

A World of Minds: Ecological Psychology as a Framework for Comparative Cognition

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Introduction

Comparative cognitive science explores the differences and similarities in cognitive abilities across species, along with the purported mechanisms that enable these capacities. This is a multifaceted enterprise which benefits from the contribution of many fields, all of them unified by a broadly evolutionary perspective that seeks to find out how widely specific mind-related functions are distributed in nature.

As with any scientific discipline, empirical research in comparative cognition is deeply influenced by the theoretical frameworks or paradigms that researchers adopt and the commitments these entail. In this case, most researchers adopt a computational-representational approach, which entails that cognition is brain-based information processing. This commitment, far from being innocuous, has profound effects on *what* they study (e.g., how they conceive of the different cognitive abilities), *how* they study it, and even *which* organisms they submit to study.

Consider, for instance, the comparative study of decision-making. According to Olmstead and Kuhlmeier (2015), most explanatory frameworks of decision-making in comparative cognitive science are based on neuroeconomics and take mammalian brains as their primary empirical models. This creates a challenge when attempting to study decision-making in non-mammalian organisms—one that becomes even greater when studying non-animal species. Although there is empirical evidence to suggest that some species of plants, fungi, bacteria, and protists exhibit complex patterns of behaviour akin to decision-making

(Latty & Beekman, 2010; Lee et al., 2023; Reid et al., 2015; Segundo-Ortin & Calvo, 2022; Sheldrake, 2021; Smith-Ferguson & Beekman, 2020), doubts nevertheless persist as to whether these capacities can exist without a nervous system (Adams, 2018; Alpi et al., 2007; Mallatt et al., 2020; Taiz et al., 2019).

Building on these considerations, this chapter examines how the principles of ecological psychology—an influential alternative to traditional cognitivist (and neurocentric) theories of perception-action and perceptual learning—can be applied within comparative cognitive science. Section 1 introduces the main theoretical and methodological foundations of ecological psychology compared to traditional, inference-based models of perception and action (for a comprehensive description, see Blau & Wagman, 2023; Segundo-Ortin & Raja, 2024), and explores the types of research questions that arise when adopting an ecological perspective in comparative cognitive science. Section 2 offers a comprehensive historical review of the most important empirical studies of perception and action in non-human organisms up to the present day. This section closes by focusing on the case of plants, which highlights the broader applicability of ecological psychology compared to traditional neurocentric perspectives. Finally, the chapter adopts a philosophical perspective, considering how a Gibsonian-inspired comparative cognitive science helps to mitigate anthropocentric biases and deepen our understanding of cognition across diverse forms of life.

1. Fundamentals of an ecological comparative psychology

The first distinction between ecological and inference-based (computational) theories of perception concerns where the process of perception begins. Whereas inference-based approaches assume that perception begins with the reception of impoverished stimuli, ecological psychologists believe that perception is a matter of detecting information that is made available in the temporally extended structural properties of some ambient energy array. To see this idea more clearly, think of what happens when the light emanating from a bulb propagates into a room filled with objects. As the light is reflected from the surfaces of the objects, it gives rise to different patterns, textures, gradients, shadows, etc., that structure the light, and which can be detected as an observer occupies different points of observation. Importantly, this structuring occurs according to deterministic laws, meaning that “there is *only one* situation that could produce this distribution of light and *only one* distribution of light that could have been produced by this situation” (Blau & Wagman, 2023, p. 38). Since a particular situation in the environment (α) lawfully generates a unique distribution of light

(β), the occurrence of β non-ambiguously corresponds to, and guarantees, the presence of α . In ecological terms we say that β “specifies” α , whereby this specification forms the basis of the ecological notion of information: that is, β provides information about α in virtue of being specific to it.

Crucially, because the structural properties of an ambient energy array are non-ambiguous regarding the environment’s features (its composition, layout, etc.), organisms with the appropriate perceptual systems can perceive the latter *directly* by paying attention to (or detecting) said properties. Thus, according to the ecological approach, “[p]erception is not the process of inferring a meaningful environment from meaningless stimulation. Rather, it is an ongoing process of detecting meaningful information that yields meaningful experience” (Thomas et al., 2019, p. 238).

