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On the significance of biogenic approach in comparative cognition

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ABSTRACT

Comparative cognition is an interdisciplinary field of animal behavior, inherently premised on varying foundational perspectives, whether researchers acknowledge it or not. The distinction between anthropogenic and biogenic approaches serves as a useful framework for categorizing the two primary starting points in cognitive research. Based on these classifications, it becomes evident that comparative cognition research incorporates elements of both approaches. Based on empirical research on comparative cognition, it can be observed that comparative cognition tends to be biased towards the anthropogenic approach. While we do not advocate for abandoning the anthropogenic approach, embracing the biogenic approach offers substantial advantages. These advantages include not only practical benefits such as increased empirical research productivity but also significant intellectual gains. Although the biogenic approach does not imply a commitment to a specific philosophy, it shares a high degree of affinity with embodied cognition. We, thus, further suggest that the biogenic approach to comparative cognition can effectively align with the recent trends in ecological psychology and enactivism. Such a shift in approach has the potential to reshape the formulation of research questions and influence the underlying ontological commitments driving the research.

1. Introduction

Comparative psychology has a relatively long-standing history within the field. During the course of its history, various conceptual positions diverged to shape the field. In the standard history of psychology, Romanes is credited with founding the field (Romanes, 1884). However, comparative psychological research existed prior to Romanes (d'Isa and Abramson, 2023). Among this early work, some, like Romanes, inferred animal intelligence from anecdotal observations of animal behavior, while other studies employed experimental methods. Romanes' reliance on anecdotal evidence was quickly criticized, leading to an emphasis on the importance of experimental research (Morgan, 1903). This emphasis on experimentation persisted even after its introduction to the United States, where it aligned with the subsequent rise of behaviorism (Thorndike, 1911/2000; Watson, 1913). Furthermore, comparative psychology has been deeply influenced by European-born ethology (Griffin, 1978). Although this is a rough overview, it highlights that comparative psychology did not emerge from a single discipline but rather represents a heterogeneous field that deals with animal behavior. Indeed, a glance at contemporary textbooks on comparative psychology reveals an approach that is unbound by any specific methodology, framework, or philosophical stance (e.g., Papini, 2020; Shettleworth, 2009a) (see Table 1).

Since the advent of cognitive science, this field has increasingly been referred to as comparative cognition (Wasserman, 1993). It encompasses a diverse range of areas related to animal cognition, described as "an interdisciplinary field bringing together tools from ecology, ethology, cognitive science, developmental psychology, evolutionary biology, and neuroscience, among others " (Shettleworth, 2009b). The concept of cognition here remains largely consistent with Neisser's (1967) classical definition to study human cognition, and refers to "the mechanisms by which animals acquire, process, store and act upon information from the environment" (Shettleworth, 2009a, p. 4). As the interdisciplinary nature of this field suggests, it is not founded upon a single methodology, conceptual framework, or philosophical position. This stands in contrast to fields such as ecological psychology, which adopts a direct perception as the fundamental theory, or behavior analysis, where radical behaviorism remains central (Gibson, 1979/2014; Skinner, 1974). Note that these fields include pluralistic positions and are not committed to a very monolithic doctrine within each field (Bruineberg et al., 2023; Yanagawa & Matsui, 2025; Zilio & Carrara, 2021). Nevertheless, there are some root assumptions, such as

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the rejection of an anti-representationalism stance. This internal consistency diverges from the conceptual heterogeneity found in comparative cognition.

However, the absence of a central framework does not imply that comparative cognition is devoid of any philosophical and conceptual grounding to approach cognition of animals. We believe that Lyon's (2006) distinction between anthropogenic and biogenic approaches is useful for clarifying the traditional approaches within comparative psychology. She argued that it is beneficial to categorize cognitive research approaches into these two families. As we will elaborate later, these approaches differ primarily in whether the starting point of cognitive research is centered on humans or on other organisms. These differences give rise to various perspectives on cognition, specific research methods, interpretations, and the ideas that are emphasized. Although comparative cognition is an interdisciplinary field, the ways in which these two approaches function have not been systematically organized. Additionally, while Lyon (2006) advocated for the necessity of the biogenic approach in cognitive research, its practical scientific and philosophical significance within the specific domain of comparative cognition is not self-evident.

In this paper, thus, we first point out that although both approaches coexist in comparative cognition research, though there is a bias towards the anthropogenic approach. The subsequent two sections will touch upon the anthropogenic and biogenic approaches observed in comparative cognition. Following this, we will highlight the utility of the biogenic approach and discuss how it relates to other philosophical stances such as ecological psychology and enactivism. In the final section, we will examine the potential concerns regarding the biogenic approach to comparative cognition. Through these discussions, we aim to emphasize the significance of the biogenic approach in comparative cognition, arguing that it contributes to the scientific implementation of ecological-enactive direction and facilitates the advancement of comparative cognition research.

2. The anthropogenic approach and its ubiquity in animal cognition

The anthropogenic approach studies cognition by using human cognition as the reference point. Lyon (2006) defines this approach as follows:

> "I call the tradition that takes the human case as its starting point for the study of cognition the anthropogenic approach (from the Greek; literally, human + birth, origin)" (p. 12)

What does it mean to use human cognition as a "starting point"? Lyon (2006) highlights the cognitivist research program as a typical example of this approach. This program fundamentally conceptualizes cognition as internal information processing realized by the nervous system, where representations are formed to guide behavior. This perspective inherently includes computationalism—the notion that cognition is a computational process within the skin—and representationalism, which posits that mental representations are internally manipulated and transformed to produce behavior. In comparative cognition, the anthropogenic approach can be understood as a research tactic that begins by applying concepts of human cognition to the study of a specific species.

As this definition suggests, research that applies the traditional framework of cognitive science to animals almost invariably adopts the anthropogenic approach. For instance, cognitive concepts such as memory and attention, operationalized in human cognitive psychology, are subjected to experimental investigation in animals as well (e.g., Blough, 1991; Castro & Larsen, 1992). Moreover, many studies extend "higher cognition", seemingly unique in human, to animals. A representative example can be found in the investigation of theory of mind in chimpanzees, exploring their ability to engage in mind-reading (Call & Tomasello, 2008). Other concepts like prospective reasoning (Evans & Beran, 2012), episodic memory (Clayton & Dickinson, 1998), metacognition (Goto & Watanabe, 2012), causal reasoning (Blaisdell, Sawa, Leising & Waldmann, 2006), and cognitive flexibility (Kehagia et al., 2010) are also prime examples of higher cognition. Beyond laboratory-tested cognition, similar efforts to transpose human mental concepts to animals can be seen in studies on animal personality or behavioral syndromes (e.g., Cabrera et al., 2021). While these studies encompass a variety of cognitive concepts applied across several taxa, the researchers started framing their questions using mental terms reflective of human cognition.

Specifically, common features of the anthropogenic studies on comparative cognition include: (1) addressing concepts that are widely accepted in human cognitive research; (2) employing operationalizations of these concepts first developed in human cognitive psychology; and (3) devising and applying analogous tasks to different animal species based on these operationalizations. These characteristics collectively exemplify the scientific practice of the anthropogenic approach, as they clearly take humans as the starting point for measuring animal capabilities. This practice implicitly assumes that such operationalized concepts, when appropriately controlled and adapted, can serve as comparable constructs between humans and animals. In other words, this type of comparative cognition detaches cognition from specific behaviors that function effectively in the life histories and ecological environments of animals, instead using humans as the benchmark for cognitive research.

While ecological validity is of course critically important in comparative cognition, it is often not the first consideration in research. Instead, it tends to be scrutinized after a certain cognitive capability has been identified. For example, the ability to point to objects in order to draw another individual's attention has been considered a core referential capability and has been reported in chimpanzees (Leavens et al., 1996). Leavens, Hopkins, and Bard (2005) argued that pointing behavior develops through situational factors by comparing the behaviors of captive and wild apes, noting that this behavior is virtually absent in wild individuals. The typical sequence of consideration is: (1) identifying a cognitive capability that seems unique to humans in a specific species, and then (2) examining the ecological validity of such cognition in that species. This order of inquiry contrasts with the biogenic approach to comparative cognition, which arguably begins with the biologically significant regulation of animal behavior. It should be noted that our aim is not to criticize these research practices, but merely to describe how the anthropogenic approach to comparative cognition typically proceeds.

Finally, it is important to note that while anthropogenic does not equate to anthropomorphic, the two are not entirely unrelated. Anthropomorphism involves attributing human mental experiences to animals (Asquith, 1984). Though this attitude has been consistently criticized within comparative psychology, as long as the anthropogenic approach is rigorously applied in the aforementioned ways, it does not naively project the researcher's subjectivity onto animals. For instance, in classical conditioning, fear responses are operationalized by behaviors such as freezing or the cessation of ongoing behavior. This operationalization is accepted because it is agreed upon as a functional consequence of fear. Therefore, as long as it is employed under this functional definition, there is no harm in discussing whether "an animal exhibited a fear response to a noxious stimulus". If this were deemed anthropomorphic, it would be a flaw in the definition of the fear response concept itself and operationalization of it, rather than an issue of anthropomorphism.

