



## 2020 J.B. Johnston Club for Evolutionary Neuroscience Meeting Abstracts

Abstracts for talks scheduled for the virtual 2020 annual meeting of the J.B. Johnston Club for Evolutionary Neuroscience are listed in alphabetical order by presenting author. The final schedule of talks will be sent to the membership prior to the meeting. More information can be found at <https://www.jbjclub.org/>

### **Neuronal plasticity in large-brained mammals: Adult neurogenesis or “immature” neurons?**

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Neuronal plasticity is considered a fundamental mechanism for the nervous system to learn from experience, to establish memories, to change brain tissue architecture across time, to recover after lesion or disease, and in some cases, to regenerate lost nerve cells. Nevertheless, such plasticity can remarkably vary across animal species, in its different forms and degrees. It is generally recognized that the persistence of neurogenesis into adulthood, while quite striking in non-mammalian vertebrates (e.g., fish, amphibians, reptiles), is highly reduced in mammals. Several studies have started to investigate some biological reasons for this decrease and, most importantly, it has been shown that there is substantial variation in the different “types” of plasticity involved, suggesting that different animal lineages display evolutionary specializations. Adult neurogenesis is the persistent capacity to produce new neurons throughout life, starting from neural stem cells. Since its discovery in certain brain regions of mammals, adult neurogenesis has been intensively studied with the aim of fostering therapeutic interventions for brain plasticity, and possibly repair. Nevertheless, it is clear that in mammals, unlike fish, the stem cell niches are restricted to two-to-three small brain regions, wherein the new neurons mainly play a role in learning and in the postnatal maturation of specific neural circuits, having lost most of their reparative capacity. Despite technical limits, data mostly converge to indicate that neurogenesis is almost entirely absent in regions of the adult human brain where in rodents neuronal addition continues into adult life. Analyses carried out in dolphins, mammals devoid of olfaction, has shown disappearance of neurogenesis at the time of birth. In spite of this knowledge, we lack systematic and comparable studies assessing the actual rates of adult neurogenesis in specific brain regions of widely different animal species. The state of the art is even more complex, since some reports found high amounts of neurons expressing typical markers of neurogenesis in the human hippocampus, yet in the absence of typical signs of stem cell niches and very low levels of cell division. On the other hand, very recent studies have revealed a new population of non-dividing, “immature” neurons in layer II of the cerebral cortex (cortical immature neurons; cINs), which are generated before birth, then continuing to express molecules of immaturity. These cells appear to remain in a “stand by” or “dormant” state for very long time, maintaining the potential to differentiate into mature neurons and to integrate within existing neural circuits. The cINs were discovered in rodents and were thought to be restricted to the paleocortex. We recently demonstrated that they are abundantly present in large-brained mammals, also extending in the entire neocortex and in subcortical regions. Hence, the current hypothesis is that different populations of immature neurons can represent a “reservoir of young cells” for those large-brained species that are characterized by decreased adult neurogenesis. This view supports our previous suggestion that different types of plasticity can be the result of evolutionary trade-offs associated with brain size and other neuroanatomical specializations. For example, adult

neurogenesis in the subventricular zone of the lateral ventricles, which is linked to olfaction, is highly reduced in humans and substantially absent in dolphins, while robust in rodents. Accordingly, the cINs might represent an evolutionary developmental mechanism for plasticity that varies among mammalian species, granting a reservoir of young cells for the neocortex of large-brained species.

### **Variation in auditory sensitivity of salamanders reflects ecomorphological diversity of the inner ear**

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The vertebrate inner ear is an elaborate structure housing the auditory and vestibular end organs, and its morphology has been found to reflect auditory function and the sense of balance. Many studies have used morphological assessment of the membranous labyrinth of the inner ear as a proxy for understanding variability in auditory capabilities and locomotor performance, and even as predictors of the ecological drivers (e.g., habitat type, foraging style, locomotor mode) underlying the complex evolutionary history of extant vertebrates. We have recently shown that there is interspecific structural variation in the salamander inner ear that correlates with habitat usage; in particular, we found that the ventral portion of the inner ear endocast housing the acoustically-sensitive saccule, lagena, and auditory papillae demonstrates parallel enlargement among independent lineages of obligate cave-adapted and facultative cave-dwelling salamander species. Here, we used auditory brainstem response recordings to assess sensitivity to airborne sound and seismic vibration in eight ecologically diverse salamander species in order to correlate physiological performance with the structural variation observed in the inner ear. In general, all salamander species tested were sensitive to sound pressure from 50-1200 Hz and seismic vibration from 20-1200 Hz. We found a peak in sound pressure sensitivity from 200 to 250 Hz that falls within the frequency response bandwidth of the amphibian papilla. High sensitivity at lower frequencies is most likely imparted by the saccule, which is sensitive to low frequency sound and vibration from 20 to 150 Hz in most amphibians in which it has been studied. Although all salamander species in our study had similar ranges of sensitivity to sound and vibration, cave-dwelling species showed significantly greater sensitivity for low frequency (<200 Hz) sound and seismic vibration within the sensitivity bandwidth conferred by the saccule. This variation indicates that the morphological trends observed in cave-dwelling and closely related surface-dwelling species are correlated with variation in physiological sensitivity to low frequency acoustic energy. The morphological correlates of ecology among diverse species reveal underlying evidence of specialization in the salamander inner ear and suggest that physiological variation in the function of the salamander ear exists even in the apparent absence of selective pressures on the auditory system to support acoustic behavior.