Crucially, a structured pattern in an ambient energy array can only be meaningfully characterized as information in relation to some species that can detect it. For instance, whereas some aquatic animals are capable of electrolocation and hydrodynamic perception, changes in the voltage patterns of the electric field or the water provide no information to human beings. This opens the way for a comparative analysis of the different informational variables and media that species exploit when trying to perceive the environment.

The second idea we want to highlight is that, among the properties of the environment that organisms perceive directly, are affordances. Affordances are opportunities for action that a situation offers to an individual with the requisite morphology and capacities. Affordances imply a complementarity or “mutuality” of organism and environment: a bottle affords grasping for a human adult with functional hands, but may not do so for a child if their hand is too small or their motoric abilities are not sufficiently developed; and it certainly won’t do so for a goldfish, which lacks hands altogether. As such, elaborating a taxonomy of the environment’s affordances is only possible if we scale the properties of the environment to an organism’s body and capabilities. Considering this, it makes sense to ask, for instance, whether two different species perceive the same affordances when placed in the same setting.

Importantly, there is a substantive body of empirical evidence indicating that, in humans, the perception of affordances takes precedence over, and is independent of, the perception of properties of either the organism or the environment (see Segundo-Ortín & Raja, 2024). For instance, the perception of *reachability* or *passability* cannot be reduced to a simple combination of perceived bodily or tool properties (Thomas & Riley, 2014; Wagman & Stoffregen, 2020; Higuchi et al., 2011). In principle, the questions that motivated these initial empirical studies on humans can also be asked of non-human animals, providing an

opportunity to compare and contrast different species' perceptual processes, including our own (Wagman et al., 2024).

The last crucial difference between ecological and traditional theories of perception is that the former conceives of perception as an *embodied* process. In most cases, perceiving a particular property of the environment requires that the agent actively searches for it, exploring both the ambient energy array—that is, fixating attention on different structural properties, moving to create energy flow, manipulating objects to reveal their invariant properties, and so on. If this is the case, perception cannot be reduced to brain processes alone, for it involves the activity of larger “perceptual systems” (J. J. Gibson, 1966) that encompass the sensory organs, the brain, and the entire body-environment system. James Gibson captured this view when he claimed that “[o]ne sees the environment not with the eyes but with the eyes-in-the-head-on-the-body-resting-on-the-ground” (1979[2015], p. 195).

Recognizing that perception is an embodied activity raises important questions for comparative cognition. For instance, thinking in terms of perceptual systems opens the possibility of investigating the specific organs that different species put to work in detecting information, and how they use their bodies to explore and manipulate different energy arrays. Do different species use similar exploratory strategies when located in the same or in sufficiently similar contexts? What relevant differences can be found among the visual (or other perceptual) systems of different species? Do these differences affect how they perceive and respond to the affordances of the environment?

Drawing from Wilson and Golonka (2013), we argue that adopting an ecological approach to comparative cognition involves asking three questions. First, we must identify the cognitive task to be solved. As they point out, “[e]mbodied cognition solutions solve specific tasks, not general problems, so identifying how an organism produces a given behaviour means accurately identifying the task it is trying to solve at the time” (p. 2). Some tasks, for instance, are more complicated than others, and they may require the perception of a sequence of affordances that are nested in an orderly fashion, meaning that a task can be decomposed into a series of smaller tasks. The second question concerns the resources that the organism has access to in solving the task. These resources will encompass bodily resources (perceptual systems) and environmental resources (informational variables that specify the relevant affordances) alike, and the analysis of the cognitive process must include an exhaustive list of these. The third question pertains to how organisms assemble these resources. How can perceptual information specifying an object's reachability be used in conjunction with the organism's ability to perceive its own movement?

In the following section, we attempt to show how ecological psychologists interested in comparative cognition have put these questions to work.

2. Empirical applications of ecological psychology to comparative cognition

A key aim of ecological psychology is to offer an explanation of the perceptual guidance of action that can be applied to (potentially) all organisms (Turvey, 2019). Aligned with this view, Eleanor and James Gibson were convinced that we could formulate general principles of perception and perceptual learning by carefully observing and studying how different species make their way in the world (Adolph & Kretch, 2015, pp. 128-129).

