

HOW TO TEST ADAPTIVE VS EXAPTIVE HYPOTHESES

The Case of Human Language

Irene Berra¹, Telmo Pievani², and Emanuele Serrelli²

¹Department of Cognitive Science, University of Messina
²Department of Human Sciences for Education "Riccardo Massa", University of Milan-Bicocca
iberra@unime.it

ABSTRACT. The concept of exaptation, named in 1982 by S.J. Gould and E. Vrba, was recently blamed of arbitrariness and in need of a restrictive theory (Botha 2011). Our view (Pievani and Serrelli 2011) is that exaptive hypotheses can be operationalized and improved, and recent research in language evolution offers a good example. Clues coming from brain comparative studies, functional imaging and mirror systems point out that both cortical and subcortical structures have been re-functionalized during the evolution of primates and hominids, due to their plasticity and learning capacity. Ancestral constraints on acoustic communication have been retained by several vertebrate species and put to use by cognitively modern humans. Then, language results from the intersection of wider functional domains.

AN EXTENDED TAXONOMY OF FITNESS (Gould and Vrba 1982).

Aptation. The general class of any character that enhances fitness.

- 1. Exaptation.** A character not shaped by natural selection for its current utility
 - a. Exaptation type I,** derived from a functional shift with the previous function often maintained
 - b. Exaptation type II** (or spandrel in the Gould's architectural metaphor), derived from a neutral non-aptation
 - i. Cross-level spandrel.** An indirect effect of a trait over another hierarchical level, for example from organisms to groups
- 2. Adaptation.** A character resulted from ordinary natural selection.

THE SIZE EXAGGERATION HYPOTHESIS. The descended larynx has long been considered a uniquely human adaptation for articulate speech. However, several mammals lower their larynx during vocalization and at least two deer species (red deer *Cervus elaphus* and fallow deer *Dama dama*) show a resting laryngeal position comparable to that of adult humans (Fitch and Reby 2001). Usually formant frequencies provide cues of body-size, and the vocalizer might exaggerate the impression of his size by lowering formant frequencies (fig. 1). Cats, koalas and elephants are supposed to permanently descend their larynx. As a size exaggeration device or as a byproduct of upright posture, the descended larynx has been exapted for phonetic virtuosity.

