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Prehistory, neuroscience, and evolutionary anthropology: a personal journey

Emiliano Bruner

Centro Nacional de Investigación sobre la Evolución Humana, Paseo Sierra de Atapuerca 3, 09002 Burgos, Spain
email: emiliano.bruner@cenieh.es

Summary - *The relationship between anthropology and neuroscience has always been friendly but controversial, because they embrace inclusive common topics (human beings and their brains) although following distinct approaches, often more holistic and speculative in the former field, more reductionist and quantitative in the latter. In recent decades, novel disciplines have been proposed to bridge the gap between anthropology and neuroscience, mostly taking into account their common interest in human evolution. Paleoneurology deals with the study of brain anatomy in extinct species. Neuroarchaeology concerns the study of brain functions associated with behaviours that are of interest according to the archaeological record. Cognitive archaeology investigates the evolution of those behaviours following methods and theories in psychology. These new fields can provide quantitative and experimental support to topics that, to date, have been largely discussed only on a theoretical basis. Nonetheless, working with extinct species necessarily involves many limitations. Consistent theories on the evolution of our cognitive abilities must rely on the integration of different sources of information, on parallel and independent evidence from different fields, and on a proper attitude: openness and caution.*

Keywords - *Paleoneurology, Neuroarchaeology, Cognitive archaeology, Human Evolution, Brain evolution, Cognition.*

Anthropology and neuroscience

Both anthropology and neuroscience deeply embed any possible field of knowledge if one considers that humans themselves are the ones organizing and processing that knowledge through their own cognitive scaffolds. Therefore, when trying to find bridges between anthropology and neuroscience, the main problem is that there are too many. Humans are intensely characterized by their brains, which in turn cannot be investigated outside of the frame of human biology and culture. Such an intricate relationship may represent a confounding factor when trying to delineate a simplified and clear epistemological, methodological, and experimental context. Indeed, anthropology and neuroscience have been in intimate contact ever since, with blurred boundaries and complementary interests. Repeated attempts to launch the foundations of a chimerical field of *neuroanthropology* have led to stimulating but blurry results, probably because of a patent tautology. In fact, (almost) everything can fit within this all-comprehensive and elusive label, making it difficult to establish a well-defined range of methods and principles.

Despite such a tight relationship, anthropology and neuroscience have maintained, however, certain professional and cultural barriers. Anthropology is, in cultural and academic terms, a broad field, probably the broadest ever, so it lacks a precise professional profile, at least when compared with most standard disciplines. When dealing, more specifically, with biological anthropology, it has been often defined as the natural history of humankind, a definition which is frank and self-explaining, although pretty vast in terms of targets and methods. Instead, neuroscience, despite the undisputable extensiveness of the field, has a more developed sense of unity, probably because of a dominant and transversal topic, a physical "object" that is the least common denominator of all its branches: the brain. As a consequence, in anthropology, a professional career is less defined than in neuroscience. Indeed, an "anthropologist" can have obtained almost any university degree (humanities, natural sciences, biology, sociology, psychology, epidemiology, etc.) and the label can be assigned to so many distinct professional qualifications (archaeology and history, anatomy and physiology, ethnology and economics, nutrition and health, etc). I am particularly pleased to remember here a good friend and former member of the Italian Institute of Anthropology, Amilcare Bietti, one of the most competent and expert scholars in prehistoric archaeology in Italy at the end of the past century, who long held the chair of Prehistoric Ecology, and who had an official educational background in… theoretical physics! Interestingly, this interdisciplinary condition is often based on a unidirectional flow, in the sense that a medical doctor, a psychologist, or even an engineer can finally work in anthropology or even be labelled as "anthropologist", but the opposite is certainly not true: if you are an anthropologist, they will never let you perform a surgery, treat patients, or build bridges. Such unidirectional admixture, somehow, reveals a different social and academic perception (at both cultural and legal level) of these professional careers.

However, beyond the fact that anthropology can be investigated from many distinct scientific perspectives, the admixture between science and humanities is of course a major issue, in this sense, because of the profound conceptual, methodological, and educational differences between the two sectors. At first glance, such admixture sounds necessary (because of the intimacy of the biological and cultural aspects of human nature) and valuable (because of the synergies between the two approaches). However, the supposed advantages of this interdisciplinarity is often lost because the two aspects, instead of being properly integrated, are blended and confused, generating fragile and undefined professional niches. Instead, in the case of a "neuroscientist", there is usually a much narrower range of career possibilities, mostly including biology and medicine. As a consequence, anthropology is commonly seen as a field that is less specialized than neuroscience and, somehow implicitly, less rigorous. This feeling is probably amplified by the fact that neuroscience more frequently deals with topics that directly influence health, while anthropology generally concerns issues with no direct effect on human welfare.

Such differences have generated a situation in which, despite the common interests, the two fields have evolved a relationship of tolerable acquaintanceship, rather than a real emotional friendship. Neuroscientists are fascinated by anthropological topics, but they proudly maintain a separate status of "harder science". Anthropologists, instead, are proud of their condition of cultural hobos, although they love using the *neuro* prefix as much as possible in order to feel part of the *neuro* family. Of course, such subtle reciprocal flirting is not only a matter of knowledge, but it also has to do with social aspects: visibility, academic success, and financial funding.

No one's land

I defended my degree in Biology back in 1998, at the University La Sapienza of Rome (Italy), with an experimental thesis in Human Ecology, which was supervised by Massimo Cresta. He was, in my opinion, a real giant in the world of the Italian anthropology, a medical doctor who had dedicated half a century to study nutrition and biocultural interactions in diverse human populations. Cresta was the one who, at that time, introduced me as a member to the *Italian Institute of Anthropology*, and to my early assignments as assistant for the *Journal of Anthropological Sciences* (formely *Rivista Italiana di Antropologia*). In his speech where he presented my membership, he made reference to my "fruitful polemical personality and critical attitude", which, in his opinion, could definitely add to the development of the institution. Posterity will judge.

A few years before, I had spent some time at the chair of Psychobiology, being fascinated by human brain and behaviour. In fact, I had enrolled in Biology because of my enduring interest, during the whole of my adolescence, in animal ethology and Konrad Lorenz's books, then turning my attention to human ethology after reading the books of Lorenz's student, Irenäus Eibl-Eibesfeldt. I was fascinated by how a comprehensive range of biological information could be used to support evolutionary inferences on human behaviour. Unfortunately, my early academic experiences in ethology were not as good because I found there was an unexpected excess of behavioural observations and speculations, and little biology. Psychobiology was, indeed, a great alternative. With one major problem however: at least at that time, humans were the exclusive targets of psychologists and medical doctors, while biologists were orthodoxly relegated to work with animal models. There was a sort of silent agreement in the academic environment on this point and, after meeting a bunch of influential researchers in biology, psychology and medicine, I realized that such an academic pact could not be broken, at least if you are a student. I made one last extreme attempt by contacting a professor of human physiology in order to propose working on brain metabolisms and behaviour. I guess she was not aware of the recent advances in brain imaging, and I can only remember that she kicked me out of her office shouting that I was a monster, a crazy Frankenstein, supposing my intention was to apply to humans the same methods that she used with mice and cats. This is why I then redirected my university career and concentrated on zoology and ecology (mainly insects, spiders and reptiles), until my lucky encounter with Massimo Cresta brought me back to humans.