Any review of the applications of ecological psychology to the comparative cognitive sciences must begin with Eleanor Gibson. She entered the field when Howard Liddell invited her to join his “Behavior Farm” lab at Cornell’s Psychology Department. Liddell’s lab was primarily focused on studying neurosis in sheep and goats through classical conditioning. While Gibson remained sceptical about Liddle’s studies, this opportunity allowed her to work on problems related to learning and development, and to acquire some experimental skills that would prove useful in the future.

Following this, Eleanor Gibson began collaborating with Richard Walk, who led a rat lab specializing in learning. Their early experiments examined how repeated exposure influenced the development of shape discrimination. This work convinced Gibson that a theory of perceptual development could not rely solely on passive exposure to environmental features during early development but must also include active exploration as a central component.



Figure 1. A woman calling a child from across the deep side of the visual cliff. From Gibson and Walk (1960) Image taken from the US National Institute of Health website: https://openi.nlm.nih.gov/detailedresult.php?img=PMC4569749_fpsyg-06-01381-g009&req=4. Image is reprinted under CC-BY-SA 4.0.

Soon after, Gibson and Walk grew interested in depth perception, and developed their famous “visual cliff” (E. J. Gibson & Walk, 1960). The apparatus consisted of a large, clear glass platform elevated off the ground (Fig. 1). One half of the platform was covered with a solid surface (usually patterned with a checkerboard), while the other half had the same pattern on the floor beneath the glass. This arrangement created the illusion of drop (a *cliff*), even though the glass remained flat and continuous, allowing safe movement across it. They first tested the visual cliff with 90-day-old rats. The rats had been split into groups before their eyes opened, with one group deprived of light until the test. Interestingly, Walk and Gibson found that even the light-deprived rats avoided the cliff, indicating that they could perceive the possibility of falling without previous visual experience (Walk et al., 1957). Walk and Gibson then decided to test other animal species. First, they found that chicks and goats less than a day old avoided the cliffside too, whereas kittens reared in the dark needed a short training period before they avoided the cliff. Next, crawling babies, aged from six to twelve months, were tested, with the following results:

Perception of depth has developed by the time locomotion is possible in human infants. [...] However, it is also true that crawling experience makes a difference for navigation. Brand new crawlers are apt to descend to the deep side of the cliff as often as to the shallow. It’s not because they can’t perceive depth, but because they

require some experience in visually guiding locomotion before reliable selection of surface develops. (E. J. Gibson, 2002, pp. 74-75)

Inspired by this work, recent experiments have studied affordance perception in non-human animals (see Wagman, 2019; Wagman et al., 2019). For instance, empirical studies of affordance perception typically investigate the perception of so-called “action boundaries” – the point at which a given behaviour becomes impossible, making it necessary to opt for another course of action (see Warren, 1984 for a canonical example).¹ These experiments are important because they indicate that “perception reflects the fit between action capabilities and environmental properties rather than an arbitrarily defined property” (Wagman et al., 2019, p. 74). Experimental protocols originally devised to test, for example, the correlation between reaching abilities and the perception of objects’ *reachability* have been extensively applied to, among others, rodents (Cabrera et al., 2013; Jiménez et al., 2019) and dogs (Wagman et al., 2017, 2018), with results similar to those previously reported in humans. Another example is the perception of *passability* (Warren & Whang, 1987). Experiments with hermit crabs indicate that their perception of whether an aperture affords passing varies in conditions where the crabs occupy more space, similar to findings in humans (Sonoda et al., 2013). This reinforces the view that perception reflects organism-environment mutuality across species.

Interception of moving objects is another common interest among Gibsonian psychologists. Studies have shown that, for visually perceiving animals, information about the future position of an object is specified in the pattern of optical acceleration of the target object (Serres & Ruffier, 2017; Shaffer et al., 2004). The same can be said for another well-studied variable: time-to-contact or *tau*. Even though *tau* was originally studied for human drivers and plummeting gannets using visual information (Lee, 1976; Lee & Reddish, 1981), it is now recognized as a crucial variable for many non-visual navigation and approaching tasks in multiple species (Lee, 2009). Importantly, these studies show that, regardless of the anatomical differences in their perceptual systems, different species can control their behaviour based on the same informational variables.

