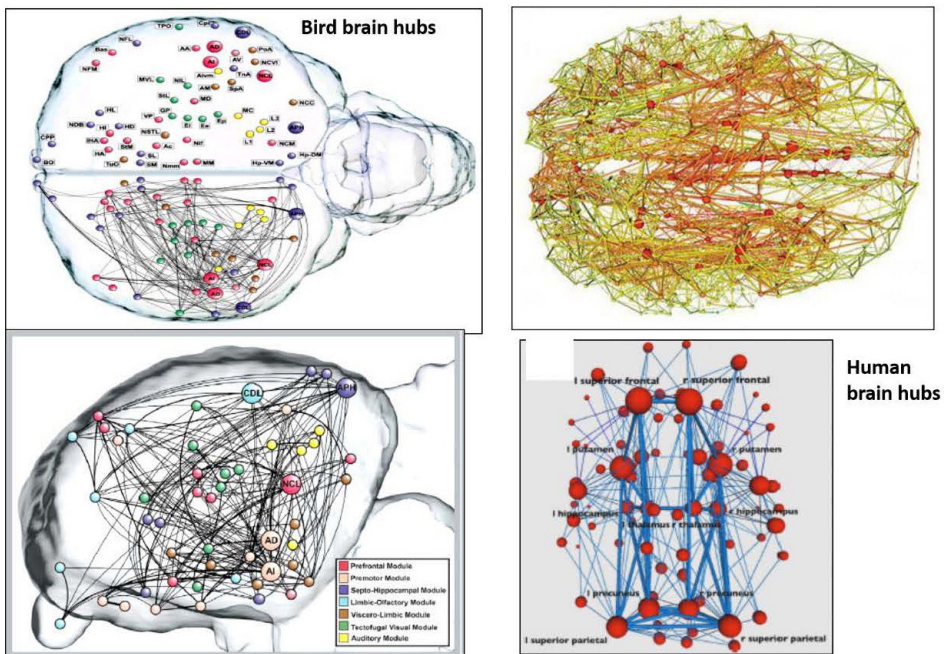
**Fig. 4.** Three aspects of the differences between mammalian and avian brains. Cortex organisation is altered in its laminar (mammals) and cluster-like (birds) construct (with permission) [17, 46]. Both avian hemispheres lack a “corpus callosum”, as demonstrated for the pigeon by silver colouration [35]. To serve information to these separated hemispheres several and unique axonal tracts are present [10, 24, 40].

## Hubs

A hub is defined as a node occupying a central position in the overall organization of a network. Nodes are connected by edges considered as structural connections or functional relationships. The connections determine whether a node has a high



degree (lot of connections) or a low degree (less connections). Networks thus can contain several groups of nodes called modules. “A module includes a subset of nodes of the network that show a relatively high level of within-module connectivity and a relatively low level of intermodule connectivity. ‘Provincial hubs’ are high-degree nodes that primarily connect to nodes in the same module. “Connector hubs are high-degree nodes that show a diverse connectivity profile by connecting to several different modules within the network” [19]. The first “hub” diagram of the avian pallium has been composed by Stingelin [49]. He discerned 10 types of cells and four types of organisations that are present in the avian hemisphere pallium. Adding organisation-density values to the cell types (8 values discerned: 8 high and 1 low) a nexus diagram could be made. *Globus pallidus (paleostriatum primitivum)* came out highest, while the lateral striatum (*paleostriatum augmentatum*) belonged to the lowest qualified structures. Each pallial subparts contained its own node value see [40]. The connectivity matrix of the avian forebrain was studied by graph theory showed a connective core of hubs based on modular networks [46]. The nodes are characterized by an overload of connections that can be named according to their module organisation: prefrontal, premotor, septo-hippocampal, limbic-olfactory, viscerolimbic, tectofugal-visual and auditory module (Fig. 5).



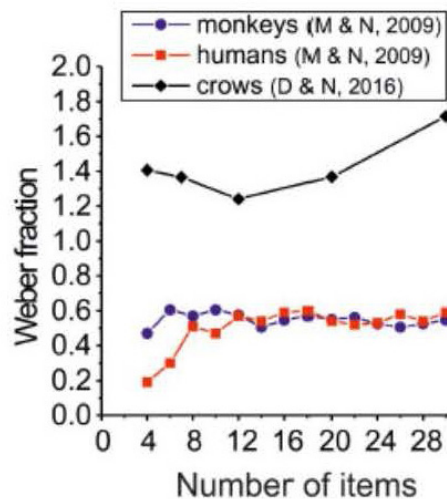
**Fig. 5.** Bird brain hubs are restricted to one hemisphere. Human brain hubs contact the hubs of the other hemisphere. Moreover the “intensity” of the connections over the corpus callosum belong to the strongest ones (thickness of the blue lines indicates the intensity of the interhemispherical connections) (with permission) [19, 46].