The curious twist of fate came, anyway, after my degree dissertation in human ecology (a biocultural analysis on aging in rural areas) when, after some years of collaboration working on primate skulls in the Museum of Anthropology "Giuseppe Sergi" of the same university, Giorgio Manzi invited me to join to his laboratory of paleoanthropology, finally through a PhD grant on biomedical imaging, morphometrics, fossils, and brain evolution. At the end of the 90s, computed tomography and geometric morphometrics were the new, charming and enigmatic cutting-edge techniques, and he proposed to apply these methods to the reconstruction of the endocranial casts in fossils species, especially in Neandertals. Three years later, after an exciting period of improvised exploration in pixel science, multivariate statistics and comparative neuroanatomy, I defended my PhD in human paleoneurology. The president of the board was the professor of Psychobiology, Alberto Oliverio, an amazing scholar, a brilliant person, and a key reference in the field. After the dissertation, he told me, with patent satisfaction, that he was so glad that, finding the door closed, I had managed to enter through the window. The first research article which integrated digital anatomy, geometric morphometrics and paleoneurology was published in 2003 (Bruner et al. 2003).

Prehistory and neuroscience

In the following decade, with the beginning of the millennium, anthropology and neuroscience began developing more practical and outlined professional relationships, largely because of the shared methodological (computed and molecular) tools. Also, science at that time was increasingly spreading through the dissemination market, and novelty is always a major key, in this sense. Cross thinking and innovation have a certain appeal when dealing with mass-media and with the general public, and this probably prompted further the collaboration between the two fields. Three disciplines that were profoundly enhanced by this new stage of interdisciplinary bridging are paleoneurology, neuroarchaeology, and cognitive archaeology. Despite the fact their definitions are blurred and their boundaries overlap, these three fields roughly deal, respectively, with brain anatomy, brain functions, and psychological aspects of behaviour.

Fossil brains

The term *paleoneurology* (more properly it should be called *paleoneurobiology*) refers to the morphological study of brain anatomy in fossil species (Bruner 2015, 2017, 2019; Bruner and Beaudet 2023). Of course, the brain does not fossilize and, actually, there is no fossil brain at all. Paleoneurology concerns the study of the endocranial casts (called *endocasts*; Holloway et al. 2004), namely the positive mould of the endocranial cavity (Fig. 1a,b). This cavity is principally shaped by the growing brain (Moss and Young 1960; Enlow 1990; Richtsmeier and Flaherty 2013), and therefore it can be reasonably used as a proxy of the overall brain form (Zollikofer et al. 2013; Neubauer 2014; Dumoncel et al. 2021). One can estimate the size of the brain (the cavity is roughly 10% larger), or try to localize major cortical references (sulci and gyri) that can be used to make inferences on gross proportions of lobes or areas. Of course, the morphological imprints of the cortical regions on the bone surface are not so easy to interpret. Most cortical brain elements do not leave corresponding traces on the endocranial morphology and, when they do, those traces are blurred and smooth. Essentially, on an endocast, gyri can tentatively be localized as "bosses", and sulci as "depressions". In some cases, the position or extension of a cortical region can be extrapolated indirectly, when the neighbouring regions are visible. In any case, such approximation requires personal experience, and a certain amount of speculation. The localization of these anatomical references allows comparisons, within and between species, for what concerns the size, shape and proportions of cortical regions that can have some functional implications. When present, conspicuous differences in brain proportions between two taxa are presumed to match some kind of neurobiological, behavioural or cognitive difference, even if the exact functions involved can be hard to detect.

Also the vessels running through the meningeal layers (such as the middle meningeal artery, the venous sinuses or the emissary veins) leave their imprints on the endocranial surface or through the bone thickness, providing information regarding blood flow in osteological samples and extinct species (Píšová et al. 2017). Like for the cortical traces, however, also in this case, some vascular elements can leave no traces at all, and the interpretation of these traces requires caution. Nonetheless, at least the available imprints are easier to match with specific vascular components, because their marks are definitely sharper. In this case, a major problem concerns the scarce (or null) information we have on the functional meaning of the vascular variants.

In any case, as stressed previously, there is no real brain to work on, and this is an important limitation of the field. In this sense, the term "brain" is indeed misleading, and should not be used too often when dealing with endocranial casts. An endocast can only reveal the rough appearance of the brain, which is definitely less than a brain itself. It only deals with macroscopic external anatomy, and it cannot reveal features that do not influence the morphology of the braincase. So, when dealing with extinct taxa, it is not the same to say "its brain was" or "its endocast suggests that", and caution is definitely recommended.

The field of paleoneurology is in no way new, and it was developed in the past century by extraordinary palaeontologists such as Franz Weidenreich, Phillip Tobias, or Ralph Holloway, among others. Endocasts were traditionally made by moulding the cranial cavity (or a part of it) with physical materials, ranging from plaster to modern epoxy resins. Making endocasts was a real technological challenge, involving a profound knowledge of the materials and of the fossils themselves. Results were amazing, although they suffered many limitations due to the physical nature of the moulds (resolution, deformation, reliability, reproducibility, access to the cavity, and safety of the specimens). This is why a major renaissance of the field, in the last 20 years, was associated with the employment of digital tools from biomedical imaging, mainly computed tomography (Gunz et al. 2009; Bruner et al. 2018a). Such digital tools have really prompted a new stage for paleoneurology, in which endocasts are reconstructed by using virtual replicas, with high resolution, faster procedures, exceptional