However, the preceding discussion might only apply to certain idealized or firmly established concepts (such as "association"). In practice, cognitive concepts, when referenced against humans, often drift from their strict definitions. Greenwood (1999) noted that this kind of "surplus meaning" is often attached to mental constructs, and this is a practical feature of such hypothetical constructs. Indeed, de Waal (1999) recognized that while anthropomorphism carries the risk of

attributing nonexistent cognitive functions to animals, he also warned against anthropodenial—the erroneous rejection of cognitive functions that should exist.[1] In his view, when studying phylogenetically close species to human, like primates, the risk associated with anthropodenial in the anthropomorphism-anthropodenial trade-off is higher. As mentioned, strictly applying the anthropogenic approach should prevent errors stemming from anthropomorphism. Nevertheless, in the real practice of comparative cognition, this risk remains significant. However, in our view, the biogenic approach minimizes the problems associated with this anthropomorphism-anthropodenial dichotomy. We will elaborate on this point in Section 5.

3. The biogenic approach and its practice in animal cognition

For many psychologists, the attempt to study animal cognition by referencing and taking human cognition as the starting point has become almost self-evident. As a result, opportunities to adopt alternative approaches seem rare. However, Lyon's (2006) biogenic approach to cognition is presented as a compelling alternative to the anthropogenic approach. She succinctly defined the biogenic approach as "The tradition that starts with the principles of biology is the biogenic (life + birth, origin) approach" (p.12). Among these biological principles, evolution is, of course, central. In fact, Lyon identified 'continuity' as the first characteristic of the biogenic approach. Yet, in modern comparative psychology, few would deny the continuity between humans and other animals, or more generally, between species. Even within the anthropogenic approach, or even anthropomorphic and anthropocentric positions in comparative cognition, continuity remains a significant perspective (e.g., de Waal, 2019).

It poses, thus, a question: what distinguishes the biogenic approach from the anthropogenic approach? Lyon (2006, p. 16) continued as follows.

The point is that the anthropogenic explanatory agenda is determined by considerations that may or may not be biological in nature. In biogenic approaches, biology determines how inquiry proceeds to explanation.

As this quotation suggests, the distinction between the biogenic and anthropogenic approaches arises from the "starting point" of inquiry. The important point to note here is that the biogenic approach does not constitute a directive to discard cognitive concepts derived from human psychology, and conduct research purely as a biological endeavor. In other words, when it is stated that biology determines the inquiry, it means that the behavioral phenomena of animals guide cognitive research, not that cognitive concepts should be eliminated. Lyon (2006) provides Piaget's (1970) genetic epistemology as an example of the biogenic approach in psychology. Piaget did not merely apply adult cognitive concepts to study infant development. For him, the ontogeny of infants was a process of adaptation, and it was from such biological principles that he derived empirically testable questions (Gillièron, 1987, pp. 247–266). Other than adaptation, Piaget drew ideas from biology, such as continuity, variation, and homeostasis (Goodwin, 1982). Indeed, concepts used to explain behavior in Piaget's theory, such as schema and intelligence, are derived from human cognition; however, the starting point for his inquiry was biological, embodying biogenic approach.

To clarify, it is entirely possible to adopt an anthropogenic approach while providing biological explanations for cognitive phenomena or psychological events. Cognitive neuroscience, which investigates the neural correlates of cognitive concepts derived from humans, exemplifies such a research area. In contrast, the biogenic approach begins by focusing on the biological processes of a specific animal. This includes a broad range of phenomena, such as the organism's chemical networks, physiological functions like homeostasis, self-organizing processes, and interactions with its environment as a whole. These processes are structured hierarchically, yet all contribute to maintaining the organism's unity. How, then, is this related to cognition? The biogenic approach takes seriously the notion that cognition is a biological function (e.g., Maturana, 1970). Although this is an evident fact for most comparative psychologists and biologists, it carries implications for how cognitive research should be conducted. Lyon (2006) identified various features of cognition, such as being a phenomenon of self-sustaining control, involving interactions with the environment to fulfill intrinsic ends (normativity), and being selective toward certain aspects of the world (selectivity), among others.[2] These characteristics are not independent; rather, they are inherent to the concept of biological function and contribute to the self-sustaining process of an organism. Biogenic research on comparative cognition would aim to specify such organism-environment interactions within the organism's niche. From this perspective, "To enable successful action and interaction within a niche is arguably what cognition is for" (p. 27).[3]

To apply the biogenic approach in comparative cognition research, one must first focus on the species-specific behavioral phenomena, life history, ecology, and unique organs of the animal in question. One pioneering study in this regard is the research on the foraging behavior of jays (Kamil & Bond, 2006). Jays are foragers of moths, which have evolved to blend seamlessly with tree patterns. Kamil and colleagues demonstrated through psychological experiments in the laboratory that jays improve their foraging success by enhancing their sensitivity to detecting moths with specific patterns. In other words, the jays employ selective attention, a cognitive concept originating from human cognitive psychology (e.g., Hommel et al., 2019; Treisman, 1969), to aid in their moth predation. However, as emphasized earlier, the difference between the biogenic and anthropogenic approaches lies in their "starting point". The research on jays originated from their intriguing foraging behavior rather than from the question of whether animals possess cognition similar to that identified in humans.

Interestingly, studies on tool use by New Caledonian crows serve as excellent examples of both anthropogenic and biogenic approaches. These crows are known to craft stick-like tools in the wild to extract insects hidden within decaying wood (Hunt, 1996). This behavior, accounting for nearly half of their nutritional intake, underscores its ecological importance (Rutz et al., 2010). In terms of cognitive research, the critical question is what underpins this behavior. From a biogenic perspective, realizing such tool use requires overcoming the physical constraint of a relatively rigid beak, which is less flexible than a human hand. To investigate this, researchers measured the visual and positional relationships of tools when grasped by crows and found that the visual control of the tool's tip was appropriately adjusted (Martinho, Burns, von Bayern & Kacelnik, 2014). It has also been revealed that the New Caledonian crow possesses a wide binocular visual field and a straight beak, which serve as morphological foundations supporting the stability of this grip (Matsui et al., 2016; Troscianko, von Bayern, Chappell, Rutz & Martin, 2012). From a motor control perspective, the sensory-motor dexterity potentially supporting the crows' tool use has been examined through studies on motor learning in crows of the same genus (Kanai, Matsui, Watanabe & Izawa, 2014; Matsui & Izawa, 2017, 2019).

[1] The concept of 'heuristic anthropomorphism' is also presented as a stance for highlighting intriguing aspects of animal behavior. However, this approach is not intended as an interpretative conclusion in animal behavior research but rather as a strategy for identifying what should be studied (e.g., Kracher, 2002). Therefore, it falls outside the scope of this paper.

[2] In addition to these characteristics, she added valency, anticipation, randomness reduction, and interdependence between functions.

[3] It is important to note that the "success" here is relative to their niche and the interactions within it. For example, consider a rat with electrodes implanted in its reward system, which engages in self-stimulation via lever pressing, neglecting food. While this behavior is clearly non-adaptive, it aligns with the animal's 'purpose' in that context.

Thus, the holistic examination of the life history, body structure, and sensorimotor capabilities of an animal displaying intelligent behavior exemplifies research practice of biogenic approach to comparative cognition.

Conversely, studies based on the traditional anthropogenic approach also exist for New Caledonian crows. These include research on naive physics and inferences regarding hidden causal agents (Jelbert, Taylor, Cheke, Clayton & Gray, 2014; Taylor et al., 2012). These studies reference cognitive concepts related to human cognition. While we have distinguished the two approaches in the researches regarding crow cognition, comparative psychologists and ethologists studying New Caledonian crows seem not to particularly differentiate between these approaches. Indeed, in the papers we have cited, the same authors were involved in studies belonging to both approaches. Does this mean that the distinction between the anthropogenic and biogenic approaches is trivial in scientific practice? We do not consider it so. The biogenic approach offers distinct advantages, which we will discuss in the next section.

4. Promoting biogenic approach

The previous section introduced several research lines utilizing the anthropogenic and biogenic approaches to comparative cognition. As previously mentioned, a significant portion of research involves applying concepts developed in human cognitive science to animal studies, which inevitably biases the research towards an anthropogenic approach. Moreover, comparative psychologists may not tend to explicitly apply these approaches in their own works. However, we firmly believe that there are distinct advantages for comparative cognition researchers who explicitly utilize the biogenic approach. This section illustrates these reasons in detail.