### **The Zombie Plot Thickens—A Tale of New Stings from the Jewel Wasp’s Crypt**

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The emerald jewel wasp (*Ampulex compressa*) is renowned for subduing the American cockroach with 2 stings. The first sting is made into the 1<sup>st</sup> thoracic ganglion, temporarily paralyzing the roach’s front legs. The second sting is into the roach’s brain, resulting in the long-term pacification (zombification) of the roach. The wasp then leads the cockroach to a hole where it lays an egg on the roach’s middle leg before barricading the entrance and departing. Since they were first described by Francis Williams in 1942, dozens of studies have investigated the effects of the wasp’s 2 stings. Here I report that 4 additional stings have been overlooked. These stings are made after the wasp leads the roach to a hole, just prior to oviposition. Three of these stings are made into the 2<sup>nd</sup> thoracic ganglion. These three stings result in extension of the roach’s middle leg—the wasp’s target. Extension of the roach’s middle leg facilitates proper egg placement by the wasp, which is critical for larval wasp survival. The function of the 4<sup>th</sup> newly discovered sting, made at the base of the front leg, is uncertain. The results reveal a new “neural manipulation” by a sophisticated parasitoid.

## **Cutting across structural and transcriptomic scales translates time across the lifespan and maps frontal cortex circuitry development in humans and chimpanzees**

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How the unique capacities of human cognition arose in evolution is a question of enduring interest. It is still unclear which developmental programs are responsible for the emergence of the human brain. The inability to determine corresponding ages between humans and apes has hampered progress in detecting developmental programs leading to the emergence of the human brain. I harness temporal variation in anatomical, behavioral, and transcriptional variation to determine corresponding ages from fetal to postnatal development and aging, between humans and chimpanzees. This multi-dimensional approach results in 137 corresponding time points across the lifespan, from embryonic day 44 to ~55 years of age, in humans and their equivalent ages in chimpanzees. I used these data to test whether developmental programs, such as the timeline of prefrontal cortex maturation, previously claimed to differ between humans and chimpanzees, do so once variation in developmental schedules is controlled for. I compared the maturation of frontal cortex projections from structural magnetic resonance (MR) scans and from temporal variation in the expression of genes used to track long-range projecting neurons (i.e., supragranular-enriched genes) in chimpanzees and humans. Contrary to what has been suggested, the timetable of prefrontal cortex maturation is not unusually extended in humans. This dataset, which is the largest with which to determine corresponding ages across humans and chimpanzees, provides a rigorous approach to control for variation in developmental schedules and to identify developmental programs responsible for unique features of the human brain.

## **Variation in Oculomotor Nuclei Size Reflects Behavior in Birds**

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The control and modulation of eye movements by cranial nerve nuclei is highly conserved across vertebrates. Eye movements allow organisms to scan the environment and bring stimuli of interest to regions of high receptor density on the retina. Moreover, convergent eye movements allow for stereoscopic vision and compensatory eye movements during self-motion permit image stabilization. Despite the importance of eye movements for many behaviours, there is tremendous variation in the degree and types of eye movements that occur across species. Whether variation in eye movements, including accommodation and pupillary reflex, is associated with the size of the brainstem nuclei responsible for these movements has not, however, been tested. Using unbiased stereology, we quantified the volumes and numbers of neurons of the oculomotor (III), trochlear (IV), abducens (VI) and Edinger-Westphal (EW) nuclei across 60+ species. Overall, the volumes of the oculomotor nuclei were positively correlated with brain volume, but differences in the allometric relationships were found among clades. With respect to volume, owls had the smallest III and IV nuclei, relative to brain size, likely because their tubular eyes do not permit eye movements more than a few degrees. Conversely, hawks have relatively large III and VI nuclei. Hawks have bifoveate retinæ and likely require extensive eye movements to bring objects of interest in register with these high-density areas of retinal specialization. In contrast, New World vultures had relatively small oculomotor nuclei. Like hawks, vultures have retinæ with central and temporal areas of specialization, but they scavenge rather than hunt live prey. The enlargement of the oculomotor nuclei in hawks might therefore reflect the need for dynamic eye movements while pursuing and capturing highly mobile prey. Even within some orders, the relative size of the oculomotor nuclei covaried with behavior. For example, within waterfowls, the merganser had a relatively large EW nucleus, with relatively more neurons, compared with other ducks. The merganser is the only pursuit-diving duck we examined and the relative enlargement of EW in this species likely reflects the dynamic accommodation and pupillary reflexes needed for effective underwater vision. Thus, the relative size of the oculomotor nuclei reflects some of the interspecific variation in behavior both within and across avian clades.