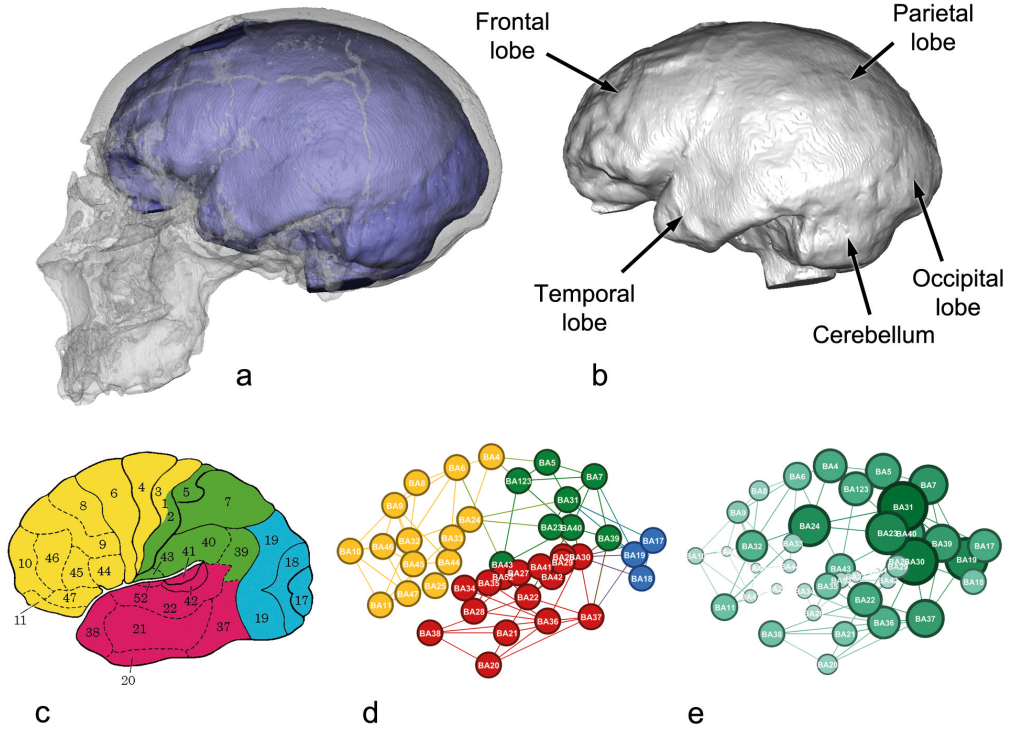

***Fig. 1** - Digital morphology allows the reconstruction of fossil skulls and endocasts (a; here, the digital replicas of Saccopastore 1 – Bruner and Manzi 2008), and paleoneurology largely deals with the anatomical study of cortical (brain) information (dimensions, proportions, sulcal patterns and meningeal vascular channels) available from the endocranial form (b). Besides neuroanatomy, functional craniology is crucial in paleoneurology in order to investigate the structural relationships and reciprocal influences between anatomical elements. Taking into account the major anatomical regions (such as Brodmann's areas; c), network analysis can be employed to analyse the topological and spatial relationships between cortical elements (d) to quantify the spatial properties and anatomical burden of the system's elements (e; here, the spatial closeness; Bruner 2022).*

reliability, and with the possibility to analyse the form and features of these virtual objects through computed quantitative techniques.

However, as mentioned above, a cast of the endocranial anatomy is certainly not a brain, and the anatomical information that can be obtained from an endocast is scarce. Nonetheless, it is also, without doubt, valuable, because it is the only direct information we have on the brain morphology of extinct species, and this is something which is definitely crucial in a taxon (humans) that has evolutionarily invested so much in encephalization. Brain size is, in this sense, a simplistic but pertinent variable. Brain size changes, in fact, do not provide any information about what brain regions underwent expansion or reduction, or whether the change was due to neurons or other cerebral tissues. Also, most human species displayed a pronounced overlap in their brain size range, which suggests that this factor is relevant but in no way decisive, when dealing with species-specific cerebral or cognitive differences. Nevertheless, the absolute and relative increase in brain size in different human lineages, at least on average, is undisputed, and it is often associated with increasing behavioural complexity. Therefore, we should consider that brain size can tell, at least in part, an interesting part of the story.

Among distinct species of the human genus, we can also observe differences in cortical proportions, or at least hypothetical differences, largely associated with changes in the frontal, parietal and temporal cortex. In this case, caution is mandatory at least for three reasons. A first limitation is linked to the fact that, as mentioned previously, the assessment of cortical territories (lobes, gyri and sulci) on an endocast is a matter of smooth boundaries and subjective interpretations. Metrics obtained from such flat and blurred surfaces are, indeed, tentative. At present, there are still few studies making inferences on the extension of specific brain regions in fossil humans. Most morphometric analyses of fossil endocasts are in fact based on cranial references (namely, landmarks of the skull, and not of the brain) or on surface models (namely, generalized geometrical forms with no anatomical correspondence). Both approaches may be useful to investigate the shape of the endocranial space, but not the variations associated with brain cortical changes. The former approach (models based on cranial references) deals with bony elements (like bregma, lambda, the cranial base and so on), which do not mark the position or extension of specific cerebral regions or areas. The latter (surface models) considers the endocranial space as a homogeneous and undifferentiated object (a sort of balloon), neglecting the anatomical contribution and diversity of its regions and cortical components. Tautologically, most analyses employing skull and surface landmarks to study brain morphology are not able to provide any substantial information on cortical evolution and, in general, only detect the influence of the cranial bones on the neurocranial variability.

A second crucial issue in paleoneurology concerns the integration between brain and braincase, namely the reciprocal influences and constraints exerted, during growth, development and evolution, by soft and hard tissues. In fact, some morphological brain changes can be due to real changes in cortical volumes and proportions (primary changes), while in other cases they can be due to spatial constraints of the cranial system (secondary changes). It can be hard to discriminate between these two alternatives, or their admixture. In this case, studies of modularity and integration between skull and brain are pivotal, and propaedeutic to any paleoneurological inference (Bruner et al. 2015; Zollikofer et al. 2017). Network analysis has been recently applied to brain topology, in order to localize those regions that have a marked "anatomical burden", because of their position or role within the spatial organization of the cerebral system (Figs. 1c,d,e; Bruner et al. 2019; Bruner 2022). Networks are commonly employed in neurobiology to study the patterns of brain connectivity, namely, the functional connections between neurons (e.g., Bullmore and Sporns 2012). Instead, in anatomical network analysis, network models are used to study the physical contact between the anatomical parts in order to provide information concerning their spatial properties and geometrical constraints (Rasskin-Gutman and Esteve-Altava 2014). This information is crucial to interpret most macroscopic cerebral changes we can detect in living or fossil species, and to distinguish between primary and secondary changes. This approach can be applied to investigate the spatial organization of the brain and the reciprocal topological influences of the brain elements (gyri, sulci or areas), or to analyse the architectural organization of the whole skull-brain system, modelling the contiguity between brain, bones, and even muscles, connective tissues and other organs (eyes, airways, etc.).

A third cautionary note on paleoneurology and cortical proportions concerns the association between brain morphology and behaviour, which is often based more on intuition and speculation than on consistent information. The current evidence on possible correlations between brain anatomy and cognition suggests that, when there is some kind of relationship, it is generally poor, and insufficient to support any robust prediction. Namely, even for those cases for which there is a proven correlation between brain anatomy and cognition, such association deals with broad and generalized functions, and it is characterized by an outstanding individual variability. As a consequence, it may be hard (and speculative) to understand precisely what behaviours can be partially influenced by a given cortical change and, even so, such an influence would be a matter of average effect, with important idiosyncratic differences among subjects. It is worth noting, in this sense, that common neurosurgical and neuropsychological practice suggest that minor changes in the brain anatomy (such as those associated with lesions or pathological conditions) can imply dramatic behavioural or biological changes, while large modifications can sometimes imply minor or null functional consequences. In sum, a correlation between anatomy and behaviour, when present, is useful to reveal and quantify a biological factor associating functional and structural changes, but it is generally not useful, *per se*, to provide reliable predictions on the cognitive performance of a species or of an individual.

