



Are there disciplinary boundaries in the comparative study of primate cognition?

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ABSTRACT

A view continues to gain momentum that regards investigation of the cognition of great apes in captive settings as affording us a model for human cognitive evolution. Researchers from disciplines such as comparative psychology, anthropology, and even archaeology, seem eager to put their theories to the test by using great apes as their chosen experimental model. Questions addressed currently by comparative psychologists have long been the object of attention by neurophysiologists, psychobiologists and neuroscientists, who, however, often use rodents and monkeys as the species of choice. Whereas comparative psychology has been influenced greatly by ethology, much neuroscience has developed against a background of physiology and medicine. This separation of the intellectual contexts wherein they have arisen and flourished has impeded the development of fluid interaction between comparative psychologists and researchers in the other disciplines. We feel that it would be beneficial for comparative psychologists and neuroscientists to combine research endeavours far more often, in order to address common questions of interest related to cognition. We regard interdisciplinary cross-pollination to be particularly desirable, even if many comparative psychologists lack deep expertise about the workings of the brain, and even if many neuroscientists lack expert knowledge about the behaviour of different species. Furthermore, we believe that anthropology, archaeology, human evolutionary studies, and related disciplines, may well provide us with significant contextual knowledge about the physical and temporal background to the evolution in humans of specific cognitive skills. To that end, we urge researchers to dismantle methodological, conceptual and historical disciplinary boundaries, in order to strengthen cross-disciplinary cooperation in order to broaden and deepen our insights into the cognition of nonhuman and human primates.

1. Introduction

The idea of investigating the cognition of great apes in captive settings in order to serve as a model for human cognitive evolution can be traced back to the influential studies of Wolfgang Köhler in the island of Tenerife at the beginning of the twentieth century. Köhler designed a series of very ingenious tool-using experiments that helped him to attribute complex cognitive abilities to chimpanzees, such as the capacity for insightful problem-solving. Much has changed from these literally and figuratively isolated pioneering attempts to gauge the cognitive potential of our closest living relatives, when today we observe the current popularity that chimpanzees enjoy as a model for reconstructing human cognitive evolution. Researchers from various disciplines, including anthropology, neuroscience, philosophy, psychology,

primate ethology, archaeology, economy, linguistics, and even aesthetics (Brosnan, 2021; Fitzpatrick, 2020; Heesen et al., 2019; Luncz et al., 2015; Mühlenbeck et al., 2016) seem eager to put their theories to the test by taking great apes as their experimental model of choice. The scientific press, as well as social media, are especially lured to studies with great apes that investigate what once were thought to be unique human behaviours (e.g., tool-use and tool-making, “theory of mind”, normative understanding, “ritual behaviour”, etc.) and the interest and repercussion of these studies reaches its climax whenever chimpanzees appear to outperform humans. Indeed, reports of individual chimpanzees (e.g., Ayumu) that appeared endowed with extraordinary cognitive abilities (Inoue and Matsuzawa, 2007) rivalling those of humans have made the front page in the media, giving us humans a necessary and timely cure of humility.

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However, the abundance of disciplines that make recourse to great apes in general, and in particular to chimpanzees and bonobos, in order to pursue their scientific interests, not to mention the exponential growth that comparative psychology has undergone since Köhler's day, cries out for theoretical and methodological unitary frameworks that could help to organise and make better sense of the data generated. The current rate of data production is so vertiginous that theoretical models to make sense of these data cannot keep pace with it. This may help to explain the level of mixed results found in studies that allegedly investigate the same cognitive abilities in the same species (e.g., in great apes). The different interpretations of the data obtained in experiments tackling "mental state attribution" and "memory" in chimpanzees is a clear example of this, and a matter of great concern, given its evolutionary significance (for comprehensive reviews see [Manrique and Walker, 2017](#); [Read et al., 2022](#)).

Another factor that may help account for mixed results is the lack of fluid dialogue and effective exchange between disciplines. Although comparative psychology has ancient historical roots ([Dewsbury, 1978, 1984](#)), it is relatively young if we refer only to well-controlled experimental investigations. Therefore, it would be appropriate for contemporary comparative psychologists to drink more often from the deep well of knowledge available from the long-standing disciplines of experimental psychology, neurophysiology/neuroscience, etc., in order to inform their own investigations. With specific regard to cognition as the product of brain activity, it seems especially pertinent to review work conducted by neurophysiologists and neuroscientists. Alas, this happens less often than might have been hoped for. Also, because cognitive skills have been shaped by and are deployed in response to specific environmental challenges, other disciplines such as anthropology and archaeology can provide the necessary physical and temporary context to interpret the behaviour of different species and permit more ecologically-valid interpretations. In the following sections, we present a few illustrative examples whereby closer collaboration between comparative psychologists and experts from other well-established disciplines (e.g., neuroscience and neurophysiology, clinical and/or experimental psychology, anthropology and archaeology) could render the results obtained with different species easier to relate and compare. Moreover, additional valuable information could have been extracted in other experiments were the exchanging of knowledge and techniques between disciplines to have taken place, with only a minor increase in cost. This is not intended as a criticism of any of the disciplines involved, but merely to suggest how closer cross-disciplinary collaboration could bare richer fruits and benefit greatly the progress of science.