## The marsupial visual system gives new insights into the evolution of parallel visual pathways in mammal: A comparative study

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The thalamofugal pathway (ThFP; retina- thalamic lateral geniculate nucleus (LGN)- primary visual cortex) is the more developed visual pathway in most mammals. A synapomorphic characteristic of the mammalian ThFP is that the LGN of each hemisphere receives ipsi- and contralateral visual projections from conjugate portions of the hemi-visual fields. In non-mammalian amniotes, the predominant visual pathway is the tectofugal pathway (ToFP; retina-optic tectum/superior colliculus- nucleus rotundus thalami/pulvinarcomplex-DVR/extrastriate cortex). A defining feature of the ToFP is a massive diffuse and bilateral projection from the optic tectum to the sensory thalamus. This trait can be regarded as the ancestral tetrapod condition, since it has been reported in all members this clade: birds, non-avian reptiles, amphibians and mammals. However, the prevalence of this trait in mammals is uncertain. Bilateral tecto-pulvinar projections are consistently found in rodents; nevertheless, controversy arises when considering other groups of mammals, including marsupials, primates and carnivores, in which most tracing studies only report ipsilateral projections. This situation poses several intriguing questions on the evolutionary history of the mammalian visual system: At what point(s) of their evolution, and under which visual ecological scenarios, did mammals evolve the hemidecussated ThFP and lose the contralateral ToFP? Are these events correlated? Aiming to clarify these questions, we performed a comparative analysis of the general organization of the visual system between the nocturnal arboreal marsupial *Thylamys elegans* and the diurnal/crepuscular ground dwelling rodent *Octodon degus*. This comparison is of interest, since *T. elegans* holds a key phylogenetic position, as it belongs to Didelphidae, a basal family of American marsupials. We found in both species that an intense expression of calretinin defines a caudal (PulC) and a rostral (PulR) partition in the pulvinar complex. In both species, the PulC receives a diffuse bilateral tectal projection, while the rostral pulvinar receives an ipsilateral topographic projection. However, compared to *O. degus*, the contralateral projection appears significantly reduced in *T. elegans*. In addition, morphometric measurements indicate that the SC/LGN ratio is significantly smaller in *Thylamys* than in the degus, while LGN/PulC ratio is approximately twice as large in *T. elegans*. Thus, when comparing *T. elegans* to *O. degus*, main components of the ToFP appear significantly reduced, while main components of the ThFP appear significantly enlarged. In line with these results *T. elegans* displays a wide binocular field, and a surprisingly highly elaborate LGN composed of several alternate ipsi- and contralateral retinorecipient layers, comparable among mammals to that of primates. Our results strongly support that a bilateral ToFP projection is the conserved ancestral condition of mammals and suggest possible visual ecological scenarios that may have led to a decreased ToFP and to a specialized ThFP in some members of the mammalian lineage.

## Artificial gene networks and high throughput analysis of in-situ hybridization data reveal the impact of experience and species on cortical Id2 and RZRb expression during development.

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The mammalian neocortex is subdivided into discrete cortical fields. Early in cortical development, morphogens are expressed at different cortical locations, which later influence the expression of downstream genes involved in cortical arealization. Prior research has shown that the expression patterns of these downstream genes vary over time and can be modified by experience. Using *in-situ* hybridization (ISH), most of these studies have not directly quantified cortex-wide gene expression, providing only qualitative descriptions of overall patterns and/or targeted quantifications of within-area expression between experimental conditions. Here, we present a semi-automated method for quantifying an entire series of ISH or histologically processed brain tissue in a high-throughput manner. The spatio-temporal analysis of fluorescent in situ hybridization (Stalefish) application allows for cross-species, age-group, and condition comparisons through reconstructed 'heatmaps' of the spatial pattern and intensity of gene expression and fMRI-analysis-based template matching. These heatmaps can be used to make direct comparisons between different experimental conditions and as training data for artificial neural networks, which recreate patterns obtained across multiple genes, developmental timepoints, and conditions of sensory experience. To test how similar early sensory experiences between species affect patterns of gene expression, we bilaterally enucleated mice (*Mus musculus*) and short-tailed opossums (*Monodelphis domestica*) early in development and used the Stalefish application to quantify cortical expression of Id2 and RZRb mRNA present at the time of would-be eye opening. Our results show that at the time of eye opening, sighted mice and opossums show similar patterns of Id2 and RZRb expression, but bilaterally enucleated animals have alterations