Firstly, promoting the biogenic approach within comparative cognition can serve as a powerful means of addressing the fundamental question of behavioral evolution within this field (Table 1). The primary goal of comparative cognition is to elucidate how animal cognition has been shaped throughout behavioral evolution and what role it has played. To achieve this, it is essential to examine the selective pressures and fitness adaptations associated with cognition—a task that has already been undertaken in some studies (e.g., Cauchoix & Chaine, 2016; Shettleworth, 2009b). However, many individual studies in comparative cognition remain focused on demonstrating specific behavioral abilities in certain species or identifying interspecies differences. To overcome this challenge, Schwartz, Pournaghdali, and Hess (2023) suggest that collecting data under more ecologically valid conditions can provide crucial evidence about the selective pressures that influenced the evolution of metacognition.

Furthermore, I believe that the breadth of the problem space that the biogenic approach can address is another critical factor. Under the biogenic approach, all behaviors in which animals engage with their environment in complex ways become subjects of comparative cognition research. This could involve anything from the complex social behaviors of large primates, the electric communication of electric fish, which obviously humans cannot perceive, to the learning capabilities of jellyfish (Bielecki, Nielsen, Nachman & Gar, 2023; Call & Tomasello, 2008; Moller & Bauer, 1973). Even in the case of plant cognition, which has sparked considerable debate in recent years, there is no a priori reason to exclude it from the scope of cognitive research (Castiello, 2021; Lee, 2023). The key is to identify the regulatory processes underpinning observed behaviors and critically assess whether they can be meaningfully described as cognitive. In contrast, the anthropogenic approach inevitably limits the scope of comparative cognition research to the range of cognitive concepts already established in human studies (see also section 6 on this point).

Despite our highlighting the utility of the biogenic approach, we do not intend to diminish the importance of the anthropogenic approach. While the range of issues that the biogenic approach can address may be broader, the anthropogenic approach is particularly effective for addressing critical issues within our human society. It is almost self-evident that the anthropogenic approach to cognition holds significant value in understanding the evolution of human cognition (Liu & Konopka, 2020). Moreover, human-derived cognitive concepts can possess practical value in biomedical research (Little et al., 2021).

Third, a long-standing issue in comparative cognition is the significance of "comparison" itself, and the biogenic approach offers valuable insights in this regard. For one, the method of comparison has historically been criticized for either not being used or being used inadequately (Beach, 1950; Macrì & Richter, 2015). Furthermore, psychologists have struggled to reach a consensus on the theoretical significance of interspecies comparison (Hodos & Campbell, 1969). Of course, there are studies that seek to overcome the difficulties of interspecies comparison through multi-laboratory collaboration, and we do not intend to deny the significance of such efforts (MacLean et al., 2014). Nevertheless, some of comparative cognition research is fraught with challenges. For example, studies investigating self-recognition using mirror tests are a typical example of the anthropogenic approach. The problem with this standard test is that it is influenced by the repertoire of self-directed behaviors, biomechanics, and effector morphology constraints of the animals, as well as their motivation to perform such behaviors. In reality, the assumption that self-recognition, typically examined with the mark test, is an identical cognitive category shared between humans and animals is questionable, and its likelihood appears low (Bräuer, Hanus, Pika, Gray & Uomini, 2020; Pepperberg, Garcia, Jackson & Marconi, 1995; Wittek et al., 2021). In other words, this type of cognitive concept may not be a 'natural kind.'

However, with the biogenic approach, the identification of real animal cognitive behavior comes first, and the scientific question revolves around how the animal interacts with its environment. Therefore, there is no need to be preoccupied with the procedural difficulties of direct

Table 1
Typical Formulation of Research Questions Based on Anthropogenic and Biogenic Approaches in Comparative Cognition It is important to note that the questions listed here do not encompass all possible inquiries within these two approaches.

Anthropogenic question in comparative cognition
Does a particular cognitive ability or process exist in a specific species?
To what extent is the existence of this cognitive ability more probable compared to other more parsimonious "kill-joy" hypotheses, such as those based on associative versus cognitive frameworks?
If this cognitive ability is present, how sophisticated is it compared to that found in humans or other species?
Is the mechanism underlying this ability the same process as in human cognition?

Biogenic questions in comparative cognition
Through what types of regulatory activities does an individual of a specific species interact with its environment? (What significance do these activities have for the individual?)
How does the cognitive activity persist as the individual-environment coupling?
What ecological information about the environment allows for this interaction? (What is the minimal environmental condition necessary for this coupling?)
What is the overall biological organization of the organism that permits this coupling, including physiological, bodily, and movement aspects?

comparison. One might worry that this approach could reduce the field to a mere catalog of specific animal behaviors. However, this has not been the case in the field of ethology. A glance at a standard ethology textbook reveals research on a wide range of behaviors, such as sociality, communication, habitat selection, and mating, across various taxonomic groups (e.g., Rubenstein & Alcock, 2018). It is common for experiments to be fine-tuned for each taxonomic rank, such as class, order, or even finer classifications. Yet, it is hard to argue that ethology research is merely a catalog collection. This is because there is a shared purpose or hypothesis among the research community, allowing for meaningful cross-referencing of findings, even without direct procedural comparisons. While there have not been many examples of testable hypotheses proposed within the biogenic approach to comparative cognition, there are exceptions, such as the conditions for the evolution of tool use (Rutz & Clair, 2012).

Moreover, adopting the biogenic approach in comparative cognition allows researchers to distance themselves from the biases of anthropomorphism or anthropodenial. The danger of rejecting anthropomorphism lies in denying cognitive functions that animals inherently possess, while the problem of rejecting anthropodenial is the opposite. This trade-off is similar to the false-positive and false-negative dichotomy in statistical hypothesis testing. This conflict arises when applying cognitive concepts, which originate from humans, to interpret animal behavior. However, in the biogenic approach, one can commit the conceptual stance that cognition refers to the interaction where animals are actively engaged with their environment, functioning in a specific manner. Thus, in this approach, cognition is not something to be interpreted; rather, it is a natural fact found within the coupling of organisms and their environment. The focus of cognitive research should be on explaining this fact, while the fact itself is merely a matter of observational and measurement reliability.

We argued that the biogenic approach is a valid strategy for comparative cognition for the reasons outlined above. However, it is important to note that this does not constitute an argument for discarding the anthropogenic approach. According to Lyon (2006), the anthropogenic and biogenic approaches differ in the theories they adopt and the keywords associated with cognition. Nevertheless, the fact that these are distinct approaches does not imply that one theory is inherently superior or more comparable than the other. Therefore, adopting one of these approaches does not require the rejection of the other. For instance, there is no issue with someone who emphasizes the biogenic approach also utilizing the anthropogenic approach when addressing a specific cognitive issue, such as whether animals have human-like episodic memory in animals.

Let us also address the relationship between the biogenic approach to comparative cognition and evolutionary psychology here. Traditional evolutionary psychology posits that mental concepts function as an adaptive toolkit (Barkow et al., 1992; Cosmides & Tooby, 2013). This 'notorious adaptationism' has been repeatedly criticized (Dupré, 2016; Rellihan, 2011; Richardson, 2010). Rellihan (2011) argued that evolutionary psychology discusses the evolution of the mind through the lens of climbing a static adaptive landscape, while offering minimal evidence to support its evolutionary hypotheses. This concern applies to both biogenic and anthropogenic approaches, though it is particularly pressing in the anthropogenic approach. Explaining animal behavior through human-derived cognitive concepts risks interpreting such behavior in terms of human cognitive adaptivity. While this is not an inevitable pitfall of the anthropogenic approach, it remains a persistent risk. In many comparative cognition studies, avoiding this issue heavily relies on the interpretive restraint of researchers. Similarly, the biogenic approach also faces the risk of anthropocentric adaptationism if it misinterprets how an organism's behavior functions within its niche. However, as long as the biogenic approach remains aligned with its foundational premise of considering organism-niche interactions, this risk is lower compared to the anthropogenic approach. In this respect, the two approaches have the potential to form a complementary relationship.

In sum, there are several reasons for comparative cognition researchers to incorporate the biogenic approach. Nevertheless, we reiterate that promoting the biogenic approach does not mean that the anthropogenic approach should be abandoned. Indeed, Lyon (2006) herself pointed out the usefulness of the biogenic approach while also acknowledging that both approaches are complementary and should not be exclusively chosen. The current state of cognitive science does not allow one approach to fully subsume the other. While a framework that integrates both approaches may emerge in the future, it seems that, for now, they will continue to function complementarily in scientific research. However, there is another reason to promote the biogenic approach: it has a deep connection with emerging frameworks in cognitive science philosophy that have been actively discussed in recent years.

5. Relating biogenic approach in animal cognition to other philosophical stances

In this section, we will connect the biogenic approach with other philosophical perspectives that share a deep affinity with it, shedding light on its implications for comparative cognition. The biogenic approach is not merely a suggestion to focus on biological processes such as ecology and physiology; rather, it serves as the starting point for framing cognitive research. The perspectives that resonate strongly with this approach and that, we believe, can provide productive insights for the future of comparative cognition are ecological psychology and enactivism.