2. Potential benefits derived from stronger cross-disciplinary collaboration

2.1. Instances of experimental psychology and neuroscience-related disciplines informing comparative psychology

The first study we analyse had a profound impact in both the scientific community and the social media. This study reported the extraordinary working memory abilities of a juvenile chimpanzee (Ayumu) that appeared to outperform humans in a visuospatial working memory task ([Inoue and Matsuzawa, 2007](#)). In this task, a series of numbers are flashed simultaneously on screen for a very short time, and, as soon as the experimental subject touches the first number of the series, the other numbers are masked, and the chimpanzee has to touch the position the numbers had vacated in ascending order. This task is similar to the Corsi Block Tapping Task (henceforth CBTT), which is a widely-accepted task of visuospatial working memory in humans which is included in the most popular intelligence tests (e.g., Wechsler) (see [Kessels et al., 2000](#)). In the computer adaptation of the CBTT, a series of squares are flashed in random positions on the screen and, as soon as the last square light vanishes, the person whose memory is being measured must touch the position that the squares had vacated in the same order

in which they had previously lit up. Note that in this CBTT computerised version the experimental subject must chain mentally the position occupied by each illuminated square with the position occupied by the next illuminated square until consigning the whole sequence into memory. In stark contrast, all the numbers to be recalled in the Inoue and Matsuzawa task were simultaneously displayed on screen and it was not until the chimpanzee had touched the first number in the series that the remaining numbers were masked. The fact that all numbers to be remembered were shown simultaneously on screen allows an experimental subject to deploy different encoding strategies. Indeed, it is possible to consign to memory a specific shape that connecting the dots could create instead of fixing on the positions of the individual numbers and their order of appearance ([Busch et al., 2005](#)). That strategy is unavailable to participants in the original standardised CBTT because the position on screen of each square is shown discretely and serially, so that never are two (or more) positions revealed at once. Transforming a random array of dots into a single coherent image would be akin to chunking, in that now what needs to be consigned into working memory is a single object (e.g., one chunk of information), instead of several positions (e.g., several objects) on screen, which reduces the load of information to be encoded ([Cowan, 2001, 2010](#)). This fact alone renders the memory task of Inoue and Matsuzawa hardly comparable to the original standardised CBTT ([Busch et al., 2005](#)), casting doubt on whether the adaptation with chimpanzees is a valid measure of their visuospatial working memory. Another reason that renders the results with chimpanzees difficult to compare with previous results is that the experimenters manipulated the time exposure to the to-be recalled numbers, instead of the time elapsed between the disappearance of the numbers and their posterior recollection. Fuster and Alexander registered the activity of prefrontal cortex and dorsomedial thalamic nucleus while rhesus monkeys performed a delayed-response memory task: elevations of electric activity in these areas that followed the disappearance of the stimuli were taken as proof of concept for the existence of working memory ([Fuster and Alexander, 1971](#)). This suggests that elevation of electrical activity in the absence – not in the presence – of the to-be-recalled items is a reliable indicator of working memory. Indeed, traditional studies on memory preferentially target the time elapsed between encoding and recall, since it is assumed that the longer the waiting interval, the bigger the demands posed on memory. Overall, the unorthodox and inflexible administration and adaptation of a classical memory test limits the interpretability and comparability of the results obtained from chimpanzees with regard to those obtained previously from other species.

Another example that illustrates how comparative psychologists and primatologists interested in the study of cognition could benefit further from incorporating previous knowledge accumulated by experimental psychology, neuroscience, and neurophysiology into their research is the study of spatial navigation. The idea of animals forming mental maps that assist open field navigation pioneered by [Tolman \(1948\)](#) challenged the behaviourist reductionist view of memory as a collection of rigid stimulus-response associations, and marked the advent of the cognitive revolution that unfolded subsequently. It is important to note that Tolman did not regard cognitive maps as graphical representations of three-dimensional space, but more broadly as a way of connecting information flexibly to assist reasoning and/or problem solving. This point has been underscored conveniently by other influential authors whose careers have been devoted to investigating how the hippocampus functions ([Eichenbaum, 2017](#); [O'Keefe and Nadel, 1978](#)). Regardless of the notion we may favour as to what constitutes a mental map, what undoubtedly is well-documented is that lesions to the hippocampus hinder the ability of animals (e.g., rats) to find its way in an open field, while seemingly sparing other types of memory (e.g., cued-based recognition, conditioned responses, habit learning, etc.) ([Basile et al., 2020](#); [Bussey et al., 2000](#); [McDonald and White, 2013](#)). The discovery of place cells—cells that fire when the experimental rats occupied specific places in an open field—further strengthened the view that the

hippocampus is critical to spatial navigation (O'Keefe & Dostrovsky, 1971; O'Keefe and Nadel, 1978), notwithstanding its potentially wider involvement in declarative memory and/or flexibility of thinking (Eichenbaum, 2017; O'Keefe and Nadel, 1978).

