

## Social learning and origin of the language faculty by means of natural selection

Fabio Di Vincenzo & Giorgio Manzi

*Dipartimento di Biologia Ambientale, SAPIENZA Università di Roma, Rome, Italy*

e-mail: fabio.divincenzo@uniroma1.it

Language faculty (henceforth LF) and social learning (henceforth SL) are closely related biological phenomena. In both humans and apes, the cortical areas involved in SL (emulative and imitative) are anatomically associated with areas that allow the LF in *Homo sapiens*; in addition, SL exhibits a functional coupling of semantic and computational aspects, which phylogenetically precede any evidence of language. It is likely that the SL capacities of our Plio-Pleistocene ancestors increased due to the advantages drawn from passing technical skills and knowledge required to access essential nutrients for brain expansion (encephalization). We believe that it is within this context that the LF, and its related cortical and functional complexities, might have been selectively promoted. Only within an evolutionary (i.e. Darwinian) framework of this kind, it may be possible to gain a clearer understanding of the ongoing debate on the role of FOXP-2 genes in the evolution of the LF and in the phylogenetic relationship among highly encephalized hominin species (Benitez-Burraco & Barceló-Coblijn, this forum).

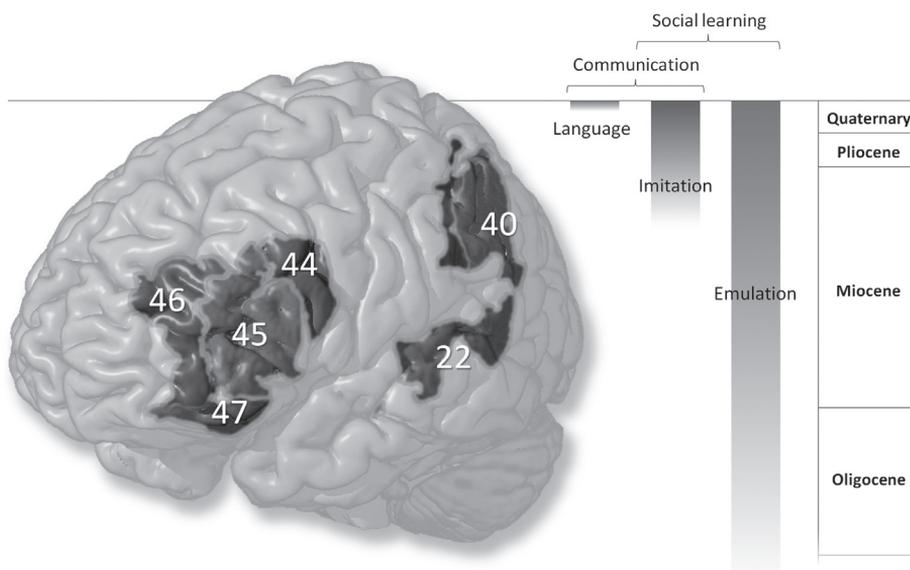
### A Darwinian synopsis

“From the hand to mouth” perspective on the origin of language (e.g. Corballis, 2002) received acceptance within the scientific community after it was found to be in accordance with many neurophysiological findings. This evidence includes the congruence between the left hemispheric lateralization of right-handedness and the linguistic function, as well as the homology between the

human brain BA 44 (a component of Broca’s area, which is not only involved in speech, but also in hand and mouth motor functions) and the monkey premotor area F5 (Petrides *et al.*, 2005). A crucial issue in this view is the biological disposition shared by the Anthrozoidea to interact empathically (*alias* semantically) with observed meaningful (goal-directed) oral and manual activities according to the properties of the *mirror neurons*, whose distribution largely overlaps the cortical areas associated with the LF in modern humans (e.g. Rizzolatti & Craighero, 2004).

In keeping with these observations, scholars (e.g. Rizzolatti & Arbib, 1998; Corballis, 2002) have proposed that gestural communication, based on signs and pantomimes, provided the exaptive scaffolds for the subsequent evolution of the vocal language. According to this point of view, an evolutionary *continuum* exists between the recognition by monkeys of the functional meaning of motor activities (such as grasping) and the semantics of language. However, language is a modality-independent communicative system and, thus, gestural language may be as complex as oral language, both semantically and syntactically. In order to work properly within a linguistic system (oral or gestural), syntactic structure – based on recursive nested dependencies (Hauser *et al.*, 2002) – needs to overcome a threshold of minimal functionality. Therefore, from which original non-linguistic domain (if any) might syntactic ability ultimately have emerged?