Ecological psychology, pioneered by J.J. Gibson, fundamentally asserts that perception is action-oriented (for a textbook nicely introduced ecological psychology, see Segundo-Ortin and Raja, 2024). Gibson argued that the environment is replete with ecological information that specifies affordances, which organisms seek to 'pick up'. Here, ecological information means a covariant structure between the embodied activity of the organism and the process of the environment. In other words, ecological information must specify the opportunities for action available to the organism, or affordances (Gibson, 2014, p. 131). In this sense, ecological information is determined by the dual nature of the environment's facts and what the organism's body can do (Carvalho & Rolla, 2020). Thus, the goal of the organism is not to create a mental copy of the world, as this is unnecessary.

The concept of affordance refers an opportunity for action that is offered by an environment surrounding an organism. It is, as Gibson (1966, p. 285) argued, both a fact inherent in the environment and simultaneously a "value." Crippen (2020) discusses the slime mold (*Physarum polycephalum*) as a nice exemplary case of a non-neural organism that survives by utilizing such values. The slime mold is a communal unicellular organism, yet it exhibits remarkable locomotor capacity. It marks its path with a secretion of slime, which it then avoids (Nakagaki, 2001), resulting in the network of optimal transportation (Tero et al., 2010). In the case of slime molds, the ecological information regarding the paths they have traversed persists in the environment. By picking up this information, the organism identifies negative affordance that prompts avoidance behavior.

The idea that affordance has both positive and negative aspects may give the impression that affordance is a construct generated within the brain. However, an important notion within affordance theory is its realism. Gibson asserted as follows (1967/2019, p. 410; emphasis original):

The *affordances* of the environment are permanent, although they do refer to animals and are species-specific. The positive and negative *valences* of things that change when the internal state of the observer changes are temporary. The perception of what something affords should not be confused with the "coloring" of experience by needs and motives. Tastes and preferences fluctuate. Something that looks good today may look bad tomorrow but what it actually *offers* the observer

will be the same.

Affordances, therefore, are not mental constructs but real properties of the environment. Gibson (1966) equated value with affordance (p. 285), but this does not imply that the extraction of affordances is invariant. While the appearance or smell of a peanut typically offers a positive affordance—namely, edibility—it may evoke a negative affordance for someone who has developed an allergy, signaling harm and avoidance (Crippen, 2020). The valence of an affordance is a property as it is perceived with reference to an observer (Gibson, 1979/2014, p. 137). Therefore, its actualization depends on the organism's activity of picking up corresponding ecological information. This process is contingent on the organism's bodily structure, organization, and immediate state. The perspective implies that comparative cognition grounded in ecological psychology should focus on identifying the ecological information that organisms pick up during continuous activity and how it aids in regulating their behavior.

Indeed, Gibson's successor, Reed (1996), succinctly stated, "From an ecological approach, psychology must take *an animal's encounters with its surroundings* as the fundamental phenomenon to be explained" (p.184, emphasis original). There, it was pointed out that the primary task for comparative psychology is to explain the encounters between diverse species and their environments without reducing them to human-centered laws. He adamantly opposed the notion of reconstituting internal cognitive processes of animals as human analogies under mechanistic metaphors such as stimulus-response machines or computers. This stance contrasts sharply with the anthropogenic approach, which adheres to a cognitivist program of representationalism, yet aligns closely with the biogenic approach.

By emphasizing the niche in which animals reside, some may perceive the biogenic approach to comparative cognition as merely behavioral ecology through field observations. While it goes without saying that behavioral ecology is crucial to comparative cognition (c.f., Healy et al., 2009), we do not consider laboratory experiments to be irrelevant in comparative cognition. Interestingly, it is known that lawfully structured environmental stimuli scale the perception of affordances according to the anatomical features of animals (Wagman, Langley, Farmer-Dougan, 2017). In their study, Wagman et al. (2017) presented food to various dog breeds at progressively higher heights. The results revealed that the height at which dogs transitioned from head-only reaching to rearing (i.e., reaching with the head and torso) scaled with animals' shoulder height. For dogs, head-only reaching is low-cost and stable, but limited in range, presenting a trade-off. Such laboratory experiments are essential for examining the information animals use to make behavioral choices, highlighting an important role of comparative cognition grounded in ecological psychology.

Next, enactivism, initially proposed as the "enactive approach" by Varela et al., 1991/2017 in "The Embodied Mind," posits that for organisms to maintain themselves, they must engage with their environment through sensorimotor systems, creating "sense" (sense-making) in a cycle that continuously informs their actions. For Varela and his colleagues, cognition was the active process of self-maintenance by the organism. Organisms equipped with sensorimotor systems engage with the environment in ways that maintain their bodily integrity, sustaining themselves as autopoietic systems. Life itself is a process of self-maintenance, that is, autopoiesis, and basic form of cognition is the act of constructing a meaning of the environment through embodied actions within this process, which is called 'enaction' (Maturana, 1970; Varela et al., 1991/2017). Precisely, Thompson (2007) define sense-making equals to enaction (p. 158)[4]:

Sense-making is viable conduct. Such conduct is oriented toward and subject to the environments' significance and valence. Significance and valence do not preexist "out there," but are enacted, brought forth and constituted by living beings. Living entails sense-making, which equals enaction.

The life is autonomous in the sense that produces and sustains its own (Thompson & Stapleton, 2009). The idea that living processes and basic form of cognitive processes share a common structure as autopoietic systems is known as the mind-life continuity thesis, which remains a central theme in enactivism and embodied cognition (Kirchhoff & Froese, 2017; Thompson, 2007).[5]

For enactivists who emphasize life-mind continuity, cognition is regarded as an emergent phenomenon arising from the interaction between an autonomous agent and a meaningful environment (De Jesus, 2016). Thompson (2007) elaborates on the concept of an autonomous agent (p. 43):

An autonomous system, however, is defined by its endogenous, self-organizing and self-controlling dynamics, does not have inputs and outputs in the usual sense, and determines the cognitive domain in which it operates.

From this perspective, cognition is seen as a process involving the environment within the organismal cycle, and the persistence of such a cycle is itself a process of life. Therefore, the question of what cognition is cannot be divorced from the question of what life is (Wheeler, 2011). Why is, then, enactivist thinking fruitful for the biogenic approach to comparative cognition, given that comparative cognition does not aim to directly address the nature of life? A clue can be found in Thompson and Stapleton (2009), where they stated that cognition in the enactive approach begins with the following question. (p.p. 23–24)

[…] the enactive approach starts from the question of how a system must be organized in order to be an autonomous system—one that generates and sustains its own activity and thereby enacts or brings forth its own cognitive domain.

If one adopts enactivism as a framework for conducting a biogenic approach to comparative cognition, the process of self-maintenance generated by persistent behavioral cycles is a locus of psychological phenomenon.[6] Slime mold is, again, suggestive example for the biogenic approach to comparative cognition from the standpoint of enactivism. The navigation of slime molds is not based on memory stored in the neural system, as they do not possess, but rather on externalized memory (Reid, Latty, Dussutour & Beekman, 2012). Through this externalized memory, slime molds take in nutrients and use it for self-maintenance. Their interaction with the environment through their sensorimotor cycles is a process that signifies the places they have passed through as paths they should avoid. Comparative psychologists adopting the biogenic approach need not hesitate to call this process cognition. On the other hand, human memory-based navigation typically involves cognitive maps. Although we do not wish to deny the

[4] Other enactivists use the term "sense-making" with somewhat different nuances. For instance, there are affective uses (Colombetti, 2010), an emphasis on situated norms (Sepúlveda-Pedro, 2024), and a stronger claim regarding sense-making as a sufficient condition for life (Froese & Di Paolo, 2011). However, in this paper, we are agnostic regarding which interpretation is most appropriate, focusing instead on arguing that the enactivist framework is valuable for a biogenic approach to comparative cognition.

[5] Note that others do not emphasis life-mind continuity for their principle. See Ward et al. (2017).

[6] Note that we do not intend to claim that enactivism or ecological psychology are equivalent to the biogenic approach. Indeed, Lyon (2006) noted that adopting an enactive (embodied) cognition is not equal to adopting the biogenic approach. Our intention is also to emphasize that enactivistic and ecological perspectives are valuable starting points for the biogenic approach to comparative cognition.

concept of cognitive maps, equating the formation of cognitive maps with spatial navigation would lead to the conclusion that slime mold behavior is not cognitive. This way of thinking is more likely to occur if comparative cognition only adopts the anthropogenic approach.

It should be noted that enactivism and embodied cognition encompass a range of perspectives, with varying degrees of emphasis and nuance in their claims (Gallagher, 2023; Ward, Silverman, & Villalobos, 2017). What unifies these positions is a shared focus on the central role of the body in cognition. Nonetheless, as Gallagher (2023) refers to with the term "weak embodied cognition," where action-oriented representation plays a significant role in cognition (Clark, 1997). Although the concept of action-oriented representation is inherently neutral with respect to its orientation towards biogenic or anthropogenic approaches, empirical research on this topic tends to favor the latter. In practice, many studies on embodied cognition in humans focus on examining the impact of the body and environment on traditional human-centered cognitive concepts (Fincher-Kiefer, 2019). Therefore, although research from this perspective distances itself from traditional cognitive science by not treating cognition merely as an abstract computational process, the cognitive concepts it employs tend to remain close to traditional ones. As a result, it is likely to approach the anthropogenic one.