Researchers in neuroscience and behavioural physiology have investigated spatial navigation extensively by using rats and the Morris water maze as the experimental subject and apparatus of choice, respectively. The basic procedure in these investigations consists of introducing a rat into the maze and registering whether – and how – it escapes the water by reaching a slightly submerged platform. The platform is not directly visible as the water is intentionally tainted and the rat needs to rely on allocentric cues in order to place it. An important distinction is made, regarding how the experimental subject learns to locate the platform, between using a visible landmark placed in the immediate vicinity (e.g., a flag on top of the platform), or triangulating its position on the maze based on the location of various external stimuli present in the experimental room. The first strategy hardly requires spatial orientation skills as the rat needs only to direct its head toward the visible landmark and keep track of whether its trajectory deviates from the established course while assisted by visual, proprioceptive and sensorimotor self-generated feedback. On the other hand, triangulation of distal cues to locate the submerged platform requires some spatial representation of the layout. Supporting this idea, lesions of the hippocampal system have dramatic effects on the ability to locate the platform by using the external cues (allocentric task), but do not preclude the ability to find the target location by relying on a visible landmark positioned next to the platform (response learning or egocentric task) (de Bruin et al., 2001; Rice et al., 2015). Controls here are mandatory to discern whether rats use one strategy or the other in order to locate the target platform. Such controls consist of using curtains to block visual access to allocentric cues, or removing them entirely, in order to establish whether rats are still able to locate the submerged platform, and of shifting the position of these cues or of the maze by some degrees in order to determine whether spatial orientation is disrupted accordingly. If these manipulations hinder performance, then generally it is assumed that the rats were using external cues to guide their behaviour and that their performance relied heavily on the integrity of the hippocampal system. If, on the other hand, the manipulations have little effect on performance, then the task is likely to require a taxon system and generally is regarded as a response learning task. In recent times, primatologists and comparative psychologists have shown great interest in exploring spatial orientation/navigation in great apes both in the wild (Ban et al., 2019; Janmaat et al., 2013; Normand and Boesch, 2009) and in captive settings (Mendes and Call, 2014; Menzel et al., 2002). In line with what we have described for the studies that used rats as the experimental subject, researchers that investigate spatial navigation in apes correctly differentiate between, on the one hand, finding a target position by relying on discrete cues in the environment that signal a specific location, and, on the other, deploying strategies that require consideration of the spatial layout of the environment, for instance by exploiting its geometry or by a configuration of distal landmarks (Janmaat et al., 2013; Kanngiesser and Call, 2010; Mendes and Call, 2014; Menzel et al., 2002). However, these studies often lack relevant additional controls in order to confirm the use of distal landmarks or of the spatial layout representation of the environment for finding the target locations. We briefly discuss a study by Menzel et al. (2002) to illustrate this point. The experiment by Menzel and colleagues intended to investigate the ability of a young bonobo named Kanzi to use lexigram information in order to find specific locations in an enclosure of woodland. They cite Muller et al. (1996, p. 669) in proposing that “*the ability to find a straight-line path between any pair of points in the environment, so that any point can serve as a starting location and any other point can serve as a goal*” is positive evidence for the ability to form cognitive maps in animals. In their study, Menzel and colleagues used signs posted in different locations within the enclosure in order to indicate to Kanzi where to find a desired object (food or toy) by means of lexigrams.

Success in finding the designated objects above chance level was taken as evidence of Kanzi's spatial navigation skill. The authors acknowledged that Kanzi's route from each starting location to the goal location was never a straight line, which would have provided evidence that the bonobo had formed a mental map of the layout. Instead, he made some detours, but overall was able to find the target locations in a seemingly efficient manner. When inspecting the different routes taken by Kanzi in order to find the target locations, there was found to be extensive overlapping with humanly-made trails, which opens the possibility that Kanzi was using visual discrete features of the environment in order to find the designated locations. All in all, it is difficult to tell whether Kanzi had formed a mental representation (e.g., cognitive map) of the environment that had helped him to connect two distant points at any given time (his position and that of the goal location) or else had learned to follow paths until approaching the intended location and then used visual inspection to locate the target objects. The doubts could have been resolved if, as is systematically done with rats, a control condition had been implemented that rendered as uninformative any feature landmarks that were immediately accessible. For instance, several trials could have been run in which the human trails had been eliminated or otherwise altered in order to force Kanzi to use the geometry of the enclosure or distal landmarks in order to find his way to the goal locations. If he had managed to find the locations despite the trails having been erased, this would have offered incontrovertible evidence that Kanzi had been able to form mental maps of the enclosure which allowed him to navigate it spatially, in a manner resembling what is termed “survey” or “metrical” navigation. This is way-finding at its most sophisticated, consisting of organising and relating all known locations in a common framework of reference (Franz and Mallot, 2000; Trullier et al., 1997), which is precisely what Tolman considered necessary in order to form a cognitive map (Tolman, 1948).