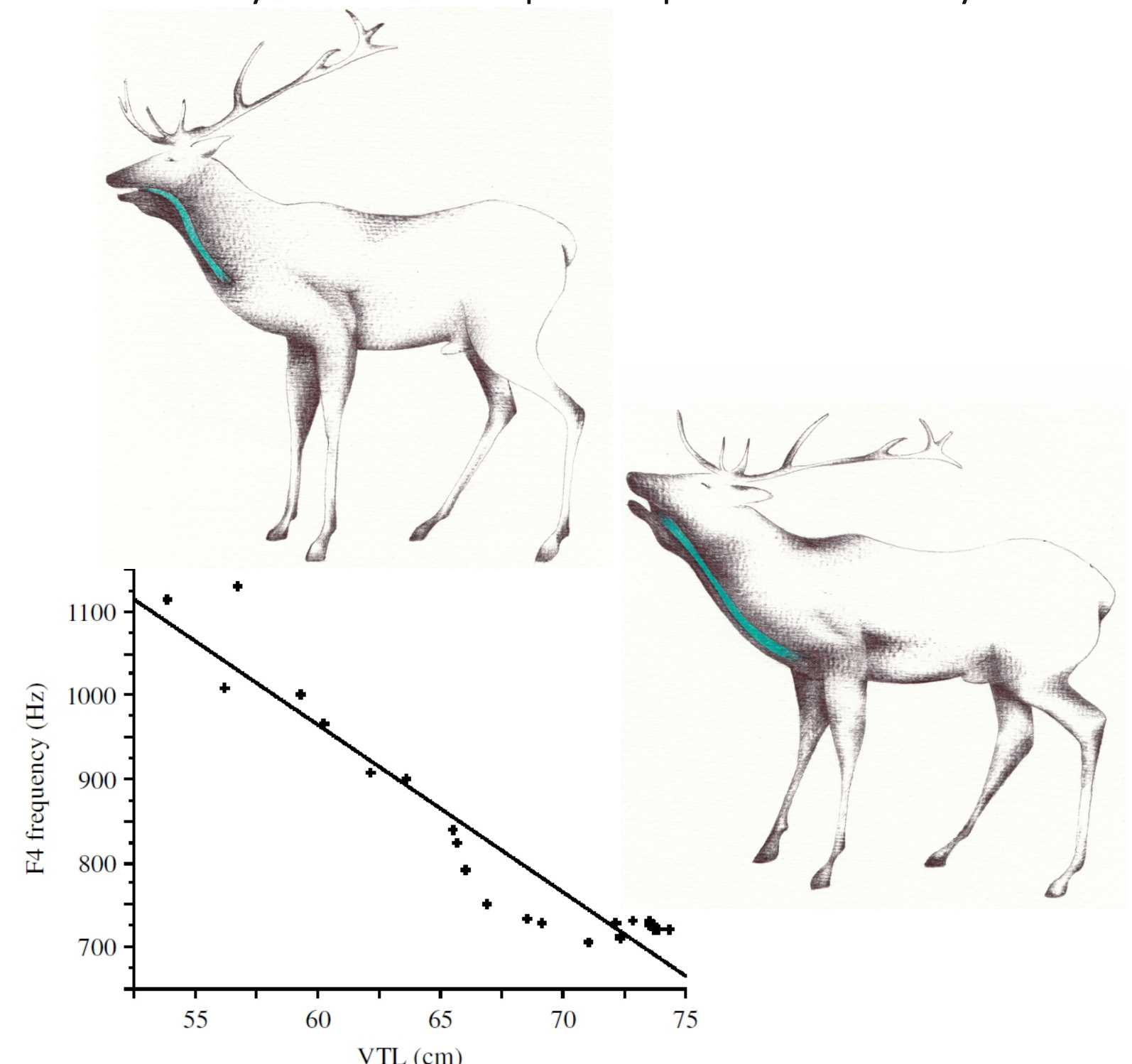


Fig. 1. The descended larynx of a red deer in resting position and during vocalization. Formant frequency (on the y-axis) decreases as the larynx descends. Vocal-tract length (VTL) on the x-axis. From Fitch and Reby (2001), redrawing.

CONVERGENT EVOLUTION. To account for the origin of language is as difficult – or maybe as easy – as to account for how fish evolved into terrestrial vertebrates. Darwin's renowned solution for this transition was probably incorrect, but the principle still holds. An exaptive hypothesis has been proposed for acoustic communication during water-to-land transition of Devonian tetrapods. Given that mudskippers (Gobiidae) (fig. 2) are semi-terrestrial gobies living in intertidal habitats, their vocalizations have been studied to test this hypothesis (Polgar et al. 2011). Probably, tetrapods' most recent common ancestor exploited the opportunity to explore terrestrial environments with acoustic adaptations to water. Furthermore, this exaptation may be convergent even in other soniferous benthonic teleosts, such as toadfish (Batrachoididae), well-known for male vocalizations during courtship (Rice and Bass 2009).