in their patterns of gene expression. Additionally, we found that artificial networks representing gene interactions were capable of reproducing the Id2 and RZRb expression phenotypes observed in mice and opossums, and that enucleation altered the structure of these networks. Together, these data directly show that differences in experience, and not species, can drive alterations in the pattern of Id2 and RZRb expression.

### **Cortical interlaminar astrocytes are generated prenatally, mature postnatally, and express unique markers in human and non-human primates**

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Interlaminar astrocytes (ILAs) are an astrocyte subtype in the cerebral cortex that have a soma in layer I and long interlaminar processes that course perpendicular to the pia into deeper cortical layers. We previously performed a comparative study of ILAs in 46 species of therian mammals. We described *rudimentary pial* ILAs with short GFAP<sup>+</sup> processes confined to layer I, and *typical pial* ILAs with long GFAP<sup>+</sup> processes exiting layer I and extending into deeper cortical layers. ILAs are present in all mammals, and that primates have the highest number of ILAs and the most morphologically complex ILAs. ILAs have been described in postnatal animals, but exactly when they appear during development has not been determined. We studied ILA developmental origin and differentiation of ILAs in prenatal and postnatal cortex by analyzing GFAP<sup>+</sup> and S100b<sup>+</sup> ILAs in mouse, rhesus macaque, chimpanzee, and human. We found that ILAs are present in the prenatal brain and increase in number and morphological complexity throughout development. We compared the expression of specific markers in ILAs across development in mouse and macaque and found some similarities in protein expression by mouse rudimentary ILAs and macaque typical ILAs but noted key differences that may indicated distinct functions across species. These data provide new information on ILA astrogenesis and function in the developing cerebral cortex.

### **Sequence heterochrony in insect brain development leads to an immature form of the central complex: a fly-beetle insight**

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Animal species differ greatly in their adaptations of brain structure and function. Stark differences can even occur in one individual at different life stages, as is often the case for brains of larval and adult forms of holometabolous insects. All such differences occur during development, but the evolutionary mechanisms behind them remain poorly explored. Here, we want to present our work on two holometabolous insects, *Drosophila melanogaster* and *Tribolium castaneum*, where life stage differences between larva and adult, and differences between those species, are dramatically apparent. Interestingly, the central complex, facilitating multiple behavioural elements behind spatial orientation, is conserved between species at the adult stage, but differs strongly between larvae and adults of one species as well as between larvae of different taxa. We will present our work involving genome editing and establishing transgenic lines which allowed us to visualize cells expressing the conserved transcription factor *retinal homeobox*. With such comparative transgenic lines, we labelled *genetic neural lineages* in both *Drosophila* and *Tribolium*. This approach was essential to compare the development of homologous neural cells between species from embryo to adult. We identified a much more complex picture of different types and degrees of heterochronies involving the central complex than originally assumed. These include heterochronic shifts in developmental events in embryonic and pupal stages. Moreover, we provide, to our knowledge, the first example of *sequence heterochrony* in brain development, where developmental steps changed their position within the developmental event progression. We show that through this *sequence heterochrony*, an immature developmental stage of the central complex gains functionality in *Tribolium* larvae. This immature larval form differs strongly from its adult counterpart, meaning that *Tribolium* has a specific set of central complex neuropils for each stage of active locomotion. We believe that the *Tribolium* larval central complex

can be used in the future to characterise which behaviours can be facilitated with a functional, but immature, neuropil, promising to further shed light on the function and evolution of this intriguing brain area.