Applying the criteria of the so-called “Chomsky hierarchy” (Chomsky, 1956) to the study of the archaeological record, Longa (2013)



**Fig. 1 - The cortical network forming the MNA (Iacoboni, 2005) is homologous to the areas devoted to language on the left side of the human brain; these areas are also part of the mirror system (e.g., Rizzolatti & Craighero, 2004). According to Brodman's numeration, 44 to 47 relate to Broca's area and associated prefrontal areas, 22 to the area of Wernicke, 40 to the inferior parietal lobule in correspondence of the angular and the supramarginal gyri. On the right, the neural functions associated with this cortical network are reported according to observations in extant Anthropoidea, thus in a putative chronological/evolutionary sequence.**

recognizes the occurrence of recursive syntactic structures in the motor procedures associated with the manufacturing of geometric engravings of the upper Palaeolithic, which display the same embedding relationships as those found in natural language (i.e. context-sensitive or type 1 grammars). Other scholars have already highlighted hierarchical structures based on nested dependencies in manipulative tasks such as knotting (Camps & Uriagereka, 2006; Barceló-Coblijn & Gomila, 2012) and tool-making (e.g. Holloway, 1969; Greenfield, 1991, Geneste *et al.*, 1997; Di Vincenzo, 2011; Di Vincenzo & Manzi, 2013; Shipton *et al.*, 2013).

While some scholars have long claimed that there is a causal relationship between improvements in tool-making abilities and the evolution of language, others view any resemblance as being merely superficial (for a review, see Vaesen, 2012). Brain imaging analyses actually only

reveal the partial involvement of “linguistic” areas during simulations of Oldowan and Acheulean knapping activities, performed by both naïve and expert toolmakers (e.g., Stout & Chaminade, 2007), which thus challenges the hypothesis of a direct link between tool-making and language. However, widespread brain activation – which appears to be widely congruent with patterns of processing and coding of linguistic information – is attained during observation (by non-experts) of object-directed motor sequences (by experts) and, more extensively, during phases of planning for subsequent replication of the motor behaviour learned by imitation (Buccino *et al.*, 2004; Vogt *et al.*, 2007), tool-making included (Stout & Chaminade, 2011).

Thus, there is increasing evidence that supports the causal role played by the evolutionary enhancement of SL (in both apes and humans) in the origin of the LF (in humans alone). From

a functional point of view, imitative SL combines – as it does in the LF – two distinct levels of comprehension (Byrne & Russon, 1998): 1) an *action level imitation* (ALI), which allows “semantic” comprehension of the functional meaning of each observed motor act, and 2) a *program level imitation* (PLI), which ensures the recombination of each motor act (units of meaning) into a new, hierarchically ordered, motor behaviour, which is similar as possible to the observed model. Worthy of mention is a similar process that allows language to assemble syntactic structure into sentences.

Neurophysiologically, ALI depends on the *high level resonance* properties of the *mirror neurons* found above all in Broca’s area (BA44/F5) (Rizzolatti *et al.*, 2002), whereas the PLI mainly involves the left dorsolateral prefrontal cortex, most likely area 46, which plays a key role in sustaining the *working memory* (Vogt *et al.*, 2007). The superior temporal lobe and sulcus (STS) and the posterior parietal lobe (BA 40, homologue to area PF in monkeys), which are all part of the mirror system, also play a central role in imitative processes and form, together with the prefrontal areas, a functional network that Iacoboni (2005) refers to as the *minimal neural architecture* for imitation (MNA), i.e. the same as that found on the left side of the human brain which also subserves the LF (Fig. 1).

Furthermore, Stout & Chaminade (2012) pointed out that imitation of praxis (tool-making) is sufficient to intentionally influence the thoughts of the observers by inducing the same kind of high-level goal inference required in verbal communication. Di Vincenzo (2011) and Di Vincenzo & Manzi (2012, 2013) stressed the relevance of features of SL to sustain, both functionally and anatomically, the evolution of the LF in the Pleistocene when sociality, diet, technology and brain expansion (encephalization) in the genus *Homo* evolved according to a positive feedback in such a way as to face new ecological conditions.