Of course, in the case of macroscopic evolutionary changes, one can suppose that "something" has changed in the neural organization and, therefore, in the cognitive functioning. According to the traditional view on cortical parcellation, the brain is formed by areas with distinctive functional roles (e.g., Van Essen and Dierker 2007). In this case, changes in cortical (or subcortical) proportions suggest that the functional balance and integration of these areas has changed, with some consequences on the cognitive processing. Alternatively, the brain patchwork can be seen as formed by overlapping growth and developmental gradients, generally connecting the sensorial (primary) inputs (Huntenburg et al. 2018). In this case, changes in brain proportions reveal different patterns of sensorial integration and, consequently, of information processing.

An interesting case study deals with the parietal cortex, which, in modern humans, displays a distinctive morphology (larger size and more complex organization) in regions which are crucial nodes for specific modern human behaviours (Bruner 2018; Bruner et al. 2022). The parietal cortex integrates information from body and vision, and its increase would be expected to reveal an enhancement of the corresponding processing capacity. Mental imaging, graphic ability, tool-use, haptic dexterity or projectile technology are all features particularly related to modern behaviour, and largely depend on visuospatial functions associated with the activation of the parietal cortex. These same functions are also a fundamental part of the working memory system, which is the basic network that assists executive attention, decision making, planning and fluid reasoning (Wynn and Coolidge 2004; see below). The fact that we find complex parietal morphology and complex visuospatial behaviour in the same species (*Homo sapiens*) is probably not due to chance. Nonetheless, it must be once more stressed that paleoneurology regards anatomy. Inferences on cognition should be based on multiple and independent sources of information and anatomy is, per se, a complementary issue within a wider approach to cognitive evolution. At the same time, it is also clear that, when dealing with neuroscience, cognition and human evolution, the anatomical information on brain morphology in extinct hominids should not be neglected.

A final relevant note on paleoneurology regards the fact that this field is not only rooted in anatomy, but also intrinsically developed within the research context of general anatomy. Namely, research on fossil hominids requires a proper knowledge of anatomical functions and variations in living hominoids. This seems obvious, but, in common practice, it is not always so. Many features investigated in paleoanthropology are not sufficiently well known in our own species, and this is a major limitation to the development of robust and reasonable evolutionary hypotheses. This scarce knowledge concerns all the principal topics investigated in paleoneurology, namely the skull, the brain, and the vascular system. It is patent that modern humans can supply large samples of living (physiologically active and anatomically complete) subjects, while the fossil record provides only partial, fragmented and distorted osteological pieces of few specimens. Fossil samples, simply put, cannot reveal the biology, functions, development and variability of most anatomical traits. Neither can they support the proper application of consistent statistical methods. It is therefore necessary to investigate a character (its biology, functions, development and variability) in modern populations, before making any speculations on the fossil evidence. Unfortunately, quite often, such speculations are not reinforced with this necessary background, and many research papers in the field are developed through descriptive (i.e., non-quantitative) analyses of poorly known anatomical features. These kinds of studies, when accompanied with firm and conclusive statements, can seriously harm the reliability and reputation of the discipline, although they may be successful in selling sensationalist titles and attractive journal covers. Indeed, we can say that working in paleoneurology means most of all working on the brain and skull of modern humans and modern primates, then applying the results from those neontological studies to specific paleontological cases, when possible.

Archaeology and the brain

Biomedical imaging has led to a major advance by virtue of its capacity to explore the internal anatomical structure also in living subjects, in hard (computed tomography – CT) and soft (magnetic resonance imaging – MRI) tissues. The same toolkit has also provided, in the last twenty years, the possibility to investigate metabolic functions, by integrating imaging with the detection of biological signals associated with tissue activation (for example, functional MRI or Positron Emission Tomography – PET). The term *neuroarchaeology* generally refers to those studies in which functional imaging is employed to investigate brain activity during the execution of behaviours that are relevant according to the archaeological record (Stout and Hecht 2017). The most frequent example is tool-use and tool-making (Stout and Chaminade 2007). In this case, subjects are brain-scanned while performing tasks associated with lithic knapping, in order to investigate what regions of the brain are activated in different technological situations (Fig. 2). For example, it has been observed that while Oldowan knapping largely relies on parietal activation (body and space functions), Acheulean knapping involves a wider fronto-parietal system, probably associated with executive functions and decision-making (Stout et al. 2015). Similarly to paleoneurology, also neuroarchaeology largely deals with anatomy. However, because of the functional implications, in this case, hypotheses on cognitive evolution are more direct, and less speculative.

These methods are particularly powerful, although not exempt from limitations. First, these kinds of techniques are pretty expensive, time-consuming, and complicated in terms of logistics. Therefore, in general, samples are not so large and the statistical power is hence limited. Furthermore, tasks are conducted in laboratory conditions, and applying these procedures in realistic (field) situations is hardly feasible, at present. There are also technological limitations, which are often underestimated (Bruner and Ogihara 2018). These methods are based on large chains or numerical transformation and algorithms, including normalization steps and automatic segmentation of the anatomical regions, which are transformed into digital models made by pixels. All these steps may introduce biases or operational choices that can substantially influence the results, passing unnoticed in many cases (see Gronenschild et al. 2012). Instead, all too often, these transformations and assumptions are taken for granted, with scarce caution regarding their possible effects on the final outputs. It is also worth noting that most of these techniques rely on some biological signal associated with neural activation, and not with neural activation itself. For example, they are used to detect blood flow variations or oxygen consumptions. We assume that more blood or oxygen in a given brain region means more activity and therefore a direct implication of that region in a specific function, but this rule of thumb has not been properly assessed, and may have important exceptions or weaknesses.

A final note concerns the risks due to the noticeable charm generally associated with these methods, which are indeed appealing and attractive in terms of mass-media attention and public reaction. This indisputable success may overestimate their results and applications, skewing the research feedback towards science marketing and sensationalistic attitudes.