### **Corollary discharge evolution in mormyrid electric fish**

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During animal communication, sensory responses to self-generated signals are inhibited by internal copies of motor commands, which are referred to as corollary discharges. Corollary discharges are found across various taxa and sensory modalities, but little is known about how they have evolved as signals diversified. Mormyrid fishes generate stereotyped electric pulses (electric organ discharge [EOD]) for communication and electrolocation. The EOD duration varies extensively across species, ranging from 0.1 to >10 ms. In the electrosensory communication pathway, a corollary discharge provides brief, precisely timed inhibition that effectively blocks responses to self-generated EODs in the nucleus of the electrosensory lateral line lobe (nELL) in the hindbrain. However, this corollary discharge inhibition was only studied in species generating short-duration EODs. How have these corollary discharges coevolved with the diversification of EOD duration? Is longer EOD duration associated with longer corollary discharge inhibition? Here, we compared corollary discharges in 7 mormyrid species having varied EOD duration. For each individual fish, we measured EOD duration, and then measured corollary discharge inhibition by recording evoked potentials from the extero-lateral nuclei in the midbrain, which are the downstream targets of nELL. We found that the duration of corollary discharge inhibition was weakly correlated with EOD duration, but the inhibition delay in long-EOD species was longer than short-EOD species. In addition, we found that electrosensory receptors responded to self-generated EODs with spikes occurring in a narrow time window immediately following the first peak of the EOD, which occurred at a longer delay in long-EOD species compared to short-EOD species. Finally, we compared the time courses between the EOD and corollary discharge using an identical time reference and found that the inhibition overlaps the first peak of the EOD across species. These results suggest that this corollary discharge inhibition has evolved to shift its timing without changing its duration, which enables it to optimally block responses to self-generated signals while minimizing the window of insensitivity. To our knowledge, our findings provide the first evidence for evolutionary change in sensorimotor integration in relation to communication signal diversification.

### **Organization of telencephalic- “ponto”-cerebellar pathways in birds.**

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Birds, like mammals, have relatively large forebrains and cerebella. In mammals, there are extensive projections to the cerebellum through the pontine nuclei originating from several parts of the cerebral cortex. As in mammals, the telencephalon of birds sends descending projections to several nuclei that in turn project to the cerebellum, but the organization of these pathways has not been studied extensively. Birds have two nuclei at the base of the brainstem thought to be homologous to the pontine nuclei of mammals, the medial and lateral pontine nuclei (PM and PL). Additionally, birds are unique in that they have a pretectal nucleus, the medial spiriform nucleus (SpM), that resembles a pontine nucleus insofar as it receives projections from the telencephalon and projects to the cerebellum. In mammals the organization and function of these forebrain-ponto-cerebellar pathways has been studied extensively, but much less is known regarding the equivalent pathways in birds. In this study, using pigeons, we injected anterograde tracers in different subregions of the two main outputs of the pallium, the wulst and the arcopallium. Additionally, we injected retrograde tracers in the different sagittal zones of folia VI to VIII the cerebellum. First, we found that the wulst and the arcopallium project to the medial and lateral subdivisions of SpM, respectively. Furthermore, the projections from the rostral somatomotor wulst and the caudal visual wulst are to separate but adjacent regions in the medial SpM. This modality specific segregation of telencephalic inputs to SpM is similar to the organization in mammals, where different sensory and motor cortical areas project to different regions of the pontine nuclei. Second, with respect to the pontine nuclei in pigeons, PL receives a projection from the visual arcopallium but not the auditory region, while PM receives only a small projection from the rostral (somatomotor) wulst. Interestingly, the visual wulst does not project to PM or PL. Third, we found that the subdivisions of SpM project to different sagittal zones of folia VI-VIII in the cerebellum. The lateral, arcopallial-receiving zone of SpM, projects to the more medial zone of the cerebellum (zone A1), while the more medial, wulst-receiving area of SpM projects to the more lateral zones (A2-C). Similarly, PL projects to zone A1, and likely zone E, while PM sends projections to zones A2 and C. Our results suggest that the organization

of telencephalic inputs to SpM in birds parallels that of the projection to the pontine nuclei in mammals and reinforces the notion that SpM is analogous to the mammalian pontine nuclei. Further, our results suggest that the two main outputs of the forebrain in birds, the arcopallium and the wulst, are separated in the cerebellum. These results are an important step towards understanding cortico-cerebellar interactions in birds, and the role they may play in motor and cognitive tasks.

## **Evolution of visual pathways in teleosts and topographic organization of the tectal projections to the nucleus prethalamicus**