Another study by Mendes and Call (2014) investigated the capacity of chimpanzees to remember different food locations after minimal exposure (1–2 trials), both after 24 h and after 3-months. The researchers hid three bananas in a non-directly visible spot of the indoor enclosure (an area resembling a wood, with different types of trees and vegetation) into which they released the chimpanzees in pairs. They waited until the chimpanzees had found the hiding place. Then they tested whether chimpanzees remembered the location of the hideaway by running additional trials with the bananas hidden in the same spot. The results showed that chimpanzees could find the hiding place even when three months had elapsed, if provided with the appropriate cues (presence of the experimenter in a look-out) that signalled that there were bananas to be found in the enclosure. We believe that this study is well-designed and well-conducted and the results are appropriate and informative. We think, however, that useful information regarding the way the chimpanzees found the bananas could be obtained by running a follow-up study or including additional control conditions in the initial experiment. The external cues in the water maze helped to decide whether rats orientate spatially or else use visual landmarks positioned on the submerged platform. In a similar way, distinctive and very ostensible new features (e.g., high posts with coloured flags) could be added to the indoor enclosure in the experiment by Mendes and Call that, in triangulation with the position of the bananas, could give away the hiding places. When chimpanzees show proficiency in finding the bananas several manipulations could be implemented, such as changing the starting position of the apes or rotating the position of the posts in order to see whether those changes affect the ability to find the hideouts. Mendes and Call did not run these additional control conditions because their experimental question was whether the apes found the bananas after long spans of time had elapsed, yet knowing the searching strategies of the chimpanzees and whether they were feature-orientated or spatially-orientated would be extremely informative. To the best of our knowledge, no study on spatial navigation with apes conducted in a natural or semi-natural environment has ever used control conditions in order to find out which specific strategy apes deploy in order to find

their way, and researchers almost invariably end up making informed guesses. In stark contrast, running this control condition is almost mandatory when investigating spatial navigation in rats in the laboratory. We think that if there was fluid dialogue between neuroscientists/neurophysiologists and comparative psychologists or, better still, if they worked in collaboration, then the experimental designs could be enriched further in order to extract additional valuable information when testing new animal species.

2.2. Comparative psychology and ethology informing experimental psychology and neuroscience

The emergence of the genetic revolution and the characterisation and successful implementation of genomic tools to manipulate genetic sequences, such as epigenetic and combinatorial systems for gene expression, gene silencing techniques, and optogenetics, has advanced research in behavioural neuroscience significantly in the last two decades. However, such tools have been developed in but a limited number of species, thus reducing the generalisability and applicability of the findings. The problems of the model species approach, most typically exemplified in studies in behavioural neuroscience, have been accentuated for practical reasons, including the fact that small animals, such as *Drosophila* and mice, are more economical and easier to breed and maintain in colonies in large numbers. However impractical it may be to study complex behaviour and to develop modern neuroscience techniques for a wider range of animal species, it is important to enhance awareness of such limitations and potential pitfalls, of which there are many examples, in order to stimulate an enriched dialogue between comparative psychologists, ethologists, and behavioural neuroscientists. Indeed, many important breakthroughs, leading to transformative technical advancements or greater understanding of the molecular and neural mechanisms mediating complex behaviour, have been sparked by the use of “unconventional” species. For example, the work of Sir Alan Hodgkin and Sir Andrew Huxley in the squid led to the discovery of the neuronal basis of cellular communication (Hodgkin and Huxley, 1952). The research of Eric R. Kandel in *Aplysia californica* broke new ground in understanding the molecular basis of sensory habituation, long-term facilitation, classical conditioning and memory storage and recall (Hawkins et al., 2006; Kandel et al., 2014). Furthermore, the observation that certain proteins in green algae control movement in response to light led to the more recent discovery of optogenetics, an invention widely attributed to Ed Boyden and Karl Deisseroth (Boyden et al., 2005) but advanced by Zhuo-Hua Pan in a paper submitted in 2004 and later published in 2006 (Bi et al., 2006). Optogenetics is a revolutionary technique that allows genetic manipulations to turn neurons and circuits on and off *in vivo*, thus revealing how neurons connect and contribute to complex behaviour. Such discoveries in alternative model systems indicate that the concentration of research around a single model system could lead neuroscientists to miss out on important technical and conceptual innovations. Moreover, there is the additional problem of specialisation. Complex neural systems mediating high-order perception and complex function, such as high-level vision and social behaviour, are highly specialised, and often popular animal model systems, involving mice, rats, or pigeons, are re-purposed in order to study such processes, owing to practical and budgetary considerations, though the species may be far from ideal for such studies. There are, for example, notable difficulties in trying to force a square block through a round hole, and a good example of this is the study of vision in rodent models due to the poor visual acuity of rats and mice, and their poorly developed visual cortex (Baker, 2013). Similarly, the study of social behaviour in model species such as rodents is severely hampered by loss of genetic diversity in captivity and by the limited social interaction afforded by laboratories and animal facilities in general. It has been shown that humanly-driven artificial selection, inbreeding, and adaptation to captivity, in mice have led to the loss of many important behavioural traits that are exhibited by mice in the wild, with a greater