In contrast, "strong embodied cognition", which does not view cognition as representational but rather as the process by which organisms maintain themselves through their coupling with the environment, naturally gravitates toward the biogenic approach. While the empirical studies with enactivism still remain rare in comparative cognition there are some attempts that better align with it than traditional cognitivism (Cheng, 2018; Merritt, 2015, 2021). For example, Merritt (2021) argued that dogs' cognition is better characterized by enactivism than traditional cognitivism. The relationship between dogs and humans spans over 10,000 years, with archaeological evidence indicating a close association since the Stone Age (Miklósi, 2014). Thus, the environment humans occupy constitutes their niche. As a result, dogs' cognitive activities exhibit numerous distinct characteristics. Among these, Meritt (2021) argued that interspecies "play" with humans serves as an exemplary case of cognition unfolding through dynamic interaction. For dogs, human actions themselves are integral to the manifestation of their cognition. The cognitive processes demonstrated in agility training or play involving gestures presuppose the presence of humans, and cannot be disentangled from their niche. Meritt contends that this perspective is better understood through enactivism, which conceptualizes cognition as arising from embodied interactions, rather than through cognitivism, which characterizes cognition solely within the individual, isolated from the environment. Starting from the activities within a given niche, considering the cognition of specific species and linking this to empirical research aligns with the way of thinking with biogenic approach.

Lastly, one may concern that two positions we introduced may not be compatible, given that ecological psychology explicitly adopts realism, but enactivism does not. Indeed, enactivism has criticized ecological psychology for emphasizing its own uniqueness by highlighting aspects (e.g., Varela et al., 1991/2017). However, it was argued that these are, in fact, not in opposition (Crippen, 2025; Segundo-Ortin et al., 2019). The apparent tension not only hinders the progression of philosophical debates but may also introduce unnecessary confusion when these approaches are applied to comparative cognition. Nevertheless, the relation between two stances is still in active debate: some argued that ecological psychology and enactivism are compatible in some ways, with no irreconcilable conflicts between them (Bruineberg et al., 2023; Crippen, 2020; Segundo-Ortin, 2020). Others highlighted the distinction between two stances (Heft, 2020; Hutto, 2017; Varela et al., 1991/2017). For instance, Hutto (2017) criticized certain terms used in ecological psychology (such as the "use" and "pick up" of ecological information) as unclear, and are at risk of being interpreted within a representational approach, while Segundo-Ortin (2020) clarified that these criticisms stem from misunderstandings.

We anticipate a collaborative and productive relationship between two; however, resolving the tension between them is beyond the scope of this paper. Yet, we just highlight one specific point: the strong view of embodiment is compatible with ecological psychology. Indeed, Crippen (2025) observes the following regarding enactivism: "If everything is enacted, transformed, and thus imbued with value, then apparent worlds become the sole ones. This renders apparent worlds real because we forfeit the baseline option for a truer alternative, which is another reason why constructivism does not always negate realism." Gibson's notion of "pick up" might appear to imply that organisms passively await information from the world to some enactivists, but this is clearly a misconception. Eating, for example, is an exploratory, stimulus-producing process involving chewing and tongue movements. These are active sensory engagement rather than mere reception. Drawing on such cases, Crippen (2025) argues that the traditional divide between organisms' sense-making, in which they enact aspects of their environment (enactivist constructionism), and ecological realism no longer marks a substantive difference. In his view, the enactivism notion of constructing worlds by interaction is not inherently incompatible with the realism of ecological psychology. The role of neural activity within this framework, while still lacking consensus, has been approached through various hypotheses: as part of the closed sensorimotor loop of a biological agent (Di Paolo et al., 2017); as a form of dimensionality reduction to extract information from high-dimensional environments (Favela, 2023); or as the synchronization of neural activity with events occurring at an ecological scale ('resonance', Raja, 2018). Although it remains contentious which of these perspectives is most constructive for empirical research, they all share a common rejection of the notion that the central nervous system serves to form representations—specifically, to reconstruct entities from impoverished environments.

6. Defending biogenic approach to comparative cognition

In the final section, we aim to address potential concerns of the biogenic approach to comparative cognition. As previously noted, the field of comparative cognition has been predominantly shaped by an anthropogenic perspective, and the biogenic approach remains outside the mainstream. Our goal is to demonstrate how the biogenic approach can positively contribute to the field. Nevertheless, we imagine that some readers may harbor concerns about this approach. While it may not be feasible to provide exhaustive responses to all potential concerns, we will present persuasive defenses to the best of our ability. Through these defenses, this section also seeks to highlight the merits of the biogenic approach.

First, some may suspect that the biogenic approach unjustifiably extends the concept of cognition to biological processes, thereby reducing cognitive research to pure biology. On this point, we wish to reiterate that the biogenic approach to comparative cognition does not seek to eliminate the concept of cognition.

We consider that the biogenic approach is not a form of eliminativism of mind. Kotsko (2014) compared Burrhus Skinner's radical behaviorism and Paul Churchland's eliminative materialism, noting that while the former equates mental concepts with interactions between organisms and their environments,[7] the latter reduces them to neurobiological processes. Despite their different reductionist targets, both perspectives converge in asserting that terms related to mental functions lack explanatory role for behavior. Both approaches anticipate that, as research advances, explanations involving mental concepts will gradually be replaced—for Skinner, by terms tied to contingencies of reinforcement and theories of verbal behavior, and for Churchland, by

[7] However, it should be noted that Skinner's radical behaviorism is not a form of reductionism in the conventional sense (see Yanagawa & Matsui, 2025).

neurophysiological concepts. In contrast, the biogenic approach serves primarily as a framework for organizing inquiry and does not entail the claims made by these positions. However, it does not explicitly reject them either, maintaining a neutral stance toward their assertions.

Another reason that the biogenic approach does not entail a reduction to biology can be found in the choice of research topics. Even if a cognitive scientist adopts a biogenic approach, the phenomena requiring explanation remain the varieties of capacities involved in producing behavior, such as sensation/perception, memory, value judgment, learning, decision-making, and communication (Lyon et al., 2021). These capacities also constitute typical research topics in comparative cognition (Shettleworth, 2008). Of course, these are also addressed within biology. However, considering that cognitive science is inherently an interdisciplinary field, researchers in comparative cognition need not worry that their areas of inquiry will be excluded by the biogenic approach.

Furthermore, the biogenic approach has the potential to influence research methodologies. Zhang and Ghazanfar (2018) found that the development of vocal communication in marmosets is driven not by cognitive development in the brain but by a shared central pattern generator that transitions babbling to social vocalizations through the development of lung mass. From the conventional perspective of human cognitive development, social communication is typically understood as a function of the brain. However, their study begins with the biological fact that vocalization is constrained and modulated by the body in which it is embedded. From this standpoint, they employed dynamical systems modeling and behavioral experiments to offer a novel explanation for development of social vocalization, which is undeniably a psychological phenomenon. This research exemplifies an implicit adoption of the biogenic approach. Additionally, there is report suggesting that even in human cognition, not only neurons but also immune cells contribute to mental processes (Ciaunica, Shmeleva, & Levin, 2023). While their study focused on human cells, similar methodologies could potentially be applied in comparative cognition. These studies achieve results not by adhering to the implicit assumption that neuronal activity alone underpins cognition but by starting from biological phenomena such as cellular functions.

Nevertheless, we must recognize that the current status of biogenic approach to comparative cognition has certain limitation, particularly when considered from the perspective of research methodologies and outcomes. Specifically, it is less systematically developed compared to the anthropogenic approach. The future trajectory of the biogenic approach—whether it devolves into a mere collection of disparate findings or evolves into a cohesive and structured research framework—will depend on the efforts of comparative cognition researchers who choose to adopt and advance this approach.