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Two ascending visual pathways to the telencephalon (pallium/cerebral cortex) are present among vertebrates. One of the two visual pathways in mammals is called the geniculate system, in which retinal inputs reach the primary visual cortex via the lateral geniculate nucleus in the diencephalon. The other pathway is the extrageniculate system that sends retinal information to the higher order visual cortex through the superior colliculus in the mesencephalon and the lateral posterior nucleus-pulvinar complex in the diencephalon. Similarly, two pathways are present in birds, reptiles, amphibians and cartilaginous fishes. In actinopterygians (ray-finned fishes), two visual pathways are present in cyprinids (goldfish and carp). In holocentrids (squirrelfish), however, a geniculate-like pathway appears to be missing and only an extrageniculate-like pathway can be found, which is relayed by the optic tectum and then the nucleus prethalamicus (PTh). To see if the loss of geniculate-like pathway occurred specifically in holocentrids or it is character common in other acanthopterygian fishes, we examined visual pathways of the yellowfin goby *Acanthogobius flavimanus*, which is an acanthopterygian like holocentrids. However, the goby represents an early branch of percomorphs, while holocentrids diverged from other acanthopterygians prior to the appearance of percomorph fishes. We found by tract-tracing methods with biotinylated dextran amine or biocytin that a visual pathway reaches the dorsal and ventral telencephalon through the optic tectum and the PTh. We also found that the PTh is composed of two subnuclei (medial and lateral) and the tectal projections to the lateral subnucleus (PTh-l) are topographically organized. In contrast, the medial subnucleus (PTh-m) receives fibers only from the medial tectum. Tracer injections into the PTh labeled tectal neurons with the cell body in the superficial zone of the stratum periventriculare and dendrites extending to the stratum fibrosum et griseum superficiale, which is a retinorecipient layer. These neurons correspond to the type XIV tectal cell of Meek and Schellart (1978). Labeled prethalamus fibers reached nine regions in the dorsal telencephalon and four in the ventral telencephalon. This visual pathway in the yellowfin goby may be equivalent to the extrageniculate-like pathway. On the other hand, a geniculate-like pathway could not be found. Distribution of visual pathways in the currently accepted phylogenetic tree suggests that the common ancestor of actinopterygians probably possessed two visual systems, and later a geniculate-like pathway was lost in the common ancestor of acanthopterygians for some reason. Studies in other percomorph fishes are need for better understanding the evolution of visual pathways in teleosts.

## **Magnification of the tongue for echolocation in movement maps of the Egyptian fruit bat**

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A well-established principle in comparative mammalian neurobiology is *cortical magnification*, wherein morphological specializations associated with unique behaviors (e.g. primate hands; rodent vibrissae) have an enlarged sensory and/or motor representation in the neocortex. The Egyptian fruit bat (*Rousettus aegyptiacus*) and other members of its genus are the only megabats that echolocate, and the only known bats to use tongue clicks (vs. laryngeal vocalization) during active sonar. This study used intracortical microstimulation (ICMS) to produce the first complete motor maps in *Rousettus* or in any bat species. First, we examine the general organization of body movement representations across a range of frontal and parietal cortical regions and compare this organization to other mammalian lineages. Second, we show that forelimb and hindlimb movements can be evoked synergistically in the cortex; both of these body parts are used to control wing camber during flight. Finally, our central finding is that *Rousettus* exhibits an exceptionally large movement representation of the tongue in both M1 and S1 (3b) when compared to other mammals. Within this large tongue representation, distinct parts of the tongue (e.g. distal vs. proximal) are represented in different territories. This suggest that the evolution of

tongue-based echolocation in *Rousettus* was accompanied by the cortical magnification and differentiation of neocortical areas involved in motor control of the tongue – an exceptional example of brain-body coevolution to generate active sonar.

### **Evolutionary trajectory of the primate neocortical expansion**

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The neocortex of different primate species varies widely in terms of surface area. By contrast, neocortical thickness is much more stable. Mechanical morphogenetic processes should then lead to the formation of folds of similar wavelength, organised in a pattern influenced by global shape and global expansion gradients. We characterised this evolutionary expansion gradient by analysing MRI data from a sample of 14 primate species. We built precise neocortical surface reconstructions, and we used an algorithm minimising local deformations to infer homologies across all neocortices. In this way we created an evolutionary trajectory for neocortical expansion going from Grey mouse lemur and Galago to Rhesus macaque and King colobus. To better understand this evolutionary trajectory we fit a surface-based Gompertz model, which allowed us to map differences in expansion rate and expansion onset (heterochrony). Our results showed first a striking similarity in folding patterns among species with similar brain volume, despite their position in the phylogenetic tree, underlining the important role of mechanical morphogenetic processes in the definition of folding patterns. Second, the evolutionary trajectory we obtained showed a caudal-rostral gradient. The more caudal regions start expanding earlier and faster than the more rostral ones, which start to expand later and more slowly. Finally, we observed cases where our local minimisation approach failed to build a continuous homology. For example, in several species the parieto-occipital region develops a clear rostro-caudal sulcus, whereas many others develop a perpendicular parieto-occipital sulcus. A method for building homologies that would not only take into account local deformations but that would also integrate the physics of buckling could help us better understand the role of mechanical morphogenesis on the evolution of the primate neocortex.