Studies on fossil endocasts (e.g. Bruner *et al.*, 2003; Zollikofer & Ponce de León, 2013) demonstrate that the process of encephalization is coupled with the reorganization of many cerebral

areas. Starting with the so-called “early *Homo*” (e.g. *H. habilis*) and during the evolution of the genus *Homo*, there is the emergence of Broca’s cup (BA 47, underlying Broca’s area), which develops from the left inferior frontal gyrus and whose development determines the shift backward of the fronto-orbital sulcus; this, in turn, is characteristic of the great apes and also occurs in the australopiths (including *A. sediba*). At the same time, the inferior parietal lobule (BA 40) becomes more distinct and the temporal planes of the two hemispheres enlarge asymmetrically. Since these changes involve cortical areas typically associated with the LF in our species, they have been interpreted as evidence of the earliest appearance of language (e.g. Tobias, 1987). However, on the basis of the model of the MNA (see above), it is evident that the function associated with the original evolution of this left fronto-temporo-parietal network is SL (not the LF), given that it is shared by the Anthropoidea in varying phases of development.

Tomasello (1999) stresses the importance of imitation as a putative hallmark of human cognitive uniqueness. However, it may be argued that imitation is also present in the SL repertoire of great apes (Horner & Whiten, 2005). By applying the principle of parsimony, it presumably evolved before the split occurred between us and chimps following our last shared ancestor (>5 myrs ago), long before the origin of our species and, thus, well before our “uniqueness”.

Therefore, what is likely to have played a pivotal role in distinguishing us from our apelike ancestors is not related to any exclusive equipment, but rather to the variety of ecological conditions that allowed some features shared by the Anthropoidea to become more selectively relevant, and embrace new and more complex functions. The selective advantage associated with the ability to acquire the know-how needed to replicate complex motor tasks markedly increased when the genus *Homo* emerged around 2.5 million years ago, in concomitance with the shift to a more meat-oriented diet. It is widely recognised that the new ecological niche and the new trophic level of these early humans derived from

**Tab. 1 - Comparison of energy and nutritional components (100 g samples) available to early hominids.**

FOOD ITEM	ENERGY (KCAL)	FAT (G)	PROTEIN (G)	AA* (MG)	DHA* (MG)
African ruminant (brain)	126	9.3	9.8	<b>533</b>	<b>861</b>
African ruminant (liver)	159	7.1	22.6	192	41
African ruminant (muscle)	113	2.1	22.7	152	10
African ruminant (fat)	<b>745</b>	82.3	1.0	20–180	trace
African fish	119	4.5	18.8	270	549
Wild tuber/roots	96	0.5	2.0	-	-
Mixed wild plants	129	2.8	4.1	-	-

Note - The main sources of fatty acids and energy are bolded (data from Cordain *et al.*, 2001).

\* Essential fatty acids: arachidonic acid (AA) and docosahexaenoic acid (DHA). Since 100 mg of daily DHA are required in pregnant and lactating females for normal infant brain development in our species, the non-occasional exploitation of herbivore carcasses in the savannah, which could have been achieved only through social coordination and extensive use of tools, would have provided the full spectrum of nutrients and the energy intake to sustain the evolutionary growth of brain (encephalization) from the Early Pleistocene.