***Fig. 2** - Neuroarchaeology concerns the study of brain functions associated with behaviours that are relevant in human evolution, such as stone tool making (left). Techniques of structural or functional imaging (for example, Diffusion Tension Imaging; right) are employed to investigate the biological basis involved in those specific behaviours. Images courtesy of Dietrich Stout and Erin Hecht.*

Extinct minds

Cognition is definitely more than just a brain. Indeed, a brain fits into a box of 1300 cc., while a mind probably does not. *Cognitive archaeology* deals with the integration between methods and theories in cognitive sciences and the archaeological evidence of behaviours associated with extinct species or past populations. The former case (extinct taxa) concerns human evolution, while the latter (past or different cultures of our own species) deals with human history, and it is a promising field which remains scarcely explored. If neuroarchaeology (as suggested by the prefix *neuro*) must concern something related to the neural system (generally, the brain), cognitive archaeology is a wider and more comprehensive field, because cognition can be investigated through different aspects of the brain, of the body, and of the environment. Psychology has a long tradition, in this sense, and cognitive studies can deal with behaviour, perception, external influences, experimental paradigms, theoretical models and simulation, or physiological correlates. In evolutionary anthropology, tool-making and tool-use, social organization, landscape use and ecological factors, and other kinds of archaeological proofs, can be employed to make inferences on the corresponding behaviours, and used to provide cognitive hypotheses based on current knowledge in psychology (Wynn and Coolidge 2016).

Most theories on cognition are based on hierarchical models in which specific skills can be grouped in narrow abilities, which can be further grouped in broader abilities (see Schneider and McGrew 2018 for a detailed review). Broad abilities concern general cognitive domains (like spatial skills, fluid reasoning or learning capacity), while narrow abilities deal with sub-domains that contribute to each broad capacity, and specific skills are associated with the performance of particular tasks and behaviours influenced by those abilities (Fig. 3). Of all these levels, only specific skills can be quantified experimentally, through psychometric tests and tasks designed to measure those abilities through standardized procedures. Narrow and broad abilities are then identified, tested, and quantified through multivariate approaches able to investigate the structure of those specific scores (Factor Analysis), or according to biological evidence (developmental stages, functional and structural brain imaging, or pathologic conditions, revealing anatomical or cognitive modules associated with those abilities). A general cognitive ability (called *g* or *general intelligence*)

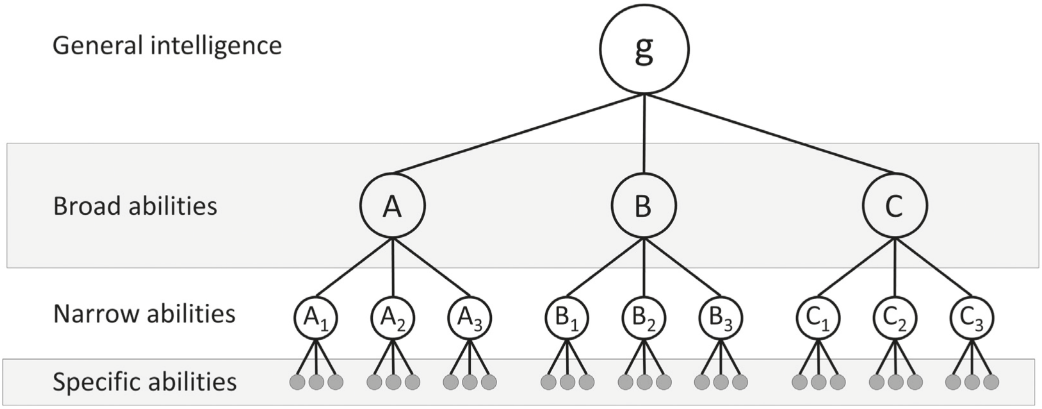

***Fig. 3** - The Cattell–Horn–Carroll theory of cognitive abilities, based on a hierarchical structure of specific skills, narrow abilities and broad abilities (after Bruner et al. 2023).*

has been hypothesized to coordinate and integrate all the broad abilities together. Of course, such hierarchical models are based on blurred and debated boundaries between abilities and functions, and must be intended as useful simplified representations of a complex mental landscape, in which real biological factors are probably mixed together with conventional and arbitrary definitions. Such models are indeed necessary to organize the science of psychological assessment in an experimental and quantitative framework.

A major aim in cognitive archaeology is to give reliable and consistent interpretations of the archaeological record according to current models of psychological structure (Bruner et al. 2023). An example is working memory, a general cognitive ability that is thought to rely on a fronto-parietal system formed by executive functions, phonological loops and a visuospatial sketchpad, and which is crucial for almost any human cultural, technological and social activity (Wynn and Coolidge 2004; Coolidge and Wynn, 2005). Working memory is involved in maintaining and handling information (most of all spatial and verbal information) while performing a task, which is something definitely essential in planning, problem solving, and decision making. A decisive feature involved in all these processes is *inhibition*, which is mandatory for most complex human behavioural, social, and cultural aspects. In fact, more than an outstanding ability "to do" something, humans are characterized by a unique capacity of "not to do", that is resisting impulsive behaviours associated with basic biological functions (eating, mating, aggression, and so on). In most animals, inhibition is generally based on emotional constraint, like fear. In humans, instead, inhibition is associated with executive attention, reasoning, and volitional (i.e., conscious) choices, and it is the very foundation of many of our unique behaviours, like those necessary to develop large and complex societies, to develop and use complex ecological and technological resources, and to develop a cumulative culture based on learning and teaching.

As already mentioned, another fascinating case-study is spatial integration, a cognitive domain that is particularly relevant in an evolutionary perspective, because it is a key factor associated with the relationship between brain, body and environment, technological evolution, visual imaging, mental experiments, social organization and consciousness (Bruner et al. 2018b; see Bruner 2023). Besides visuospatial ability (which is probably the more investigated topic in this frame, because of the importance of vision for primates, and for eye-hand coordination), spatial issues also concern all those skills associated with body management and body cognition, such as tactual, kinaesthetic, and psychomotor abilities. The integration between body and space is a crucial part of the ability to extend perception and functions to external peripheral devices (Borghi and Cimatti 2010; Malafouris 2010), namely to evolve a specialized "prosthetic capacity" necessary to delegate cognitive processes to technological components (Bruner 2021). In this sense, it is worth nothing that many recent cognitive theories include the body and the environment within the cognitive system, although the precise roles and mechanisms of all these elements must be still investigated (Wilson 2002; Kaplan 2012; Wilson and Golonka 2013).

An additional interesting ability is attention, which is a core component of general intelligence and a limiting factor in the employment of any cognitive skill (Rueda 2018). Attention, namely the capacity to maintain a cognitive task in time and space independently of inner and outer interfering stimuli, is a prerequisite to sustain almost every human activity in technological and social terms, and it is therefore expected to have experienced major changes in hominid evolution (Bruner and Colom 2022). The attention system is formed by distinct neural and cognitive modules that, although integrated, serve different functions and can evolve independently (Petersen and Posner 2012). It is to be expected that focused attention and top-down executive functions (namely, those functions associated with sustained and volitional attention), associated with a complex fronto-parietal network, underwent decisive specialization in the human genus, and particularly in *Homo sapiens*. Apart from the fronto-parietal system, sustained attention is associated with the activation of deep brain regions (like the cingulate cortex) whose morphology cannot be evaluated directly from endocasts, and are hence out of the range of any paleoneurological assessment. Behaviour and archaeology are hence the only source of information for many aspects related to the attentional skills of extinct taxa.