loss in females than in males (Chalfin et al., 2014). Thus, it is vital that behavioural neuroscientists recognise the importance of taking a more rigorous ethological approach that involves comparison to the same species and other species, both in the laboratory and in the wild. There are risks in relying on a single, or even a few, model species in order to establish firm conclusions about brain-behaviour relationships. In addition to the differences already alluded to between laboratory mice and mice in the wild, there are, for example more than 30 species of mouse, and some 2000 species of rodents, each with different sensory capabilities, natural history and behavioural characteristics. Therefore, such phenotypical diversity should also be taken into consideration in the inference process.

Although the degree of technical and conceptual refinement of modern neuroscience should not be underestimated, the selective study of a limited number of animal species may lead to the conclusion that shared genetic, molecular and neural mechanisms are responsible for regulating specific behaviours. There are numerous examples where the interplay between neuroscience, ethology and comparative psychology has shed light on interspecific differences, one of which involves the neural representation of space. Edvard Moser and collaborators showed that rat entorhinal cortex contains a directionally-orientated, topographically organised map of the surrounding space, with its unit being the grid cell, which is activated when the position of the animal coincides with any vertex of a grid representing the environment (Hafting et al., 2005). These authors demonstrated that in the rat such grid representations seem to require theta band (4–10 Hz) oscillations, such that interference between somatic and dendritic theta-band oscillations in single neurons transforms a temporal oscillation into a spatially periodic grid. However, when similar studies were conducted in the Egyptian bat (*Rousettus aegyptiacus*), an animal with an exquisite ability to localise objects in three-dimensional space, the results were different. Nachum Ulanovsky and colleagues showed that grid cells in the bat medial entorhinal cortex might exist without theta oscillations and with almost no theta modulation of grid-cell spiking, which is also required in rat-derived oscillatory interference models (Yartsev et al., 2011). This study highlights the importance of using a comparative perspective when testing hypotheses and building mechanistic models of brain function to predict behaviour.

Another excellent example of how the adoption of a comparative, more ecologically-relevant approach has led to significant advances in behavioural neuroscience can be found in the area of social affiliation and social bonding. Findings in laboratory rats in the 1980s showed that the hormone oxytocin was necessary for inducing maternal behaviour (Fährbach et al., 1984). Although laboratory rodents are not an ideal species for the study of social bonds owing to their polygamous phenotype, this early work inspired the research groups of Sue Carter and Tom Insel to turn to the prairie vole in order to study the neural basis of attachment (Carter et al., 1995; Insel et al., 1997). The vole is a mouse-size rodent found in the Midwest of North America, of which there are several species, including montane and prairie voles. These two species share 99% of their genetic code, yet they exhibit radically different social behaviours. The montane vole is a loner, nests in isolation and does not form pair bonds after mating, breeding promiscuously. In sharp contrast, the prairie vole forms long-lasting pair bonds after mating, males and females cooperate in nest building and the care of their offspring. Female prairie voles prefer the company of their partner to others, whereas males display aggressive behaviour towards other males after mating has occurred. The successful exploration of this model revealed that such remarkable differences are indeed related to the actions of oxytocin, in females, and vasopressin, in males, paving the way for many discoveries on the role of these peptide hormones in sexual behaviour, attachment, territorial behaviour, aggression, and social memory.

To end this section, we should like to emphasise the point that it is of capital importance to administer behavioural tests that are meaningful to the species under investigation. As Krakauer et al. (2017) eloquently