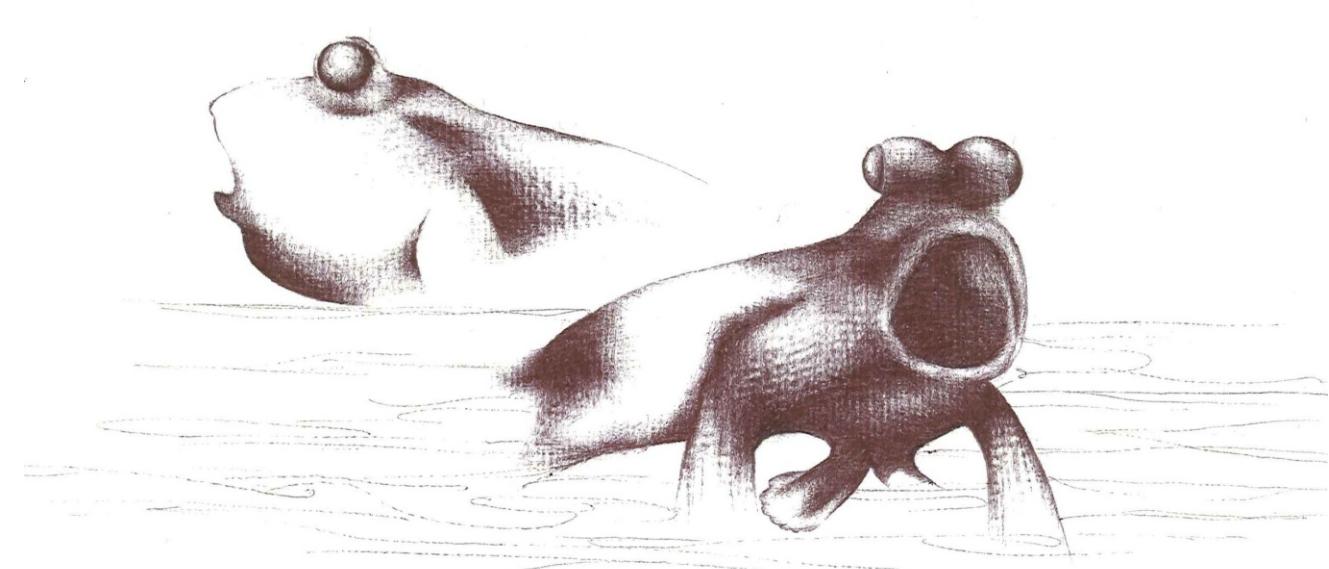


Fig. 2. Periophthalmodon septemradiatus.

INTENTIONALITY. The alarm calls of prairie dogs (*Cynomys gunnisoni*) can be viewed as an intentional system coding information by means of innate plus learned rules of categorization. The lexicon of these social rodents is both highly and regionally differentiated, suggesting representational mental states of high order (Slobodchikoff 2002). Artificial intelligence helped to corroborate this semantic diversity with neural nets. So far no non-human primate is known to have such a degree of referential communication system (vervet monkeys have only three categories of calls). To live in spatially-fixed colonies visited by the same predators every day, might have exert a selective pressure for this adaptation, which seems one of the clearest natural precursors of human language.

SOCIAL COGNITION. The evolution of language triggered off sociality in its current state, rather than being a consequence of the humans' great intelligence for complex social relationships. Several studies recognize the role of attention, emotion and motivation in handling social bonds, in simplifying learning (Lotem and Halpern 2012) and in memorizing social interactions (the so-called emotional bookkeeping, Aureli and Schino 2008). Cooperation in hunting, breeding or mobbing are found in distantly related vertebrate species, from fish and ravens to dolphins and marmosets. As tolerance, inequity aversion and consolation avoid conflicts inside the group, group-living animals protected and reproduced themselves despite group competition. These altruistic behaviours take on renewed functions with language, «from a defensive adaptation to a successful model of social organization with division of the work and new forms of exploitation of ecosystems» (Pievani 2011).