It is worth noting that all these cognitive domains patently reveal an intricate and intimate relationship between social and technical abilities (Bruner and Gleeson 2019). Primates have crucially invested, in terms of evolution, in the social group, and humans are the most social primate ever. Indeed, a large part of our brain evolution is certainly associated with our social complexity (Dunbar 2018), and this has also probably occurred through the enhancement and specialization of our intricate emotional system (Barger et al. 2014). As a consequence, it is rather difficult, in our own species, to disentangle the sophisticated network of causes and consequences linking cognition, technology, and social organization, and we must expect that major changes associated with the human phylogeny are due to a general reorganization of these three components, through balanced and reciprocal feedbacks between their associated behaviours.

Apart from considering explicit cognitive abilities, another possibility is to investigate the evolution of wider and more transversal cognitive aspects, like for example consciousness and self-awareness (Leary and Buttermore 2003). It is clear, nonetheless, that the vaster the cognitive domain, the more difficult the target is. A key problem, in this case, is to work with reliable, clear and shared definitions of such complex and blurred abilities. Then, a second spiny issue is to find proper evidence able to score or reveal the presence or degree of expression of those processes. In fact, specific skills can be directly analysed by observing the archaeological remains, while inferences on broad or imprecise mental categories will require the integration of many sources of information, and much more conjectures.

Nevertheless, in any case, it is mandatory to remember that, to work within a proper scientific perspective, testing hypotheses is an obligatory step. In fact, at present, the main limitation of cognitive archaeology is probably an excess of theoretical speculation. A consistent and sensate theoretical background is essential to any scientific discipline. However, this must be propaedeutic to a later experimental and quantitative approach, aimed at testing the reliability of the hypotheses proposed on a theoretical ground. Validation is a crucial step for any scientific perspective, and most of the current theories in cognitive archaeology have been developed, instead, on a pure conjectural base. Of course, it is easier to make theories than to make experiments, particularly in a field which is actually difficult to bring into a laboratory setting. Concluding experiments in cognitive archaeology can be challenging to design, and probably they can give only partial and general results. Nonetheless, as in any other scientific field, they are necessary to complete the puzzle or, at least, to give more information on the actual scenario. The difficulties in working on experimental settings in cognitive archaeology should not mean rejecting the experimental approach. This would mean excluding the field from the scientific paradigm.

In my laboratory, for example, we have been trying to employ methods developed in psychology to investigate behavioural and perceptual changes associated with tool-use (Bruner et al. 2018c,d; Fig. 4). Humans changed from occasional, to habitual, to obligatory tool-users in the last 2 million years (Shea 2017), and this has increased the dependency of our cognitive system on technology, offloading part of our broad, narrow and specific abilities to external (extra-somatic) peripheral elements. Although the precise roles and mechanisms of such extension is far from being understood, we must expect that we underwent a sort of specialization for the integration of these tools into the body schemes, and in their corresponding cerebral representations (Bruner 2021). Among the many cognitive abilities involved in such prosthetic extension, attention, visuospatial integration and haptics are three of the domains probably involved (Bruner 2023). As mentioned above, changes in attention may have mostly concerned the so-called top-down mechanisms, involving the executive functions associated with selecting and maintaining specific stimuli according to a conscious state of activation (Rueda et al. 2021). Visuospatial integration deals with many visual patterns that are crucial to mental imaging and eye-hand coordination (Kravitz et al. 2011). Haptics refers to the integration between tactile, proprioceptive and exteroceptive feedbacks, dealing with the somatosensory system involved in body-tool integration (Kappers and Bergmann Tiest 2013). With this in mind, a first step is to investigate the beginning of these changes, when the human hands began extending the body through dynamic touch (*sensu* Turvey and Carello 2011) on large and heavy Lower Palaeolithic stone tools, like choppers or handaxes. We used electrodermal analysis to investigate the pattern of attentional variation through the haptic exploration of these tools in order to investigate how this physical experience can influence the state of arousal (Fedato et al. 2019, 2020). Electrodermal analysis quantifies the variation of skin impedance during a task, associated with longer and slow attention fluctuations (electrodermal level - EDL) and short fast changes of general arousal (electrodermal response - EDR) (Boucsein 2012). We saw that, on average, slow attentional changes are influenced by the size, length and weight of the tool, probably because larger tools require more executive and perceptual control to integrate proprioceptive and exteroceptive feedbacks into a new body scheme (Maravita and Iriki 2004). However, handaxes trigger more punctual shifts of attention than choppers or normal stones, probably because of their increased shape and their texture complexity. We also used eyetracking to analyse how choppers and handaxes influence our visual exploration patterns, channelling our perceptual behaviour (Silva-Gago et al. 2021, 2022). Even in subjects with no expertise in archaeology, the functional region of the tool (top) and the knapped areas drive more attention than the grasping region (bottom), suggesting that our eyes might be implicitly more interested in a possible function (even in a rough stone tool) than worried about how to handle it. Nevertheless, in handaxes, the grasping region is more explored than choppers, suggesting that their increase in morphological complexity may introduce some grasping issues, when the object is within the grasping range of the body (namely, the *peripersonal space*; Cléry and Ben-Hamed 2018). Interestingly, visual exploration is not influenced by the salient features of the tool (disruption of geometry or