argue, “neuroscience needs behaviour”. Neural activation *per se* does not possess any explanatory value, unless we are able to relate this activation to an external behavioural output that ultimately lends itself to interpretation in terms of adaptive fitness or survival value. As the authors put it: “it is very hard to infer the mapping between the behavior of a system and its lower-level properties by only looking at the lower-level properties ... When we ask, “How does the brain generate behavior, ‘we are primarily asking about how putative processing modules are organized so that they combine to generate behavior in a particular task environment. Relying solely on the collection of neural data, with behavior incorporated as an after-thought ... will not lead to meaningful answers. This is a question best answered through precise hypotheses articulated in an a priori conceptual framework, careful task design, and the collection of behavioural data” (Krakauer et al., 2017, p. 481). Borrowing another example from Krakauer et al. (2017): “... once we agree that bird flight is an adaptive behavior, we then determine that it flies by flapping its wings and not by wiggling its feet. Once we have worked this out, we can start studying the feathers that make up the wing. Seen this way, understanding that the flapping of wings is critical to flight aids the subsequent study of feathers. It is unlikely that, from the outset, studying an ostrich feather in isolation would lead to the conclusion that there is such a phenomenon as flight or even that feather-like structures would be useful for flight” (Krakauer et al., 2017, p.485). What we want to press home by using these analogies is the need to put behaviour at the forefront of any experimental endeavour. It is only when we focus on the higher-level emergent properties of a complex system (e.g., behaviour) that we can make proper sense of its lower-level properties (e.g., neural activation). The main distinction is perhaps one between describing and understanding. Neuroscience can be extremely useful in describing the properties of the brain and how the orchestrated activation of millions of neurons takes place, yet true understanding only comes from considering the behaviour that this activity is supporting, and by considering it in relation to the specific situational demands. This brings us to another important question that Krakauer et al. (2017) brought up in their paper. What can we consider a meaningful behaviour? The response triggered by a discrete stimulus (e.g., flash of light or beeping sound) presented to an animal in a laboratory is not necessarily a meaningful behaviour, unless it is placed in a significant context that accentuates its perceivable utility (e.g., adaptive value). Therefore, we need to strive to provide the species under investigation with enriched environments in which the target responses triggered are commensurable and functionally equivalent to the ones elicited in their natural habitats.

A good example signalling the importance of investigating the behaviour of a species in a meaningful context is the “active vision” attributed to wild marmosets in capturing their prey. In a remarkable display of both ingenuity and technical dexterity Ngo and colleagues (Ngo et al., 2022) monitored how marmosets visually track and capture their prey in their natural habitat. What they discovered is that vision is not a source of information that is deployed passively in order to calculate/adjust the movements to be executed in a ballistic grasp prior to launching it. Instead, the dynamical biomechanical movements executed during hunting are integral to active vision, and the changes in positional behaviour serve to optimise the tracking of the prey. This discovery would have been impossible in an impoverished laboratory setting and was achieved only because all the elements that form an integral part of the hunting episode (e.g., substrates on which hunter and prey stand, differing behaviour of the insects marmosets prey upon, etc.) were considered and analysed simultaneously.

To sum up, there is, as mentioned above, a risk in considering as universally valid that research in behavioural neuroscience which is conducted on a single animal model, and often on a single sex. The comparative approach, which recognises that each species has its own behavioural phenotypes, natural environment and neural architecture and processes, could help behavioural neuroscience research in the process of characterising the neural and molecular bases of behaviour. At a practical level, this would involve the systematic testing of

behaviour in multiple animal species and the design of behavioural tasks specifically tailored to the animal species under consideration on the basis of their unique specialisations, natural tendencies and preferences. We would most certainly recommend that behavioural neuroscientists develop a working knowledge of the natural habitats, phylogeny and natural behaviour of the species under investigation and forge collaborations with comparative psychologists and ethologists to design more ecologically-valid and informative experiments.

2.3. How anthropology, archaeology and related disciplines can help comparative psychology and neuroscience to frame cognitive development in its appropriate ecological and evolutionary time context

The cognitive revolution that began in the 1950’s was greatly influenced by computer science and theoretical linguistics, and hence made use of – and perhaps even abused – the metaphor of the computer in order to represent the way our mind operates (see Fodor, 1975; Searle, 1980). The emphasis was placed on both processing of information and mental representation. In like vein, David Marr (1982) – who specialised in visual processing – proposed three levels of analysis in order to understand how information processing systems (e.g., the brain) work: 1) the computational level, specifying the goals; 2) the level of representation, along with the algorithms specifying the rules to transform inputs into outputs; and 3) the hardware implementation level, or how algorithm and representation can be realised physically. Taken to an extreme, this view neglected the context in which information is obtained, or how the information (e.g., which sensory modality) is introduced into the system (e.g., brain) in a way reminiscent of the Cartesian dualism, whereby the mind can be isolated from both the body and the environment. Perhaps as a reaction to this extreme “representationalist” approach to cognition new theories have emerged that can be ascribed to the 4Es’ cognition (e.g., Embodied, Embedded, Enactive, Extended), where cognition is regarded the product of the whole body and the situation in which that body finds itself in relation to the surrounding environment (e.g., Gibson, 1979; Hutchins, 1995; Lakoff and Johnson, 1982; Varela et al., 1991). The most iconic theory illustrating this non-representationalist take on cognition is perhaps the ecological approach to vision by Gibson (1979). In Gibson’s view, action and perception are not to be regarded as separate processes; on the contrary, they are jointly deployed to extract ecological information and exploit it in order to achieve adaptive fitness. Central to this theory is the concept of “affordances”, which are the actions that the environment and/or objects afford by virtue of their physical properties and how these relate to a specific acting agent. For instance, a handle affords the action of grasping ... It is important to point out that the same object can afford different actions in relation to different agents, or even different actions in relation to the same agent while experiencing different motivational states; thus, an apple can afford to be bitten by a hungry individual, yet thrown as a projectile by the same – “angry” – individual after enjoying a copious meal. The emphasis therefore is in the situational complementarity agent-environment. While affordances can be identified mostly perceptually, they are realised through action, hence the perception-action inseparability defended by Gibson. This ecological approach to psychology pioneered attempts to overcome the ecology-psychology dichotomy. We shall come back to this later in order to describe recent archaeological accounts that bear a Gibsonian flavour. Before that, however, we introduce some proposals originating in anthropology/archaeology that attempt to infer major evolutionary cognitive changes through the monitoring of changes in tool-making complexity. Coolidge and Wynn (2005) take combined evidence linking executive function to a few pairs of alleles, and the explosion in technological and cultural complexity observed in modern humans, in order to hypothesise that a single additive genetic mutation occurring some 60,000 to 130,000 years ago boosted human working memory capacity. Whether this singular mutation ever occurred, or, on the contrary, the increase in working memory was somewhat more gradual,