Second, it is important to exercise caution when emphasizing continuity in biogenic approach. This point was raised by William James in his critique of Thomas Huxley's "conscious automata" theory (James, 1879; 1890). Huxley's theory posits that animals, including humans, may possess consciousness, but that it has no causal efficacy and is essentially just machinery, resulting in biological determinism. The basis of this theory lies in the observation that decerebrated animals still exhibit responses to painful stimulus. James James (1879) argued that due to evolutionary continuity, there exists a gradual variation in the complexity of the nervous system (James, 1890, p. 138). Thus, James holds that the difference between humans and many other organisms with brains is one of degree rather than of kind. If the degree of consciousness correlates with the complexity of the nervous system, then variations in consciousness are likewise continuous. However, he pointed out that once the complexity of the nervous system or consciousness exceeds a certain threshold, unpredictability in behavior becomes evident. Huxley's continuity argument obscures the functional significance brought about by the degree of complexity. In a similar vein, James (1890, p.p. 128–130) reiterated his criticism, noting that the continuity between humans and animals could be used to support the claim that the same functions of the human brain also reside in the frog's spinal cord, thus critiquing the ambiguity of relying on continuity. The idea that consciousness is continuous and can be traced gradually from simple to complex nervous systems may appear persuasive at first glance. However, such a view risks collapsing into a theory that ultimately reduces consciousness to the motion of matter. This approach fails to resolve the problem of emergence of consciousness. For as soon as consciousness appears, no matter how minimal, something of a radically different kind has already come into being ("entirely new nature", James, 1890, p. 146).[8] Importantly, James' argument seems to remain valid even if consciousness is replaced with any other cognitive concept.[9]

James's critique warrants consideration even within the biogenic approach to comparative cognition. Lyon (2006) asserted that "complex cognitive capacities have evolved from simpler forms of cognition" (p. 15). In the same passage, she also notes that within the anthropogenic approach, cognition is treated as a 'kind,' whereas in the biogenic one, cognition is treated as a 'degree.' Taking James's warning seriously, we must exercise caution when treating cognition as a degree. For example, de Waal (1999) proposes a linear gradual view of 'self-awareness,' yet the meaning of the degree of self-awareness remains unclear (e.g., what does it mean for self-awareness to be "half"?), and there is no necessity presented for its change to be linear. In short, continuity does not necessarily imply that cognition and behavior are gradual, and it is essential to explore what it means for them to be continuous through both conceptual analysis and empirical verification.

Third, the idea that cognition extends beyond the brain, as proposed in theories like enactivism, has faced various criticisms, and we must address these concerns. While adopting the biogenic approach is not equivalent to endorsing the enactivism, our discussion on the compatibility between the two obliges us to provide a response. Classical perspectives, such as that of Jerry Fodor, have argued that cognition should be confined to information processing carried out by the central nervous system (Fodor, 1983). More recently, Adams and Aizawa (2010) have critiqued the extended mind hypothesis, asserting that cognition should be limited to processes within the brain. For example, they might dismiss the interpretation of slime molds avoiding previously traversed paths as externalized memory, labeling it a case of the "coupling-constitution fallacy" (Adams & Aizawa, 2010). This fallacy posits that the mere association of Y with agent X does not constitute evidence that Y is part of X. This paper does not aim to provide a general rebuttal to their criticism, as such attempts have already been made several times (e.g., Gallagher, 2018; Kagan and Lassiter, 2013; Piredda, 2017). Instead of reiterating those, we intend to highlight that the perspectives of Adam and Aizawa may in fact lead to somewhat detrimental consequences rather than effectively contributing to comparative cognition.

Clark (2010) argues that in order to defend his extended mind hypothesis, the idea that processes outside a brain constitute cognition has heuristic value to proceed empirical research. Adams and Aizawa (2010) disputed that such value is not empirically supported; however, as already discussed with slime molds, there are multiple examples in comparative cognition that inspire scientific research. Cheng (2018)

[8] This tension between continuity and discontinuity seems to have led later development toward a neutral monist worldview that no longer distinguishes between the mental and the physical.

[9] For instance, Ginsburg and Jablonka (2019) proposed the unlimited associative learning hypothesis as a evolutionary theory of consciousness. This theory argues that the evolution of consciousness results from certain biological functions (such as valuation of the external world and selective attention) and represents a 'mode of being.' This 'mode of being' emerges under a specific set of functions, implying a discontinuity between consciousness and unconsciousness. Similarly, when considering the biological functions that constitute consciousness, we must remain cautious of the possibility of such a discontinuity.

provided an overview of embodied cognition in animals, including examples such as the social interactions of dogs and the decentralized cognition of social insects. Japyassú and Laland (2017) discussed the role of webs in spider cognition. For instance, the ability of spiders to attend to their environment relies on the characteristics of their webs, which transmit vibrations. Adams and Aizawa may describe this as a coupling-constitution fallacy. However, it can be argued that the materials and structure of the spider's web, its body (including its legs as vibration detectors), and its brain have co-evolved, collectively enabling the spider's attentional processes. Comparative cognition should provide an explanation for the entire process of such phenomena. If one forces the separation of the spider's web from the spider itself, it becomes impossible to examine the phenomenon of the spider's attention. Consequently, this approach distances researchers from the fact that the spider attends to specific stimuli in the real world. In light of this, we are concerned that Adam and Aizawa's criticism may hinder the development of comparative cognition.

Comparative psychology has reflected on the tendency to view animal cognition in terms of a linear progression (Campbell & Hodos, 1991; Hodos & Campbell, 1969). Such an approach implies a scala naturae like evolution. On the other hand, if one adopts a biogenic approach, where animal cognition is seen as extending into the environment or as a form of bodily action, attention is naturally directed towards the animal's body, environment, and interaction between these. Conversely, limiting cognition to neural processes would reduce comparative cognition to a comparison of brain complexity. In fact, MacLean et al. (2014) applied self-control tasks to a number of primates and examined the evolution of self-control, finding a correlation between brain enlargement and the evolution of self-control[10]. Indeed, it may be an intriguing feature of *Homo sapiens* that process inside a head has predominant role in cognition.

Even radical enactivists, who argue that nearly all cognition occurs as contentless sensorimotor patterns, acknowledge that language is an exception (Hutto & Myin, 2017).[11] However, even if this is the case, it does not provide a rationale for restricting cognition to the head in broad range of animal kingdom. From the classical perspective that conceives of cognition as symbolic or representational manipulation, language is not an "exception" but a paradigmatic case of cognition. Indeed, for proponents of this view, what enactivists call cognition may not qualify as such at all. These two perspectives reflect a deep semantic divergence over what counts as cognition. In comparative cognition, however, adopting the latter view has proven to be more productive and conducive to empirical discovery. For instead, non-neural processes are gaining support as being worthy of the label "cognition," particularly through evidence of behavioral plasticity in aneural organisms (Papini, 2025; Smith-Ferguson & Beekman, 2020). Of course, this empirical evidence does not imply that the brain is unnecessary for cognition. Rather, it seems to naturally lead researchers in comparative cognition to the unresolved questions such as "Why did neurons evolve?" and "What did that bring to cognitive evolution?"

If Adam and Aizawa were to address this, they might still dismiss behavior that does not involve neural processes as not cognitive. Their requirements for a cognitive process, as outlined in Adams and Aizawa (2010), are that it must be "recognizably cognitive" and "take place in the brain," but this presupposes their conclusion. As already noted, such a presupposition prematurely dismisses subjects that comparative psychology should address. This harmful byproduct should not be overlooked in comparative psychology. Over more than a hundred years ago, Harvard's Spencer Jennings found even single-celled organisms exhibiting flexible behavioral plasticity (Jennings, 1906/1931). If Jennings had been constrained by the view that cognition is solely a product of the brain, the knowledge we have about notable animal behavior would be far less than what we currently possess.

[10] Please note that we are not attempting to deny the significance of their research. Self-control is clearly an important psychological function in human life. Therefore, it is a research subject where an anthropogenic approach is effectively applicable.

[11] But see also recent treatment on this issue from other enactivists (Di Paolo et al., 2018).

7. Conclusion

The current state of comparative cognition reveals a landscape where both anthropogenic and biogenic approaches coexist, though it is predominantly biased towards the former. We have discussed the significance of the biogenic approach to encourage more researchers to adopt it as their starting points. Its importance spans from fundamental issues, such as the evolution of behavior and the meaning of comparison, to more practical aspects, such as mitigating anthropomorphism. Furthermore, we have suggested that advancing the biogenic approach could pave the way for comparative cognition to align with other stances including enactivism and ecological psychology, as proposed by contemporary philosophical discussions in cognitive science. Particularly, we have emphasized that these stances offer valuable frameworks for promoting a biogenic approach in comparative cognition.

CRediT authorship contribution statement

Hiroshi Matsui: Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Yumi Hata:** Writing – review & editing, Writing – original draft, Conceptualization.

Declaration of generative AI usage

During the preparation of this work the authors used chatGPT o4 in order to refine the manuscripts written by non-native English speakers. After using this tool/service, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

Conflicts of interests

The authors do not have any conflicts of interests.

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No data was used for the research described in the article.

References

Adams, F., & Aizawa, K. (2010). Defending the bounds of cognition. In R. Menary (Ed.), *The extended mind* (pp. 67–80).
Asquith, P. J. (1984). The inevitability and utility of anthropomorphism in description of primate behaviour. In R. Harrè, & V. Reynolds (Eds.), *The meaning of primate signals* (pp. 138–176). Cambridge: Cambridge University Press.
Barkow, J. H., Cosmides, L., & Tooby, J. (Eds.). (1992). *The adapted mind: Evolutionary psychology and the generation of culture*. USA: Oxford University Press.
Beach, F. A. (1950). The snark was a boojum. *American Psychologist, 5*(4), 115–124.
Bielecki, J., Nielsen, S. K. D., Nachman, G., & Garm, A. (2023). Associative learning in the box jellyfish Tripedalia cystophora. *Current Biology, 33*(19), 4150–4159.
Blaisdell, A. P., Sawa, K., Leising, K. J., & Waldmann, M. R. (2006). Causal reasoning in rats. *Science, 311*, 1020–1022.
Blough, P. M. (1991). Selective attention and search images in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 17*(3), 292.
Bräuer, J., Hanus, D., Pika, S., Gray, R., & Uomini, N. (2020). Old and new approaches to animal cognition: There is not "one cognition". *Journal of Intelligence, 8*, 28.
Bruineberg, J., Withagen, R., & Van Dijk, L. (2023). Productive pluralism: The coming of age of ecological psychology. *Psychological Review, 131*, 996–1006.