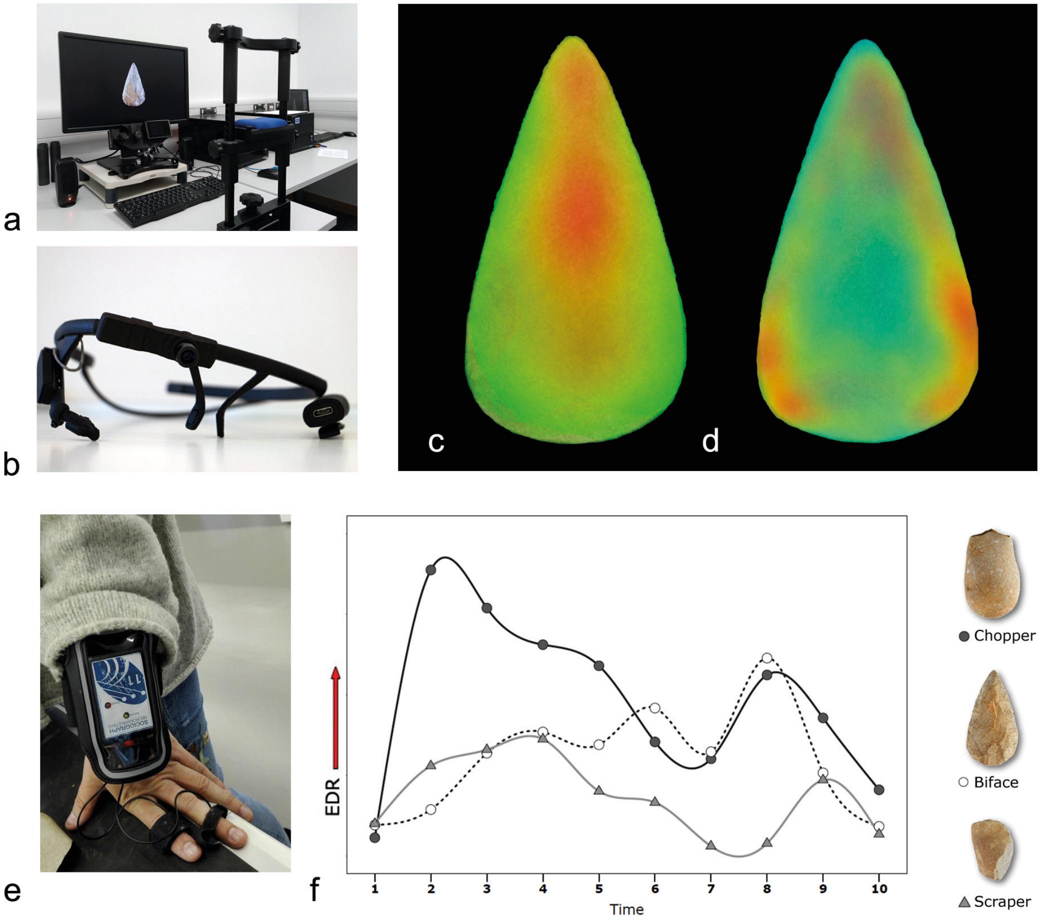

Fig. 4 - Cognitive archaeology investigates behaviours associated with archaeology records through models and methods in psychology. For example, screen-based (a) or portable (b) eyetrackers can be used to investigate the patterns of visual attention triggered by paleolithic tools (c), and compared with the distribution of the salient features of the same objects (d). Also, by using electrodermal devices (e), the fluctuations in attention and arousal can be quantified during the haptic exploration of tools (f). Images redrawn following Bruner et al. 2018c, and Silva-Gago et al. 2022.

texture), stressing that our eyes are particularly programmed for top-down attentional filters, even when exploring rough stone elements. In all these cases, it is worth noting that tool-making and tool-using is not the same as tool-sensing. Sensing is actually the first cognitive interface between brain, body and technology, and it is thought to channel the behavioural response, directly influencing skills and abilities as an active part of the cognitive process. Although these are preliminary surveys, in this sense, they open up new research perspectives on the cognitive aspects involved in our peculiar technological evolution and adaptations.

In sum, a coherent approach in cognitive archaeology includes a preliminary theoretical perspective which takes into account the behavioural evidence as inferred from archaeological remains and current knowledge and models in cognition, and then experimental or quantitative steps aimed at exploring the variables and parameters involved, as well as considering the likelihood of the corresponding hypotheses. Needless to say, conclusions in these fields must be necessarily cautious, and always based on multiple and independent sources of information. In other words, once we propose a theory on cognitive evolution, we should try to find distinct proofs that, from different points of view and for different aspects, converge on the same conclusions. Or, at least, do not reject the proposed scenario, *sensu* Karl Popper.

A natural history of human behaviour

The development of these three fields evidences a welcome progression in the epistemological approach to cognitive evolution and prehistory. The traditional and still most frequent attitude, largely employed in archaeology, is to provide a cognitive interpretation on the simple basis of the observations and personal opinions, sustained by few scattered and general references. In this case, behaviours inferred from the archaeological record are directly used to provide insights into intelligence, language, symbolism, or whatever cognitive ability, without relying on clear definitions or on a specific cognitive theory. Although such extreme speculation is sometimes necessary (and even revealing), problems arise when such personal opinions are presented as robust scientific theories, or even as concluding and firm statements. Alternative scenarios are not even considered, and the final implications are then reduced to a self-confirmed orthodoxy. Unfortunately this approach, which is probably detrimental to the reliability of the field, is still largely employed in both prehistoric and cognitive sciences, and it is supported thanks to a certain isolation of the specialized literature. In fact, a scholar in one field can generally provide a very superficial interpretation in other disciplines, because the specific readership of that field generally lacks a proper criterion to evaluate those contents. Namely, a superficial scenario in human evolution will pass unnoticed in a psychological or medical journal and, in the same way, a superficial approach to cognitive issues will not be criticized in a paleoanthropological publication.

The second stage involves the introduction of a proper cognitive model to frame the interpretation of the archaeological and behavioural data. In this case, the archaeological evidence is fitted into a specific model say in psychology or neurobiology (e.g., on working memory, consciousness, attention and so on) in order to check whether and to what extent we can speculate on the development of a given ability. This approach was already used in the past century, but more employed in recent decades, and it can be seen as the original foundation of the three disciplines presented here. Although the advance is patent, also this stage, as the previous one, is nonetheless theoretical, and conclusions have hence a major speculative background.

The third stage involves, besides a theoretical model to contrast the archaeological data, an additional crucial part: experiments. This stage is the one in which, with all the limitations described above, the three fields step definitely into the realm of scientific hypotheses. Probably, we can say that this stage is just beginning, or at least it is in a very early developmental phase.

Taking into consideration these premises, it may be useful anyway to remind some basics in evolutionary biology, which should be applied also when dealing with cognition and behaviour. A first point concerns evolutionary fitness, a concept which is often forgotten in archaeology or neuroscience. The only parameter considered by evolution and selection is reproductive success and, therefore, a feature must be intended as an "adaptation" only if it increases this factor, namely the number of offspring. For most features, we cannot have the certainty that it is so (this would mean testing species variants with crazy experiments for centuries or more!), but at least a reasonable inference in this sense is required. A major difficulty concerns the fact that most biological or behavioural features are integrated within functional and structural evolutionary and ontogenetic packages linked by pleiotropic and polygenic networks. Therefore, it can be hard to distinguish primary evolutionary changes from secondary consequences, mostly when considering that such consequences *per se* can be neutral, advantageous, or even detrimental. All too often, the term "adaptation" and evolutionary explications are used without any likely information or reasoning on this aspect.