### **Pallial Eversion Demystified: *Lhx5*- and *vGlut2a*-driven GFP-Expressions in Zebrafish Identify the Thalamic Eminences as the Missing Links between the Teleostean and Mammalian Prosomeric Amygdala Ground Plan**

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The telencephalon of ray-finned fish (actinopterygia) with its everted morphology looks strikingly different from the evaginated forebrain of mammals and other tetrapods. For more than a century, as a result, comparative neurologists could not agree on how everted and evaginated forebrains can be meaningfully compared with each other. Some classical studies viewed radial glia orientation and tela attachment sites as the most fundamental characteristics for defining homologies and considered direct comparison with the mammalian situation rather impossible (Nieuwenhuys 2009). Likewise, recent fate mapping and genetic birth dating studies in zebrafish (Furlan et al. 2017) suggested a simple outward-in pallial architecture emphasizing the incomparability to the mammalian telencephalon organization (Yamamoto, Bloch, and Vernier 2017). My contribution focuses on our most recent analysis of multiple molecular distributions such as GFAP (which labels radial glia and their processes) and the expression of *vGlut2a*- and *Lhx5*-driven green fluorescent protein (GFP) in adult zebrafish transgenic reporter lines (Porter and Mueller 2020). The results let us discover the missing evolutionary links between the evaginated and everted telencephalon ground plan. The analysis made it possible to determine major pallial and subpallial homologies to tetrapods. Specifically, we identified previously overlooked parts of the thalamic eminence (EmT) and a subnucleus of the medial amygdala, which we called the posterior medial amygdala/rostral EmT (MeAp/EmTr). Moreover, we redefined the olfactory pallial division (“Dp”) in zebrafish. What is more, based on our analyses of both radial glia distribution and tela attachments in relationship with the olfactory pallial divisions, we explained the topology of the everted telencephalon and re-defined pallial, subpallial, and EmT derivatives in adult zebrafish. The study revealed that the everted teleostean telencephalon strikingly resembles the mammalian one in terms of topology and homology despite obvious morphological differences. Thus, a complex amygdala ground plan and a dorsal pallium (mammalian isocortex) in all likelihood evolved already in a common ancestor of actinopterygians and tetrapods.



## **From complex to simple: Evolution of the amniote thalamic reticular nucleus**

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All mammals examined have a thalamic reticular nucleus (TRN) located either within or abutting the fibers of the internal capsule (lateral forebrain bundle). Using this morphological feature, a similar neuronal aggregate has been identified in both birds and reptiles. In mammals, the TRN displays certain anatomical features: specific histochemical and immunocytochemical properties; input from the dorsal thalamus and basal nuclei; and division into sectors. The TRN of crocodylians not only shares these same characters with the TRN of mammals but also displays certain significant differences. Unlike mammals, crocodylians use 2 pathways to interconnect the dorsal thalamus with the telencephalon: the lateral and medial forebrain bundles. Associated with each of these tracts is a TRN-like complex that consists of a compact group of cells sitting on top of a fiber bundle. The dorsal peduncular and perireticular nuclei are associated with the lateral forebrain bundle while the interstitial nucleus and related cells of the medial forebrain bundle are associated with this latter tract. Neurons of the TRN in mammals are commonly thought to be a homogeneous cell population in which the long axis of their respective somata is oriented parallel to the fibers of the internal capsule while their dendrites are aligned perpendicular to these fibers. Furthermore, dendrites of mammalian TRN neurons have a specialized spine morphology. Neurons in the TRN of crocodylians are heterogeneous in their soma and dendritic morphology as well as their orientation in relation to the fibers of the forebrain bundles. Also, the TRN of crocodylians contains several different types dendritic spines besides the 'fine' spines characteristic of the TRN of mammals. Thus, the TRN of mammals is much more simply organized when compared to that of crocodylians. The TRN of mammals is associated with a single fiber tract and has a uniform cell population dominated by a specific dendritic morphology. On the other hand, the TRN of crocodylians is associated with 2 fiber tracts, contains a heterogeneous grouping of cells with a variety of dendritic appendages, and its neurons have a variable orientation in relation to the fibers of the forebrain bundles. Correlated with these TRN differences between crocodylians and mammals are: (1) differences in the interconnections between the dorsal thalamus and telencephalon and (2) differences in the cellular composition of individual dorsal thalamic nuclei. These differences in forebrain organization between crocodylians and mammals are speculated to explain this variation in the TRN.