it is undeniable that working memory plays an important part in characterising human modern cognition (see Read et al., 2022). Therefore, it makes sense to try to infer changes in the working memory of our human ancestors as well as to measure it in extant non-human primates through exploring tool-use and tool-making abilities. In this vein, Matsuzawa (1996) borrowed from grammatical analysis of sentences (Chomsky, 1969, 2002) in order to infer cognitive complexity (e.g., akin to working memory) associated to nut-cracking in chimpanzees and used tree-structures to calculate the number of interdependent objects or concepts that have to be held simultaneously and related to each other. Thus, he attributed the highest level of cognitive complexity (Level 3) to instances of nut-cracking where a wedge stone must first be used to stabilise an anvil stone, then the wedge and the anvil together have to be associated with the nut, and finally the resulting combination of the three objects have to be related to the hammer stone. This traditional approach to cognition, classically adopted by archaeology, applies what we might call reverse engineering, through which complexity of the tool implements handled or produced by a species is a reflection of the complexity of the user/maker's mind. Recently, new enactivist/situated/embodied approaches have gained popularity among archaeologists that challenge the representationalist view of cognition. For instance, Lambros Malafouris (2013) introduces his Material Engagement Theory (MET) that is both ecological and enactivist, and contends that in the context of stone-knapping it is not possible to separate mind from body from environment. He questions the unidirectional assumption that mind creates technology and discusses how technology also shapes the mind. In his own words: "... I understand the impact of tool making not in a selectionist or computational sense ... Rather, I understand it in the enactive sense of learning to move with and think with through the materiality of stone ..." (Malafouris, 2021, p.4). Similarly, he coins the term creative "thinging" (Malafouris, 2014) that refers to thinking through, with and about things. He considers that this thinking through and with things comes earlier ontogenetically and evolutionarily than thinking about things (Malafouris, 2021). Material Engagement Theory is proposed to be equally useful in order to understand nonhuman primate cognition based on the same central tenets, that is, that tool use and/or manufacture are not a mere reflection and result of the cognitive skills of the user/maker but are an integral part of the process of thinking (Mosley, 2021). To end this section, we shall introduce two approaches to the study of cognition that we find difficult to ascribe to a specific school of thought, but that we feel might be useful to all disciplines involved in the comparative and evolutionary study of cognition. The first is an ingenious approach to cognition, that we could refer to as "distributed cognition," applied in bonobos by Johnson and Oswald (2001), in order to investigate the use of conspecifics as tools to influence third-parties. In their study, they recorded the behaviour of 6 bonobos and then conducted micro-analysis of 16 videos segments. They observed how the overt behaviour of individual A was directed toward B, yet caused a reaction in C. This could constitute an instance of social tool use that the authors deemed comparable to multi-tasking. What we find enticing in this study is that focal observations of target triads might have revealed nothing of interest. It was precisely by targeting the whole group and micro-analysing their behaviour individually in relation to the behaviour of all other members of the group that highlighted the critical triadic relationships. Thus, the behaviour of A toward B that caused a reaction in C was only revealed because the behaviours of the *apparently* non-interacting individuals A and C were in synchrony. This study is a salutary reminder that social complex interactions might occur in spans of space and/or time that cannot be easily apprehended and/or monitored in captivity, and therefore a distributed cognition approach can be of use to complement the data obtained in the laboratory in order to capture the bigger picture.