The spatial hemispherical distribution of the pigeon nodes does not contact the other hemisphere. Hubs regions need extra energy and are also called rich-club areas due to the possession of highly efficient neural information transfer in the brain’s network. These rich-club hub areas in the human and mammalian brain indeed heavily contact the other hemispheres (**Fig. 5**) [19].

## Cognition

Cognition is defined in the Oxford English Dictionary as “the action or faculty of knowing”. The extended definition of cognition says: “the mental action or process of acquiring knowledge and understanding through thought, experience, and the senses. It encompasses many aspects of intellectual functions and processes such as attention, the formation of knowledge, memory and working memory, judgment and evaluation, reasoning and “computation”, problem solving and decision making, comprehension and production of language”. This extended definition of cognition does not make it easier to prove its existence in birds. Only restricted utterances of cognition can be studied in birds, even if we replace language for song. Animal cognition investigates in what way birds perceive, learn, store and use information, adding the warning for anthropomorphism (see Colbert-White and Kaufman, 2019 for anthropomorphic approaches) [8, 59]. In literature e.g. the corvid’s repertoire of cognition embraces, among others, manufacture and use of tools, conspecifics support, spatial and long-term memory, and quickly recognize behavioural and numerical principles [6]. This crow cognition has been studied in relation to absolute numerosity, the abstract categorization of absolute numerical quantity [36].

The comparison between humans, monkeys and crows unmistakably shows that crows, although they have the capacity of “counting”, act worse compared to humans and monkeys (**Fig. 6**). Absolute numerosity is considered an indication or measure of intelligence. Aesop’s fable “The crow and the pitcher” tells of a thirsty crow dropping stones in a pitcher to raise the water level. The



**Fig. 6.** The smaller the Weber fraction, the higher is the discrimination accuracy of animals in absolute numerosity judgements (humans, monkeys and crows are compared; Nieder, 2020 [36]; MN, Merten and Nieder, 2009, *J Cogn Neurosci* 21: 333-346; DN, Ditz and Nieder, 2016, *Proc R Soc B* 283: 20160083).

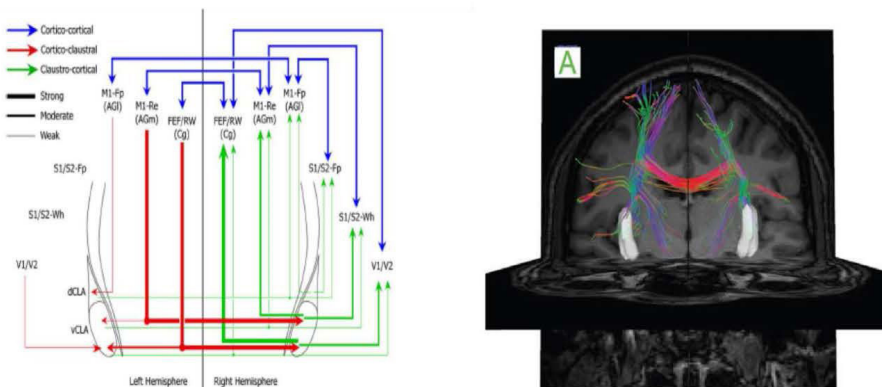
water level was initially too low to drink. These type of experiments, called “Aesopus” experiments, have been carried out frequently and all published experiments have been re-studied in a so-called meta-analysis [14]. “Does being sensitive to causal cues imply causal understanding? This question is important to evaluate experiments with ‘arbitrary’ tasks, but it is also relevant to animal cognition in general. We maintain that animals can use causal cues efficiently while lacking what we commonly label ‘understanding’. This point is far from new, as the ethological and psychological literature contains many examples of what we may term cognitive blind sight, that is, behaviour that is suggestive of cognitive complexity yet emerges from a combination of genetic predispositions, general mechanisms such as stimulus generalization, and trial-and-error learning” and at the end of their paper: “We conclude that Aesop’s fable experiments have not yet produced evidence of causal understanding” [14]. An undervalue of the innate identity of the bird’s brain occurs due to the regular position taken that bird brains are evolutionary comparable to mammalian brains and that intelligence and cognition are based on the same archaic characteristics [7]. “Cortical cells and circuits are present in all amniotes but with different macro-architectures in birds versus mammals” [25].