A second comment concerns the fact that the same behaviour can be due to different cognitive mechanisms. The brushy appearance of the human phylogeny suggests that hominids have stemmed from many independent and parallel lineages, so we must assume that different species may present different combinations of cognitive features or abilities. That is, apart from "worst" and "better" cognitive skills, there is the likely possibility of "different" skills. Namely, *Homo erectus* or Neandertals may have had cognitive abilities that we have lost, or never evolved. Also, a specific cognitive domain (like for example attention, working memory, visuospatial integration and so on) is generally formed by different and independent neural routes, and can hence evolve in a mosaic fashion. This means that the evolution of such a domain cannot be understood using a linear or progressive model based on the enhancement of a same capacity. In this sense, our interpretation of the fossil record is definitely biased by our own mental structure. For example, we tend to interpret any behavioural or cultural change in fossil species as the result of a specific reasoning capacity, although it may well be not the case at all. Our fluid reasoning (the reasoning based on intellectual abilities not related to culture) and crystallized reasoning (the reasoning aided by cultural knowledge) are for example strongly rooted in working memory and on the attentional system, so it is unlikely that extinct humans had our same capacity and mental organization, in this sense. As an extreme case, it is even possible that some evolutionary behaviours (including the ones involved in technology) were not based in a reasoning procedure, but instead on empirical approaches, or even on automatic or semi-automatic behavioural chains based on embodied (somatic and perceptual) steps, generated, channelled or influenced by sensorial and partially spontaneous responses, with scarce or null analytical (that is, conscious) components.

A third point, which can be seen as a corollary issue to the former one, concerns the interpretation of the same behaviour in different extinct human species which, for the same reasons explained above, can also be based on different and independent mechanisms. In paleoanthropology, it is very difficult to identify homology in physical traits, and this also applies to behaviours. As with any other feature, also similar behaviours can be due to parallel or convergent evolution. In the former case, similar species which are phylogenetically related and ecologically alike (as all hominids are) can independently generate similar solutions. In the latter, similar evolutionary outputs can be the result of strong selective pressure toward a specific adaptation. In any case, the same behaviour or the same technology in two human lineages should be not taken, *per se*, as evidence of a shared cognitive or cultural background. As always, multiple independent sources of evidence must be considered before presenting a comprehensive scenario on the cognitive evolution of species for which, in general, there are only limited osteological or lithic remains available.

Past and present: the ghost of actualism

The three disciplines briefly presented here (namely, paleoneurology, neuroarchaeology and cognitive archaeology) share a common limitation: they work on extinct taxa by necessarily using, as models, the living ones. In human paleoneurology, endocasts from fossil species are interpreted according to the knowledge we have on the brains of living humans and apes. In neuroarchaeology, the patterns of activation of modern human brains are used to make inference on the cognitive mechanisms of extinct neural systems. In cognitive archaeology, theories and experiments are developed on living subjects, and results are used to extrapolate cognitive scenarios of past minds. These limitations very often lead to two extreme academic reactions. On the one hand, there are scholars who think that, because of the impossibility to investigate cognition directly in fossil species, these fields must be developed on a purely theoretical basis. This perspective, as mentioned, rejects the scientific method, although in most cases the final theoretical proposals are expected (unfairly) to be treated as a scientific issue. On the other hand, there are researchers who think that, because of the impossibility to investigate cognition directly in extinct species, these fields do not merit any attention at all. Of course, a middle position looks instead, at least in my opinion, like a wiser one, namely an approach in which the information available from these disciplines is properly integrated into wider views, taking into account their possibilities and limitations.

Nonetheless, after all, these limitations are not unique or specific to research in prehistory and neuroscience, and it is hence peculiar (and suspect) to see that, in this case, criticisms are particularly harsh. In medicine, mice are often used as models for human physiology. In neurobiology, macaques are frequently used as models for the human brain, not to mention models with worms and sea urchins. In anthropology, chimpanzees have always been used as a model for human evolution, despite the fact they do not represent a human ancestor, but rather a parallel and independent lineage, and are specialized to live in an environment that is radically different from that of early humans. So, apparently, there is no reason to be exceptionally worried about the fact modern humans are used to investigate cognition and behaviour in extinct humans. In taxonomic terms, these species belong to the same genus (*Homo*), and are separated by a short phylogenetic time, when compared with most standards in vertebrate comparative biology. In sum, the problem of actualism must be taken into account, but it seems unreasonable to reject (or to support extreme criticism of) this kind of research.

Conclusion: into the mainstream

Neuroscience and anthropology have a long history of conflicting friendship. Probably, an important difference which has generated cycles of attraction and repulsion between these disciplines is the fact that the former is largely based on reductionist approaches, while the latter is definitely more holistic. In both cases, these two dispositions are often expressed through excesses: those who believe that cognition can be revealed by handling a neuron in a lab, and those depicting complex and speculative scenarios simply by handling a glass of wine on an armchair. Fields like paleoneurology, neuroarchaeology and cognitive archaeology represent a meeting point between these two extremes and, despite initial scepticism, they are presently experiencing a positive academic acceptance.

The main risk, as happens in any young field, is to be dazzled by success. As already mentioned, all too often, in these disciplines there is an excess of theoretical and speculative aspects, when compared with the experimental and quantitative counterpart. Most evolutionary issues concern questions that are hardly testable, very appealing, and inoffensive (in the sense that their conclusions do not influence our welfare and wellbeing). These three characteristics make these fields very sensitive to the fascination of marketing, and it is always tempting to do cheap science for fast vending.

At the same time, the acceptance of new disciplines from the academic system is, as usual, also a matter of personal and institutional interests and limitations, which generate obstacles and barriers when novel fields spread into the community. For example, research in such transversal topics are more difficult to publish in many traditional contexts. Multidisciplinarity is a nice term that is often employed when writing grants and the scopes of journals, but it is easier to spell than to put into practice. Many journals, despite the claims in their aims, are not particularly committed to publishing articles that go beyond the main interests of their academic entourage. Sometimes it can just be a matter of effort, because the editors may have difficulties in managing peer-reviews out of their own competence and expertise. But, in general, it is rather a matter of priorities, priorities from which pioneering issues are simply left out.

Needless to say, all the traits and features investigated in these fields are not of interest only for evolutionary anthropology, but directly bridge evolution with topics in medicine and human biology (Bruner et al. 2014). On the one hand, the information obtained from those research areas directly involves aspects that may be interesting for human health. Many endocranial traits, for example, are more investigated in paleoneurology than in medicine, even though they deal with bone biology, brain development, or the vascular system. For many of these features, we still have scarce information on the functions and variability in our own species, and no information on homology with other primates. At the same time, an evolutionary perspective can supply a different view to understand many pathological conditions or physiological processes, providing alternative interpretations that can offer new insights in diagnostic or clinical fields. Of course, working in such a multidisciplinary way does require additional efforts, which include the management of a vast literature crossing different disciplines, the coordination of teams formed by people with distinct expertise, and the awareness of working beyond the edge: some explorers will find amazing new lands, while others will find nothing interesting, and others will fall to unknown diseases, savage beasts, and hostile tribes. That's life: the real goal is not the destination, but the journey itself.

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