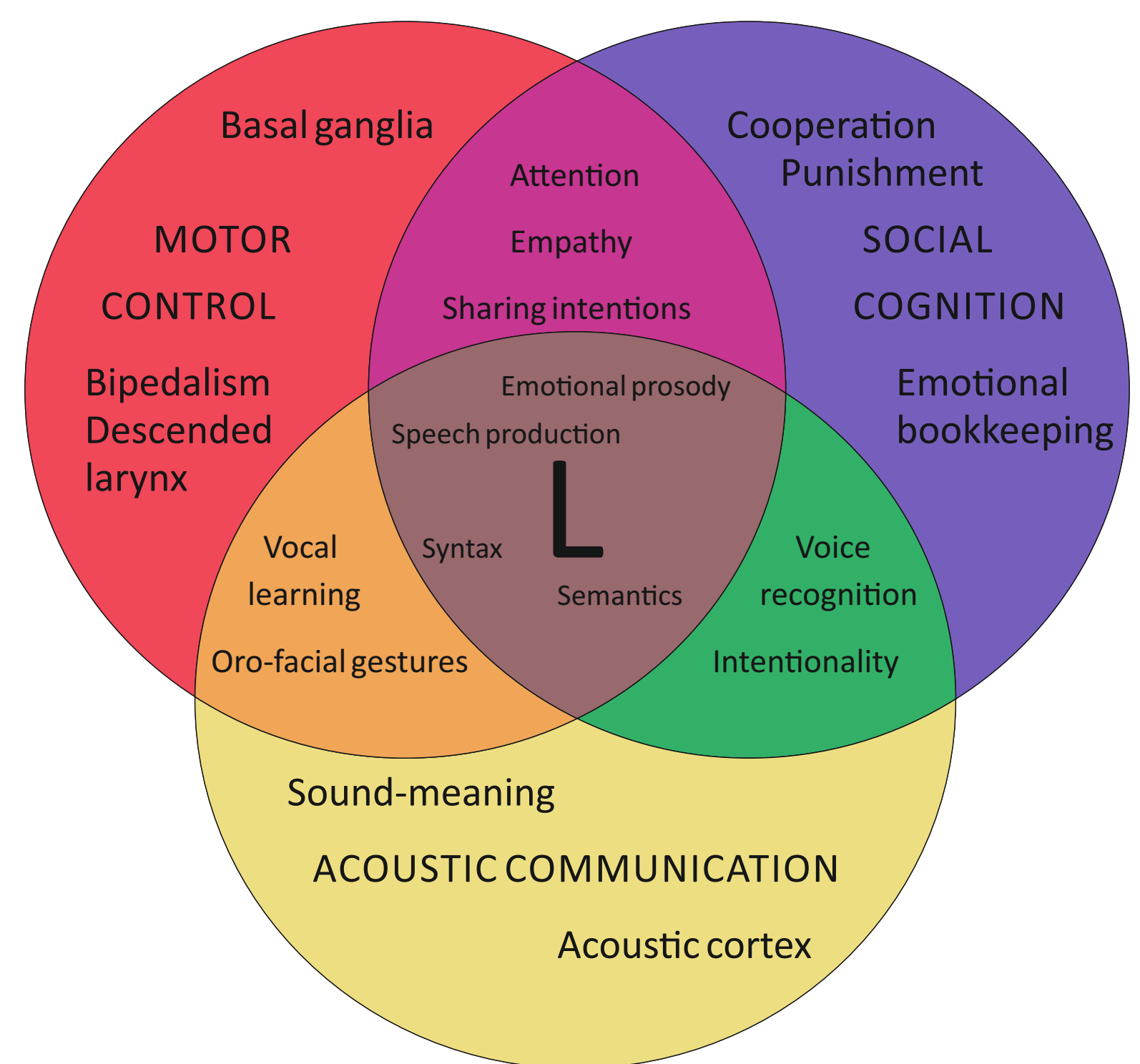


DIAGRAM OF THE MULTIPLE EXAPTATIONS OF LANGUAGE. Old structures from various functional fields acquired new roles usually integrated with the preexisting maintained ones. Language (L) is the crossroads of all these structural-functional cooptations.

REFUNCTIONALIZATION OF BRAIN STRUCTURES. Human articulate language doesn't involve clearly distinguishable structures and substructures but shows distributed functions. Nevertheless, exaptation can be often found in regions partially specialized for language but involved in neural pathways more conserved than derived. As an example, the amygdala and the anterior insula are co-opted in processing vocal emotions (Belin 2004).

Only a small portion of the auditory cortex, i.e. the superior temporal sulcus (STS, fig. 3), is specialized and more responsive to verbal sounds rather than to music or other sounds. Similarly, positron emission tomography (PET) conducted by Gil-da-Costa et al. (2006) in rhesus macaques showed that a single location (area Tpt, fig. 3) of superior temporal gyrus (STG) was largely associated with conspecific calls rather than with non-biological sounds. This area is a plausible homologue of the planum temporale (PT), the core of the Wernicke's area, and both of them carry out non-linguistic functions, such as sequence processing. In macaques, and maybe in our common ancestor (25-30 million years ago), presumptive homologues of human perisylvian areas might play a role in associating the sound and the meaning of specie-specific vocalizations and thus they may have been available for coupling sound and meaning in human language.