## **Clastrum**

The research importance of the mammalian claustrum started with the study of Francis Crick and Christof Koch (2005) “What is the function of the claustrum?” [9]. They involved the claustrum in consciousness, which encountered criticism later on [33]. Attention was supported by Yael Goll, Gal Atlan and Ami Citri (2015), while cognition was sustained by Nicola Clayton and Nathan Emery (2005) [7, 16]. This cognition model of the claustrum has been backed up by various research projects (see e.g. ten Cate and Healy, 2017, birds; Madden et al., 2022, mammals) [30, 59]. The claustrum has been divided into dorsal and ventral zones. The claustrum’s dorsal quantitative cytoarchitectonic appearance has been studied in the Anatomical department of the Sofia University [20]. The study increased the previous three or four into eight types of neurons: large, medium-sized and small multipolar, bipolar and pyramidal-like neurons, and three types of aspiny neurons. The lower ventral zone is directed towards the amygdaloid region with supposed comparable amygdaloid characteristics. The human claustrum is regarded as a multi-modal information processing network [23, 37]. The claustrum exercises cognitive control, and its activation is: or at the beginning of a task or at changing the cognitive strategy or at setting a new goal. Gender differences and variances between left and right hemisphere have been reported. Claustrum’s connections with the cortex bring cognitive task performances to the forefront in human research, especially its role in cognition control by its frontal cortex relations. Cortical-claustral contralateral projections dominate the amount of ipsilateral cortical-claustral projections in mammals. “Claustral connections enable interhemispheric transmission of certain types of modality-specific information to widely-separated cortical areas. By transmitting information from the frontal cortex

in one hemisphere to parietal and occipital regions in the other hemisphere, the claustrum provides an interhemispheric route that extends beyond the other callosal projections that interconnect corresponding sites in both hemispheres” [47]. Claustral function can be described as combining visual, tactile, auditory and emotional sensations both intra and interhemispherically. The claustrum contributes to memory storage, contiguity learning, suppression of natural urges, psychoses, recognition of fear and planning control. This is considered its integrative function between sensory and motor functions together with the reporting back to the mammalian involved cortex.

Constrained Spherical Deconvolution Tractography demonstrated the human interhemispheric and intrahemispheric connections of the claustrum (**Fig. 7**) [34]. Four types of bundles (anterior, posterior, superior, and lateral) could be discerned that connected the claustrum with the cortex. The anterior and posterior cortico-claustral bundles relayed the claustrum to prefrontal cortex and visual cortex. The superior tract involved the claustrum into sensory-motor areas, while the lateral pathway associated the claustrum with the auditory cortex. A claustral medial pathway, connecting the claustrum with the basal ganglia, is described, including caudate nucleus, putamen, and globus pallidus. “An interesting and exciting new finding is the demonstration of a bilateral connection between claustrum and contralateral cortical areas and an interclaustral communication with interconnection bundles interspersed within the bulk of the trunk of the corpus callosum” [34]. By transmitting information from the frontal cortex in one hemisphere to parietal and occipital regions in the other hemisphere, the claustrum provides an interhemispheric route that extends beyond the other callosal projections. All these interhemispheric connections are absent in birds.



**Fig. 7.** Circuit diagram of interhemispheric sensimotor cortico-claustral-cortical circuits in rats [47]. Claustral connections enable intrahemispheric and important interhemispheric transmission of certain types of modality-specific information to widely-separated cortical areas. Tractograph figure: Claustra are in white, “The whole interhemispheric claustrum connectome is showed on this figure. Some fibers of the medial and lateral pathways are visible”, (with permission) [34].

## Development claustrum in reptiles, birds and mammals

The orphan nuclear receptor Nr4a2 characterizes the claustrum, even during development as does the mature expression of G protein gamma 2 subunit (Gng2) and parvalbumin (PV) immunoreactivity [33, 43]. While in mammals and reptiles the claustrum stays an independent leaflet, its organisation in birds is characterized by a connection between its dorsal endopiriform nucleus and the subplate layer. Insula-like neurons grow internally in reptiles and birds, while in mammals an exterior localisation path is followed. “Note that reptilian and avian cell masses are layered in an outside-in pattern, whereas mammalian counterparts become stratified in an inside-out pattern” [43]. The avian claustrum has evidently its own developmental topography that is different from mammals.

## Conclusion

Despite the statement that due to similarities in avian brain connectivity and brain development comparable cognitive capacities are present in the mammalian and avian brain, the absence of a corpus callosum, the differences in cortical structure and hub organisation, the special separate claustrum topography, and the presence of an avian “split brain giving each hemisphere its own mind”, avian neuroanatomy challenges this claim.

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