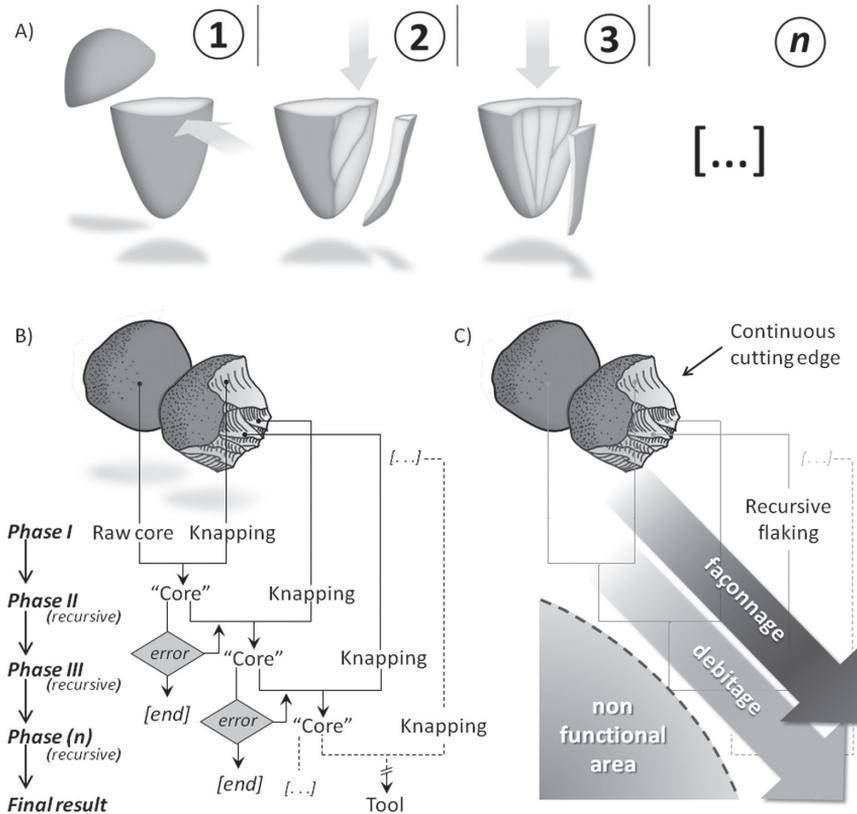
the exploitation of herbivore carcasses (scavenging) killed by the large predators, when the savannahs expanded in eastern Africa following the remarkable climate changes recorded during the Pliocene/Pleistocene transition (Hernández Fernández & Vrba, 2006). These food resources led to the intake of increased amounts of proteins and lipids, including high quality nutrients (i.e.  $\omega$ 3 fatty acids), which are indispensable to the expensive metabolism and growth resulting from enlarged brains (Tab. 1). These proteins and lipids could only be obtained by means of an extensive production and use of Paleolithic tools.

In such a context, computational and planning abilities were selectively favoured. These abilities increase efficiency, allow generativity, are less time-consuming, and reduce the possibility of tool-making errors. Moreover, they encourage apprenticeship by allowing more skilful cultural transmission while capturing the attention and intentional attributions in learners. It is likely that within the communicative context of the trans-generational transmission of motor and technical skills required for regular access to the new trophic resources, the simple recursive

ability involved in Palaeolithic technologies (Fig. 2) selectively became increasingly complex (through feedback with PLI and *working memory* storage enhancement) before being co-opted – as we suggest – in the acquisition of the LF.

In this perspective, the origin of the main features of the LF, whether functional (including the presence of recursion) or neurophysiological, can be placed within a continuous evolutionary path favoured by a constant increase in fitness, insofar as ecological factors led to a positive feedback between the enhancement of social learning and of cultural transmission and the phenomenon known as encephalization.

Co-evolution of motor praxis and sound-coding is also supported by various lines of evidence. The area F5 in monkeys responds to manual action sounds (e.g. breaking peanuts) though not, interestingly, to vocal calls (Vogt *et al.*, 2007). In chimps, Broca's homologue is activated by communicative manual gestures allied with the emission of attention-capturing vocalizations (Tagliatela *et al.*, 2011). Humans display selective left hemisphere motor facilitations in response to manual action sounds (Aziz-Zadeh



**Fig. 2 - Iteration entails repeating a given action for an arbitrary number of times, whereas recursion is the embedding of an action within another instance of itself. Both involve repetition, but recursion alone is characterized by the following items: i) each result is the input for a new productive cycle, ii) intermediate steps cannot be omitted, iii) tracking of previous related actions is required (limited by working memory storage capacity). When we apply these definitions to the Palaeolithic operational chains, we have: A) core-reduction for producing flakes is an iterative process, while (B and C) producing tools from a core (e.g. a chopping tool) involves recursion, as this consists of a hierarchically nested and embedded series of knapping actions aimed to produce a functional cutting edge. In particular, the drawing in (C) highlights how recursive flaking guarantees the efficiency of the operational chain outside the non-functional area (errors).**

et al., 2004), while the *echo-mirror neurons* present in the mirror system allow action recognition via neural matching with specific sounds (e.g. Rizzolatti & Craighero, 2004). Sounds motor facilitation is more clearly favoured in “noisy” praxical activities (e.g. tool-making) than in “mute” pantomimes, thereby allowing better acquisition and execution of new motor schemata, even through onomatopoeic imitation of the sounds associated with both observed

and displaced motor behaviours, and creating an evolutionary path to articulate speech .