In chimpanzees, the production of communicative manual gestures and vocal signals significantly activated the left inferior frontal gyrus (IFG) and the subcortical brain areas known to have strong connections to the prefrontal cortex (Tagliatalata 2008). The cortical-striatal-cortical neural circuits are relevant to speech production and perception, being responsible for the selection of linguistic stimuli, reiteration and the oro-facial coordination. The striatal nuclei is also involved in vocal and sequential learning, even in birds and rats (fig. 4).

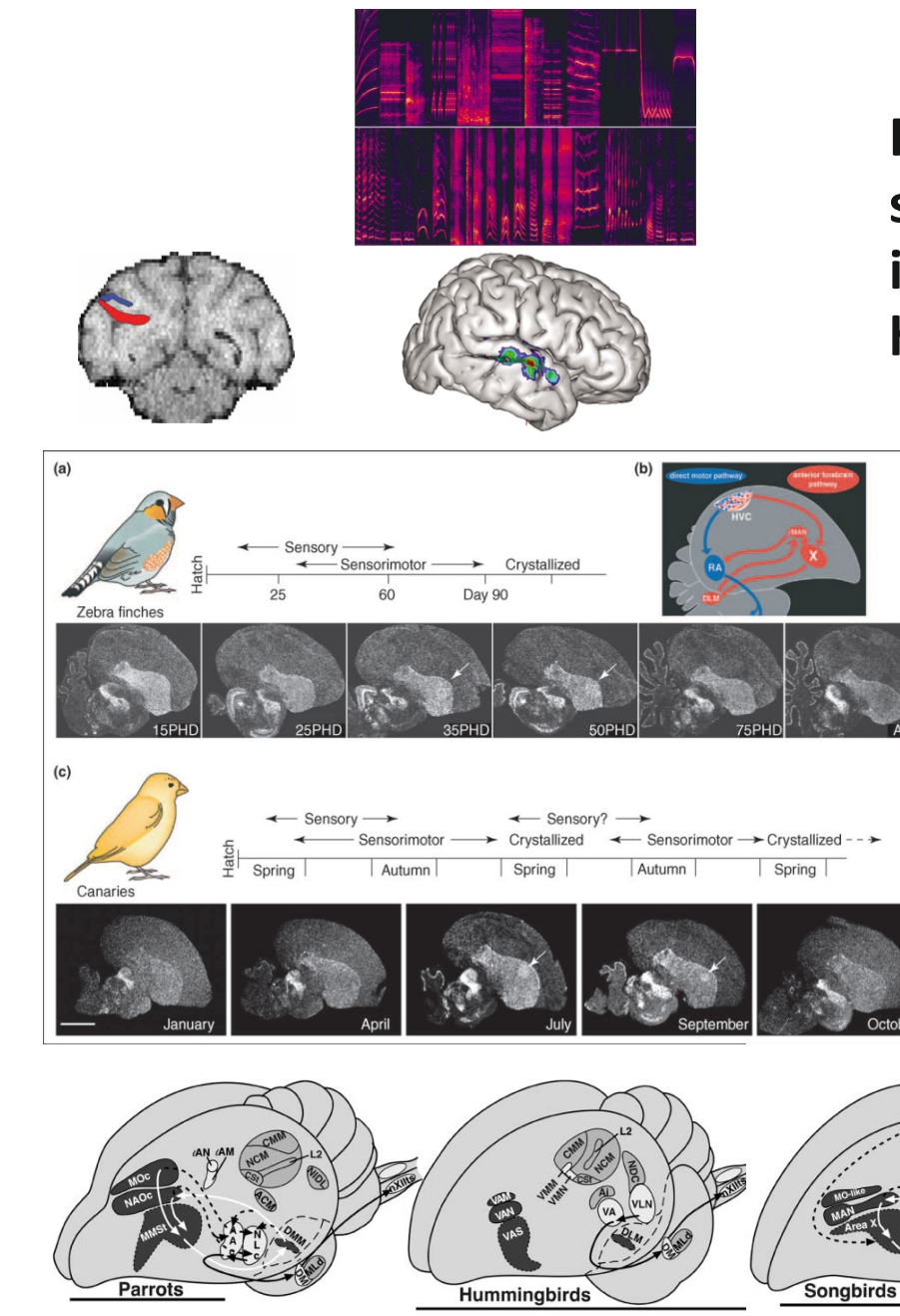


Fig. 3. Neural activity sensitive to conspecific calls in macaques and to voice in humans.