## **Convergent mosaic enlargement of brain regions related to the evolution of novel electrosensory systems**

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How do evolutionary forces affect total brain size and the sizes of different brain regions, especially if selection is acting on a particular behavioral trait? Brain region sizes generally scale predictably with total brain size, but independent, or mosaic, increases in brain region volume have been found in several lineages and may be related to the evolution of behavioral novelty. African weakly electric fishes (Mormyroidea) evolved extremely large brains along with mosaic increases in the sizes of the cerebellum and hindbrain. However, the extent to which the evolution of their behaviorally novel electrosensory system is associated with these mosaic increases remains unclear. We addressed this question using South American weakly electric fishes (Gymnotiformes) and weakly electric catfishes (*Synodontis* spp.), which have evolved novel electrosensory systems to varying degrees, independent of African weakly electric fishes. All three weakly electric lineages have evolved electric organs, while only gymnotiforms and mormyroids have evolved an additional electroreceptor type that broadens the frequency range of detectable signals. This allowed us to assess the extent to which both presence of an electric organ and electroreceptor type are associated with mosaic increases in brain region volume in independent lineages. If the mosaic increases in cerebellum and hindbrain found in the mormyroids are related to the evolution of a novel electrosensory system, we should find similar mosaic increases in gymnotiforms and synodontids. Using  $\mu$ CT scans and 3D brain reconstructions, we measured total brain and brain region volumes for multiple electrogenic, electroreceptive, and non-electrosensing species and tested for mosaic shifts between these groups using phylogenetically corrected linear regressions. We found mosaic increases in hindbrain and cerebellum in all three electrogenic lineages relative to non-electric lineages. We also found a mosaic increase in torus semicircularis in mormyroids and gymnotiforms, which is associated with an increased frequency range of detectable electrical signals relative to *Synodontis* spp. These results show that evolving a novel electrosensory system is repeatedly associated with changes in the sizes of individual brain regions independent of total brain size. Finding similar mosaic increases in multiple lineages suggests that selection can impact structural brain composition to favor specific regions involved in novel behaviors.

## Does the evolution of food-hoarding involve the modification of the appetite-regulation system?

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Food hoarding is the behavior of foraging for food, but instead of eating it, storing it for later consumption. This behavior has evolved independently in many clades, including several lineages of birds and mammals. In those groups where it has been studied, food-hoarding behavior increases when animals are hungry. In some species, the increase in hoarding after a fast is larger than the increase in consumption.

Because of this link between the regulation of food consumption and the regulation of food hoarding, we hypothesize that the brain circuitry that controls food hoarding evolved from, or at least involved a modification of, the brain circuitry that controls appetite. In both birds and mammals, the neural mechanisms that control foraging and consumption include hypothalamic neurons that express the orexigenic peptides neuropeptide Y (NPY) and agouti-related protein (AGRP), and the anorexigenic peptides pro-opiomelanocortin (POMC) and cocaine- and amphetamine- regulated transcript (CART). In hamsters, it is known that these hypothalamic neurons are also involved in the regulation of food hoarding. However, whether this is also the case in birds has not been examined. We conducted two experiments in which we compared expression of these hypothalamic neuropeptides between hoarding and non-hoarding parids, after either an overnight fast, or a recent meal. In the first experiment, we compared hypothalamic expression of NPY, AgRP and POMC between non-hoarding blue tits (*Cyanistes caeruleus*) and hoarding coal tits (*Parus ater*). Using qPCR, we found no differences between fed and fasted birds, despite the fact that birds ate more after a fast. We did, however, find that POMC expression levels were higher in blue tits than in coal tits. This is consistent with low POMC expression being related to increased foraging motivation in the hoarding birds. In the second experiment, we used *in-situ* hybridization to compare the expression of all four appetite regulating neuropeptides in the hypothalamus between coal tits and non-hoarding great tits (*Parus major*). Again, both species exhibited compensatory hyperphagia after return of food following a 1.5h fast. Furthermore, coal tits showed elevated food hoarding following a fast. Expression levels were quantified in different nuclei in the hypothalamus and will be presented at the meeting.

## Evolutionary and homeostatic changes in morphology of visual dendrites of Mauthner cells in *Astyanax*

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Mauthner cells mediate startle responses and are the largest neurons in the hindbrain of teleost fish and most amphibians. Each cell has two major dendrites thought to comprise segregated streams of sensory input; the lateral dendrite receives mechanosensory input while the ventral dendrite processes visual input. To study the effect of adaptation to different visual environments, we used *Astyanax mexicanus*, which exists in two forms: the seeing surface fish and the blind cavefish. Cave morphs have independently evolved multiple times to a life in constant darkness over tens of thousands of years. Correspondingly, we studied the short-term developmental effects of constant darkness on the morphology of the Mauthner cell ventral dendrite of surface morph larvae. We found that in this case evolution and homeostasis drive neuronal morphology in opposing directions in response to a similar extreme environment. Mauthner cell ventral dendrite of surface morph larvae increased in length and are more branched when raised in darkness, while ventral dendrite of cave morphs are smaller or absent entirely. Our study suggests function affects dendritic morphology via homeostatic mechanisms over short periods of time and via evolutionary mechanisms over longer periods of time.