A molecular substrate linking speech and praxis might be the FOX-P2 gene, which is involved not only in speech production but also in motor coordination of the hands and fingers (Vicario, 2013), as attested by the harmful effects of FOX-P2 impairment on the rapid motor sequencing ability of finger movements (Peter et al., 2011). The presence of modern-like FOX-P2 gene in

Neanderthals points not so much to a developed LF in that species, or of hybridization with modern humans (Benitez-Burraco & Barceló-Coblijn, this forum), as to the increased selective demand of the upper limbs and mouth motor fine control/coordination as well as of cognitive computational ability; thus, it is probably more closely related to mid-Palaeolithic techno-complexes than to a developed LF. It is likely that cognitive abilities, combined with others abilities suited to communication in SL, were subsumed (exapted) in LF with the origin of our species, as is suggested by the discovery of changes in regulatory factors in modern human FOX-P2 expression (Maricic *et al.*, 2013).

## References

- Aziz-Zadeh L., Iacoboni M., Zaidel E., Wilson S. & Mazziotta J. 2004. Left hemisphere motor facilitation in response to manual action sounds. *Eur. J. Neurosci.*, 19: 2609-2612.
- Barceló-Coblijn L. & Gomila A. 2012. Evidence of recursion in tool use. *Behav. Brain. Sci.*, 35: 219-20
- Bruner E., Manzi G. & Arsuaga J.-L. 2003. Encephalization and allometric trajectories in the genus *Homo*: Evidence from the Neandertal and modern lineages. *Proc. Natl. Acad. Sci. U.S.A.*, 100: 15335-15340.
- Buccino G., Vogt S., Ritzl A., Fink G. R., Zilles K., Freund H.-J. & Rizzolatti G. 2004 Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron*, 42: 323-334.
- Byrne R. W. & Russon A. 1998. Learning by imitation: a hierarchical approach. *Behav. Brain. Sci.*, 21: 667-721.
- Camps M. & Uriagereka J. 2006. The Gordian Knot of linguistic fossils. In J. Rosselló & J. Martín (eds): *The Biolinguistic Turn*. Issues on Language and Biology, pp. 34-65. Universitat de Barcelona, Barcelona.
- Chomsky N. 1956. Three models for the description of language. *IRE T. Inform. Theo.*, 2: 113-124.
- Corballis M. C. 2002. *From Hand to Mouth: the origins of language*. Princeton University Press, Princeton.
- Cordain L., Watkins B.A. & Mann N.J. 2001. Fatty acid composition and energy density of foods available to African hominids. *World Rev. Nutr. Diet.*, 90: 144-61.
- Di Vincenzo F. 2011. Toward a neuro-archaeology of the faculty of language. In E. Cosentino & M.G. Rossi (eds): *Evoluzione, mente e linguaggio*. Atti del IV Convegno del CODISCO (2010), Roma.
- Di Vincenzo, F. & Manzi G. 2012. L'origine darwiniana del linguaggio. *MicroMega*, 2012: 147-167.
- Di Vincenzo F. & Manzi G. 2013. Apprendimento imitativo ed evoluzione del linguaggio: una prospettiva darwiniana. In N. Grandi (ed): *Nuovi dialoghi sulle lingue e sul linguaggio*. Pàtron, Bologna.
- Geneste J.-M., Jaubert J., Lenoir M., Meignen L. & Turq A. 1997. Approche technologique des Moustériens charentais du sud-ouest de la France et du Languedoc oriental. *Paleo*, 9: 101-142.
- Greenfield P. 1991. Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behavior. *Behav. Brain. Sci.*, 14: 531-95.
- Hauser M. D., Chomsky N. & Fitch W. T. 2002 The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, 298: 1569-1579.
- Hernández Fernández M. & Vrba E.S. 2006. Plio-Pleistocene climatic change in the Turkana Basin (East Africa): Evidence from large mammal faunas. *J. Hum. Evol.*, 50: 595-626
- Holloway R. L. 1969. Culture, a Human Domain. *Curr. Anthropol.*, 10: 395-412.
- Horner V. & Whiten A. 2005. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Anim. Cognit.*, 8: 164-181.
- Iacoboni M. 2005. Understanding others: imitation, language, empathy. In S. Hurley & N. Chater (eds): *Perspectives on imitation: from*