Cabrera, D., Nilsson, J. R., & Griffen, B. D. (2021). The development of animal personality across ontogeny: A cross-species review. *Animal Behaviour, 173*, 137–144.
Call, J., & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences, 12*, 187–192.
Campbell, C. B. G., & Hodos, W. (1991). The Scala naturae revisited: Evolutionary scales and anagenesis in comparative psychology. *Journal of Comparative Psychology, 105* (3), 211–221.
Carvalho, E. M. D., & Rolla, G. (2020). An enactive-ecological approach to information and uncertainty. *Frontiers in Psychology, 11*, 588.
Castiello, U. (2021). (Re) claiming plants in comparative psychology. *Journal of Comparative Psychology, 135*(1), 127.
Castro, C. A., & Larsen, T. (1992). Primacy and recency effects in nonhuman primates. *Journal of Experimental Psychology: Animal Behavior Processes, 18*(4), 335–340.
Cauchoix, M., & Chaine, A. S. (2016). How can we study the evolution of animal minds? *Frontiers in Psychology, 7*, 358.
Cheng, K. (2018). Cognition beyond representation: Varieties of situated cognition in animals. *Comparative Cognition & Behavior Reviews, 13*, 1–20.
Ciaunica, A., Shmeleva, E. V., & Levin, M. (2023). The brain is not mental! coupling neuronal and immune cellular processing in human organisms. *Frontiers in Integrative Neuroscience, 17*, Article 1057622.
Clark, A. (1997). *Being there*. Cambridge: MIT Press.
Clark, A. (2010). *Coupling, constitution, and the cognitive kind: A reply to adams and aizawa*.
Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature, 395*, 272–274.
Colombetti, G. (2010). Enaction, sense-making, and emotion. In J. Stewart, O. Gapenne, & E. Di Paulo (Eds.), *Enaction: Toward a new paradigm for cognitive science* (pp. 145–164). MIT press.
Cosmides, L., & Tooby, J. (2013). Evolutionary psychology: New perspectives on cognition and motivation. *Annual Review of Psychology, 64*(1), 201–229.
Crippen, M. (2020). Enactive pragmatism and ecological psychology. *Frontiers in Psychology, 11*, Article 538644.
Crippen, M. (2025). Enactivism: A newish name for mostly old ideas? *Phenomenology and the Cognitive Sciences*, 1–25.
De Jesus, P. (2016). Autopoietic enactivism, phenomenology and the deep continuity between life and mind. *Phenomenology and the Cognitive Sciences, 15*, 265–289.
de Waal, F. B. (1999). Anthropomorphism and anthropodenial: Consistency in our thinking about humans and other animals. *Philosophical Topics, 27*, 255–280.
de Waal, F. B. (2019). Fish, mirrors, and a gradualist perspective on self-awareness. *PLoS Biology, 17*, Article e3000112.
Di Paolo, E., Buhrmann, T., & Barandiaran, X. (2017). In *Sensorimotor life: An enactive proposal*. Oxford University Press.
Di Paolo, E. A., Cuffari, E. C., & De Jaegher, H. (2018). *Linguistic bodies: The continuity between life and language*. MIT press.
d'Isa, R., & Abramson, C. I. (2023). The origin of the phrase comparative psychology: An historical overview. *Frontiers in Psychology, 14*, Article 1174115.
Dupré, J. (2016). Against maladaptationism: Or what's wrong with evolutionary psychology? 1. In *Knowledge as social order* (pp. 165–180). Routledge.
Evans, T. A., & Beran, M. J. (2012). Monkeys exhibit prospective memory in a computerized task. *Cognition, 125*, 131–140.
Favela, L. H. (2023). *The ecological brain: Unifying the sciences of brain, body, and environment*. Taylor & Francis.
Fincher-Kiefer, R. (2019). *How the body shapes knowledge: Empirical support for embodied cognition*. American Psychological Association.
Fodor, J. A. (1983). *The modularity of mind: An essay on faculty psychology*. MIT Press.
Froese, T., & Di Paolo, E. A. (2011). The enactive approach: Theoretical sketches from cell to society. *Pragmatics and Cognition, 19*(1), 1–36.
Gallagher, S. (2018). New mechanisms and the enactivist concept of constitution. In *Consciousness and the ontology of properties* (pp. 207–220). Routledge.
Gallagher, S. (2023). *Embodied and enactive approaches to cognition*. Cambridge University Press.
Gibson, J. J. (1966). *The senses considered as perceptual systems*. Houghton Mifflin.
Gibson (1967 2019) Notes on affordance. In Reed, E. & Jones, R. (Eds.) Reasons for realism: Selected essays of james J. gibson. Routledge.
Gibson, J. J. (1979). *The ecological approach to visual perception: Classic edition*, 2014. Psychology press.
Gillièron, C. (1987). *Is Piaget's "genetic epistemology" evolutionary? Evolutionary epistemology: A multiparadigm program*.
Goodwin, B. C. (1982). Genetic epistemology and constructionist biology. *Revue Internationale de Philosophie*, 527–548.
Goto, K., & Watanabe, S. (2012). Large-billed crows (Corvus macrorhynchos) have retrospective but not prospective metamemory. *Animal Cognition, 15*, 27–35.
Greenwood, J. D. (1999). Understanding the "cognitive revolution" in psychology. *Journal of the History of the Behavioral Sciences, 35*, 1–22.
Griffin, D. R. (1978). Prospects for a cognitive ethology. *Behavioral and Brain Sciences, 1* (4), 527–538.
Healy, S. D., Bacon, I. E., Haggis, O., Harris, A. P., & Kelley, L. A. (2009). Explanations for variation in cognitive ability: Behavioural ecology meets comparative cognition. *Behavioural Processes, 80*(3), 288–294.
Heft, H. (2020). Ecological psychology and enaction theory: Divergent groundings. *Frontiers in Psychology, 11*, 991.
Hodos, W., & Campbell, C. B. G. (1969). Scala naturae: Why there is no theory in comparative psychology. *Psychological Review, 76*, 337.
Hommel, B., Chapman, C. S., Cisek, P., Neyedli, H. F., Song, J. H., & Welsh, T. N. (2019). No one knows what attention is. *Attention, Perception, & Psychophysics, 81*, 2288–2303.
Hunt, G. R. (1996). Manufacture and use of hook-tools by New caledonian crows. *Nature, 379*, 249–251.
Hutto, D. D. (2017). Rec: Revolution effected by clarification. *Topoi, 36*, 377–391.
Hutto, D. D., & Myin, E. (2017). *Evolving enactivism: Basic minds meet content*. MIT press.
Japyassú, H. F., & Laland, K. N. (2017). Extended spider cognition. *Animal Cognition, 20* (3), 375–395.
Jelbert, S. A., Taylor, A. H., Cheke, L. G., Clayton, N. S., & Gray, R. D. (2014). Using the Aesop's fable paradigm to investigate causal understanding of water displacement by new caledonian crows. *PLoS One, 9*(3), Article e92895.
Jennings, H. S. (1906/1931). *Behavior of the lower organisms*. Columbia University Press.
Kagan, A., & Lassiter, C. (2013). The coupling-constitution fallacy: Much ado about nothing. *Pragmatics and Cognition, 21*(1), 178–192.
Kamil, A., & Bond, A. B. (2006). Selective attention, priming, and foraging behavior. *Papers in Behavior and Biological Sciences, 40*.
Kanai, M., Matsui, H., Watanabe, S., & Izawa, E. I. (2014). Involvement of vision in tool use in Crow. *NeuroReport, 25*(13), 1064–1068.
Kehagia, A. A., Murray, G. K., & Robbins, T. W. (2010). Learning and cognitive flexibility: Frontostriatal function and monoaminergic modulation. *Current Opinion in Neurobiology, 20*(2), 199–204.
Kirchhoff, M. D., & Froese, T. (2017). Where there is life there is mind: In support of a strong life-mind continuity thesis. *Entropy, 19*(4), 169.
Kracher, A. (2002). Imposing order—The varieties of anthropomorphism. *Studies in Science and Theology, 8*, 239–261.
Leavens, D. A., Hopkins, W. D., & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (pan troglodytes). *Journal of Comparative Psychology, 110*(4), 346–353.
Leavens, D. A., Hopkins, W. D., & Bard, K. A. (2005). Understanding the point of chimpanzee pointing: Epigenesis and ecological validity. *Current Directions in Psychological Science, 14*(4), 185–189.
Lee, J. (2023). What is cognitive about 'plant cognition'. *Biology and Philosophy, 38*, 18.
Little, A. G., Pamenter, M. E., Sitaraman, D., Templeman, N. M., Willmore, W. G., Hedrick, M. S., & Moyes, C. D. (2021). Utilizing comparative models in biomedical research. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology, 255*, Article 110593.
Liu, Y., & Konopka, G. (2020). An integrative understanding of comparative cognition: Lessons from human brain evolution. *Integrative and Comparative Biology, 60*, 991–1006.
Lyon, P. (2006). The biogenic approach to cognition. *Cognitive Processing, 7*, 11–29.
Lyon, P., Keijzer, F., Arendt, D., & Levin, M. (2021). Reframing cognition: Getting Down to biological basics. *Philosophical Transactions of the Royal Society B, 376*(1820), Article 20190750.
MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., et al. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences, 111* (20), E2140–E2148.
Macrì, S., & Richter, S. H. (2015). The snark was a boojum-reloaded. *Frontiers in Zoology, 12*, Article S20.
Martinho, A., Burns, Z. T., von Bayern, A. M., & Kacelnik, A. (2014). Monocular tool control, eye dominance, and laterality in new caledonian crows. *Current Biology, 24*, 2930–2934.
Matsui, H., Hunt, G. R., Oberhofer, K., Ogihara, N., McGowan, K. J., Mithraratne, K., Yamasaki, T., Gray, R., & Izawa, E. I. (2016). Adaptive bill morphology for enhanced tool manipulation in new caledonian crows. *Scientific Reports, 6*, 1–11.
Matsui, H., & Izawa, E. I. (2017). Flexible motor adjustment of pecking with an artificially extended bill in crows but not in pigeons. *Royal Society Open Science, 4*, Article 160796.
Matsui, H., & Izawa, E. I. (2019). Rapid adjustment of pecking trajectory to prism-induced visual shifts in crows as compared with pigeons. *Journal of Experimental Biology, 222*, Article jeb182345.
Maturana, H. (1970). Biology of cognition. *Urbana: Biological computer laboratory, department of electrical engineering*. University of Illinois.
Merritt, M. (2015). Dismantling standard cognitive science: It's time the dog has its day. *Biology and Philosophy, 30*, 811–829.
Merritt, M. (2021). Dances with dogs: Interspecies play and a case for sympoietic enactivism. *Animal Cognition, 24*(2), 353–369.
Miklósi, Á. (2014). *Dog behaviour, evolution, and cognition*. Oxford University Press.
Moller, P., & Bauer, R. (1973). 'Communication'in weakly electric fish, Gnathonemus petersii (mormyridae) II. Interaction of electric organ discharge activities of two fish. *Animal Behaviour, 21*(3), 501–512.
Morgan, C. L. (1903). *An introduction to comparative psychology*. Walter Scott Publishing Co.
Nakagaki, T. (2001). Smart behavior of true slime mold in a labyrinth. *Research in Microbiology, 152*(9), 767–770.
Papini, M. R. (2025). Behavioral plasticity in aneural organisms. *Psychological Review* (in press).
Papini, M. (2020). *Comparative psychology: Evolution and development of brain and behavior*. Routledge.
Pepperberg, I. M., Garcia, S. E., Jackson, E. C., & Marconi, S. (1995). Mirror use by African grey parrots (psittacus erithacus). *Journal of Comparative Psychology, 109*(2), 182.
Piaget, J. (1970). *Genetic epistemology*. Columbia University Press.
Piredda, G. (2017). The mark of the cognitive and the coupling-constitution fallacy: A defense of the extended mind hypothesis. *Frontiers in Psychology, 8*, 2061.
Raja, V. (2018). A theory of resonance: Towards an ecological cognitive architecture. *Minds and Machines, 28*, 29–51.
Reed, E. S. (1996). *Encountering the world: Toward an ecological psychology*. Oxford University Press.