Fig. 4. FoxP2 expression in the striatum of song learning birds.

Fig. 5. Proposed comparable vocal and auditory brain areas among vocal learning birds and humans.

THEORIES OF NEURAL REUSE, RECYCLING AND REFUNCTIONALIZATION. We should distinguish these theories (Anderson 2010) from exaptation when they concern developmental processes rather than evolutionary ones. Inheritance is a required criteria to call a trait exaptation or adaptation.

VOCAL LEARNING is found to date in three distantly related groups of mammals (humans, bats and cetaceans) and three distantly related groups of birds (parrots, hummingbirds and songbirds). The neural vocal pathways, one posterior and one anterior, are similar in birds and humans. It has argued that the evolution of these neural pathways may be under both genetic and epigenetic constraints deeply rooted in the pre-existing vertebrate brain (Jarvis 2004, fig. 5).

When ancestral developmental modules are independently co-opted by distantly related lineages, the homology is probably only partial, relative to one level and functionally not identical. A mutation in the *FOXP2* transcription factor results in impeded orofacial gestures, speech production, language comprehension and cognition. Avian *FoxP2* is highly expressed in the striatum of birds during song learning sessions. However, neither vocal-learning mammals nor song-learning birds share the human amino acid substitutions of *FOXP2* (Webb and Zhang 2005). Language evolution is likely to be a recruitment, with slight modifications, of pre-existing genetic cascades that have other regulatory functions.

“THE GREAT LEAP FORWARD”? Exaptive major transitions in human behaviours do not require to see cultural evolution as totally foreign to biological rules. In contrast, exaptive hypotheses on language have been misused to claim the uniqueness of human cultural evolution (Hauser et al. 2002). Even the greatest supporter of exaptation wrote: «(that final leap) did not result from a gradual process» (Tattersall 2008, 102). Obviously, every change happens during time, although short (fig. 6). We hope that this research poster helps to take home this message: a significant continuity exists both between language and other functional domains, and between humans and other animals.

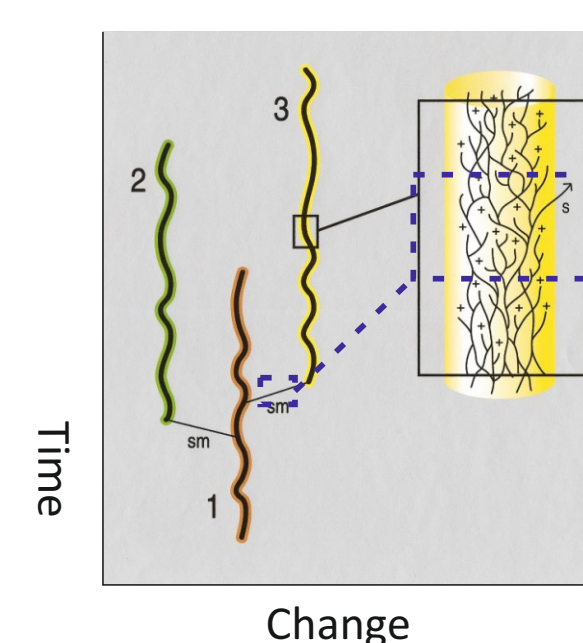


Fig. 6. Exaptation doesn't mean ex abrupto.

CONCLUSION. Aside from neurobiological studies of language, the exaptationist account is still too speculative (e.g. in anthropology). Given its patched nature, the faculty of language should be studied in a broader functional context, e.g. speech perception in relation to voice perception. In sum, exaptive hypotheses need care and attention, just like the adaptive ones. Enlarging the phylogenetic context, improving technology to identify structures and attempting the reconstruction of environmental settings to match fitness utility, help the historical comprehension of succeeding etho-ecological functions of language.

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Fig. 1-2: drawings by the first author. Fig. 3: Gil-da-Costa et al. (2006), Belin (2004). Fig. 4: Scharff and Haesler (2005). Fig. 5: Jarvis (2004). Fig. 6: Eldredge et al. (2005).