- cognitive neuroscience to social science*. MIT Press, Cambridge (MA).
- Longa V.M. 2013. The evolution of the Faculty of Language from a Chomskyan perspective: Bridging Linguistics and Biology. *J. Anthropol. Sci.* (in press).
- Maricic T., Günther V., Georgiev O., Gehre S., Čurlin M., Schreiweis C., Naumann R., Burbano H.A., Meyer M., Lalueza-Fox C., de la Rasilla M., Rosas A., Gajović S., Kelso J., Enard W., Schaffner W. & Pääbo S. 2013. A Recent Evolutionary Change Affects a Regulatory Element in the Human FOXP2. *Gen. Mol. Biol. Evol.*, 30:844-852.
- Peter B., Raskind W.H., Matsushita M., Lisowski M., Vu T., Berninger V.W., Wijsman E.M. & Brkanac Z. 2011. Replication of CNTNAP2 association with non word repetition and support for FOXP2 association with time dreading and motor activities in a dyslexia family sample. *J. Neurodev. Disord.*, 3: 39-49.
- Petrides M., Cadoret G. & Mackey S. 2005. Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature*, 435: 1235-1238.
- Rizzolatti G. & Arbib M. A. 1998. Language within our grasp. *Trends Neurosci.*, 21: 188-194.
- Rizzolatti G. & Craighero L. 2004. The mirror-neuron system. *Ann. Rev. Neurosci.*, 27: 169-192.
- Rizzolatti G., Fadiga L., Fogassi L. & Gallese V. 2002. From mirror neurons to imitation: Facts and speculations. In A. N. Meltzoff & W. Prinz (eds): *The Imitative Mind. Development, Evolution, and Brain Bases*, pp. 247-265. Cambridge University Press, Cambridge.
- Shipton C., Clarkson C., Pal J. N., Jones S. C., Roberts R. G., Harris C., Gupta M. C., Ditchfield P. W. & Petraglia M. D. 2013. Generativity, hierarchical action and recursion in the technology of the Acheulean to Middle Palaeolithic transition: A perspective from Patpara, the Son Valley, India. *J. Hum. Evol.*, 65: 93-108.
- Stout D. & Chaminade T. 2007. The evolutionary neuroscience of tool making. *Neuropsychologia*, 45: 1091-1100.
- Stout, D. & Chaminade T. 2012. Stone tools, language and the brain in human evolution. *Phil. Trans. R. Soc. B*, 367: 75-87.
- Tagliatalata J. P., Russell J. L., Schaeffer J. A. & Hopkins W. D. 2011. Chimpanzee vocal signaling points to a multimodal origin of human language. *PLoS ONE*, 6: e18852.
- Tobias P. V. 1987. The brain of *Homo habilis*: A new level of organization in cerebral evolution. *J. Hum. Evol.*, 16: 741-761
- Tomasello M. 1999. *The Cultural Origins of Human Cognition*. Harvard University Press, Cambridge (MA).
- Vaesen K. 2012. The cognitive bases of human tool use. *Behav. Brain. Sci.*, 35: 203-218
- Vicario C. M. FOXP2 gene and language development: the molecular substrate of the gestural-origin theory of speech? *Front. Behav. Neurosci.*, 7: 1-3
- Vogt S., Buccino G., Wohlschläger A. M., Canessa N., Shah N. J., Zilles K., Eickhoff S. B., Freund H.-J., Rizzolatti G. & Fink G. R. 2007. Prefrontal involvement in imitation learning of hand actions: Effects of practice and expertise. *NeuroImage*, 37: 1371-1383.
- Zollikofer C. P. E. & De León M. S. P. 2013. Pandora's growing box: Inferring the evolution and development of hominin brains from endocasts. *Evol. Anthropol.*, 22: 20-33.

Associate Editor, Rita Vargiu