Finally, we introduce active inference, a conceptual framework that we find useful for the analysis of behaviour in response to environmental demands. Succinctly stated, according to active inference theories about cerebral functioning, what is generated by the mind/brain of a sentient

creature tends to be projected forwards in time. In other words, a brain/mind incessantly predicts what likely will happen next, working as if on the Bayesian probabilistic principles of Likelihood Analysis. Therefore, a brain is not perceiving the world in the sense of building up an image of external reality in response to received sensory information. Instead, it is working the other way round: a brain builds the world outside it, before receiving or evaluating sensory information; thus, it anticipates a lived world, and then, when it samples the environment, the sensory information gathered is used to check whether its predictions hold true. Metaphorically speaking, the brain does something akin to updating a map. You do not draw a new map from scratch every time you want to include an update; instead, you superimpose on your old map what you now see, and draw on it some new feature (e.g., a new road). Doing that spares you from having to make an entire map anew: it saves you time and, most crucially, energy, namely, biophysical energy that otherwise would have to have been spent by the neurobiological activity of neurones. As part of the active inference framework, The Free Energy principle (FEP), developed by Karl Friston aspires to unify the psychological, neural and adaptive nature of living beings (Friston, 2010). While other Bayesian brain theories imply that adaptive fitness comes mainly from updating top-down predictions in response to bottom-up incoming sensory information, the FEP offers an alternative way whereby sentient creatures can achieve fitness, which is predicated in the reduction of *entropy* through action, where entropy has the meaning as defined in thermodynamics, and in this context is roughly equivalent to the discrepancy between expectations and reality. The FEP proposes that sentient creatures act so as to reduce entropy (e.g., surprisal in information theory) in their exchanges with their ecoiniche. A straightforward way to reduce entropy is to visit repeatedly a limited number of states, which could most likely be achieved by restricting behaviour to a few prototypical responses (e.g., responses typical of the species). If a set of responses has developed in a specific ecoiniche, they likely are the ones that will produce predictable outcomes and therefore those that generate minimum levels of entropy (e.g., cognitive surprisal). Recently, we have applied this logic to offer an alternative explanation to why innovation does not translate in cumulative technological complexity in chimpanzees (Manrique and Walker, 2023). We propose the existence of 'Zones of Bounded Surprisal' (ZBS), and by this concept we imply that whenever one does something new (innovate) this induces cognitive surprise in conspecifics. If the cognitive surprise is small, it may fall inside the ZBS of the observer, and hence may be registered and adopted. Once copied, an invention can spread horizontally in space and even vertically in time, and can be combined with other new innovative or inventive behaviours that may lead to cultural accumulation by "ratcheting-up". Chimpanzees and other great apes show considerable limitations in their ability, or 'Zone of Bounded Surprisal', to overcome cognitive surprisal induced by innovative or unorthodox behaviour, and hence their chances of developing complex technology are rather limited. This is but an example of how the FEP provides a framework appropriate to generate hypotheses related to individual-ecoiniche adaptations that could be useful to psychology, physical anthropology and archaeology.

3. Conclusions

We advocate a more fluid dialogue and exchange between researchers from different disciplines, which are true to the spirit of science in building cumulative knowledge and working together to solve common problems. We advocate specifically for a closer collaboration between neuroscientists (i.e., neurophysiologists, psychobiologists, neuropsychologists, etc.) and comparative psychologists, anthropologists and archaeologists interested in the comparative and evolutionary study of cognition. Because cognition is the product of brain activity it is natural for the comparative investigation of cognition to give pride of place to the brain structure and its functioning, in order to design experiments and interpret the data produced. We cannot ask comparative

psychologists to have deep expertise on the workings of the brain, nor can we ask that neuroscientists have expert knowledge on the behaviour of different species, yet we can expect both to work together so that both disciplines are cross-pollinated. The most promising way to advance in the comparative study of cognition is by joining forces with different disciplines that tackle common questions. Also, cognition is not something that happens in the void, a gratuitous expression of the computational power of our brains, yet a response to specific environmental demands, be they ecological, social or both. The ec niche can be determinant in shaping cognition, and hence it is important that anthropology, archaeology, and related disciplines, provide the appropriate background evolutionary context to help us to understand how different human cognitive skills might have originated and what specific survival challenges they were meant to solve. We want to finish by stating that some of the studies discussed here have been selected because they deal with memory, which is one of the topics with the longest tradition of experimental research. The spatial memory studies we picked were well-designed and well-executed, and the interpretation of the data was sound. Overall, they are highly informative and valuable. In fact, we are well aware that administering the control conditions required to identify the navigational strategy deployed by the apes would be very challenging and costly to implement in a semi-natural environment; in stark contrast, running additional controls in the studies with rodents is a straightforward process. Our aim is to highlight that for one specific discipline, interested in the comparative and evolutionary study of cognition, to borrow knowledge from other disciplines might not be enough; it would be preferable to put together multidisciplinary teams to tackle specific questions. We are aware that people belonging to different research teams may not always blend well, owing to personal inclinations, perceived competition, and/or lack of a shared jargon, yet we believe that it would be worthwhile to set differences apart, focus on shared goals, and collaborate more often. The proof of our commitment for a closer collaboration between disciplines is the fact that the signers of this piece belong to comparative psychology and neuroscience, respectively.

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CRedit authorship contribution statement

Héctor M. Manrique: Conceptualization, Writing – original draft, was responsible for the conceptualization of the MS and of producing a first preliminary draft. **Juan J. Canales:** took responsibility of developing the manuscript sections more directly related to neuroscience. Both authors contributed similarly to the writing of the final draft.

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