Reid, C. R., Latty, T., Dussutour, A., & Beekman, M. (2012). Slime mold uses an externalized spatial "memory" to navigate in complex environments. *Proceedings of the National Academy of Sciences, 109*(43), 17490–17494.
Richardson, R. C. (2010). *Evolutionary psychology as maladapted psychology*. MIT press.
Romanes, G. J. (1884). *Animal intelligence*. Appleton.
Rubenstein, D. R., & Alcock, J. (2018). *Animal behavior* (11th ed.). r. Sinauer Associates Inc.
Rutz, C., Bluff, L. A., Reed, N., Troscianko, J., Newton, J., Inger, R., Kacelnik, A., & Bearhop, S. (2010). The ecological significance of tool use in new caledonian crows. *Science, 329*, 1523–1526.
Rutz, C., & Clair, J. J. (2012). The evolutionary origins and ecological context of tool use in new caledonian crows. *Behavioural Processes, 89*(2), 153–165.
Schwartz, B. L., Pournaghdali, A., & Hess, K. L. (2023). Comparative approaches to the natural ecology of metacognition. *Comparative Cognition & Behavior Reviews, 18*.
Segundo-Ortin, M. (2020). Agency from a radical embodied standpoint: An ecological-enactive proposal. *Frontiers in Psychology, 11*, 1319.
Segundo-Ortin, M., Heras-Escribano, M., & Raja, V. (2019). Ecological psychology is radical enough: A reply to radical enactivists. *Philosophical Psychology, 32*(7), 1001–1023.
Segundo-Ortin, M., & Raja, V. (2024). *Ecological psychology*. Cambridge University Press.
Sepúlveda-Pedro, M. A. (2024). Sense-making in the wild: The historical and ecological depth of enactive processes of life and cognition. *Adaptive Behavior, 32*(2), 117–136.
Shettleworth, S. J. (2009a). *Cognition, evolution, and behavior*. Oxford university press.
Shettleworth, S. J. (2009b). The evolution of comparative cognition: Is the snark still a boojum? *Behavioural Processes, 80*, 210–217.
Skinner, B. F. (1974). *About behaviorism*. Knopf.
Smith-Ferguson, J., & Beekman, M. (2020). Who needs a brain? Slime moulds, behavioural ecology and minimal cognition. *Adaptive Behavior, 28*(6), 465–478.
Taylor, A. H., Miller, R., & Gray, R. D. (2012). New caledonian crows reason about hidden causal agents. *Proceedings of the National Academy of Sciences, 109*(40), 16389–16391.
Tero, A., Takagi, S., Saigusa, T., Ito, K., Bebber, D. P., Fricker, M. D., Yumiki, K., Kobayashi, R., & Nakagaki, T. (2010). Rules for biologically inspired adaptive network design. *Science, 327*(5964), 439–442.
Thompson, E. (2007). *Mind in life: Biology, phenomenology, and the sciences of mind*. Harvard University Press.
Thorndike, E. (1911/2000). *Animal intelligence: Experimental studies*. Routledge.
Treisman, A. M. (1969). Strategies and models of selective attention. *Psychological Review, 76*, 282.
Troscianko, J., Von Bayern, A. M., Chappell, J., Rutz, C., & Martin, G. R. (2012). Extreme binocular vision and a straight bill facilitate tool use in new caledonian crows. *Nature Communications, 3*(1), 1110.
Varela, F. J., Thompson, E., & Rosch, E. (1991/2017). *The embodied mind: Cognitive science and human experience (original/revised edition)*. MIT Press.
Wagman, J. B., Langley, M. D., & Farmer-Dougan, V. (2017). Doggone affordances: Canine perception of affordances for reaching. *Psychonomic Bulletin & Review, 24*, 1097–1103.
Ward, D., Silverman, D., & Villalobos, M. (2017). Introduction: The varieties of enactivism. *Topoi, 36*, 365–375.
Wasserman, E. A. (1993). Comparative cognition: Beginning the second century of the study of animal intelligence. *Psychological Bulletin, 113*, 211–228.
Watson, J. B. (1913). Psychology as the behaviorist views it. *Psychological Review, 20*(2), 158–177.
Wheeler, M. (2011). Mind in life or life in mind? Making sense of deep continuity. *Journal of Consciousness Studies, 18*, 148–168.
Wittek, N., Matsui, H., Kessel, N., Oeksuez, F., Güntürkün, O., & Anselme, P. (2021). Mirror self-recognition in pigeons: Beyond the pass-or-fail criterion. *Frontiers in Psychology, 12*, Article 669039.
Yanagawa, K., & Matsui, H. (2025). On concepts of action and behavior as the implicit point of agreement between enactivism and radical behaviorism. *Asian Journal of Philosophy, 4*, 18.
Zhang, Y. S., & Ghazanfar, A. A. (2018). Vocal development through morphological computation. *PLoS Biology, 16*(2), Article e2003933.
Zilio, D., & Carrara, K. (Eds.). (2021). *Contemporary behaviorisms in debate*. Springer International Publishing.