Ecological research in comparative cognition does not stop with *Animalia*, however. Plant behaviour, for instance, has also been extensively studied from an ecological

¹ Warren explored the concept of “action boundaries” by identifying the critical height at which stepping onto a stair bipedally becomes impossible for an individual, necessitating an alternative action such as using the arms, seeking support, or avoiding the step.

perspective despite James Gibson's own neglect of plants (Calvo & Lawrence, 2023; Carello et al., 2012; Calvo et al., 2014; Calvo, 2016; Calvo et al. 2017; Frazier, 2025; Lee & Ponkshe, 2025). General Tau Theory (Lee, 2009) tells us that control-oriented movements involve detecting temporal, rather than spatial, information, such as distance to or size of a target. Theoretically, this principle extends to non-animal organisms like paramecia (Delafield-Butt et al., 2012) and plants (Carello et al., 2012), and it is applicable, for instance, to the study of some goal-oriented growth patterns in climbing plants. One empirical hypothesis is that vines control growth-based approach to supports by detecting temporal information as specified by the tau invariant (see Calvo et al., 2014). If the hypothesis is correct, plants would control their approaching behaviour by perceiving the affordances specified by tau.

One illustrative study of tau-guided movement in plants (Tetlow, unpublished ms.) analysed the rhythmic opening of *Ipomoea purpurea* (morning glory) flowers—a process known as anthesis. Unlike tropic movements, which are directed by environmental stimuli like light or gravity, anthesis is a type of nastic movement: it follows an internal timing mechanism and unfolds independently of directional cues. Using time-lapse video, the study demonstrated that the petals' movement toward their fully open position followed a smooth, goal-directed trajectory consistent with the tau principle. This suggests that the timing and control of petal movement were not random or mechanical, but ecologically attuned, much like the visually-guided landings of birds or the gaze adjustments of primates. In this way, the study supports the idea that plants, despite lacking nervous systems, can exhibit controlled, purposive movements that conform to the same temporal invariants observed in animals—underscoring the broader relevance of tau theory for comparative cognition across life forms.

We may also turn to subterranean examples to further illustrate plant affordance perception. Root systems exploit hydrodynamic gradients and soil textures to guide their growth, and they can adjust growth direction and rate to access nutrients in the soil (Yokawa & Baluška, 2018). Likewise, roots perceive the “supportability” of the soil, and whether it affords the required stability for functional root development. As with studies on animals, this demonstrates both the mutuality of organism and environment, and shows that affordances are always scaled to the organism's perceptual and morphological capabilities. This suggests that plants, like animals, detect information directly relevant to their functional needs, revealing ecological specificity to their perceptual systems.

Interestingly, this last point opens up the possibility for a comparative study among different plant species. Consider Venus flytraps (*Dionaea muscipula*) and sundews (*Drosera*).

Both are carnivorous, yet their methods of capturing prey differ. The Venus flytrap's trap-closing mechanism is triggered by repeated stimulation of sensory hairs, while sundews use mucilaginous glands on their tentacles to ensnare insects. These species perceive and exploit different affordances, reflecting their specific ecological adaptations.

Extending ecological psychology to plants illustrates the broad applicability of the theory's principles (Frazier, 2025; Lee & Ponkshe, 2025), allowing us to extend our comparative analysis beyond animals and to build a broader, more inclusive understanding of cognition that spans different biological kingdoms.

3. Fighting anthropocentrism

In recent years, researchers in comparative cognition have highlighted a range of biases that permeate the field, potentially undermining our ability to accurately identify and document both the continuities and differences in cognitive abilities across species.

One common bias is anthropomorphism. Broadly speaking, anthropomorphism is defined as “[t]he attribution of human psychological, social, or normative property to a non-human animal, usually with the suggestion that the attribution isn’t justified” (Andrews, 2020b, p. 262). Debates about anthropomorphism and how to avoid it are common currency in the field. However, as Andrews (2020a) suggests, it is not clear what being anti-anthropomorphic implies. On the one hand, some researchers argue that we must avoid describing non-human behaviour in “mentalistic” or folk-psychological terms, preferring more “behaviouristic” notions instead—e.g., using “affiliative relationship” over “friendship.”

Even though we sympathize with the use of operationalized terms over mentalistic ones, we note the risk of applying double standards when claiming that mentalistic terms should be avoided for non-human species only. In fact, as Wynne (2007) argues, the problem of folk-psychological terms is that, often, they offer an *appearance* of explanation uniquely (see also Penn 2011). Wynne illustrates this point by comparing the use of the term ‘remorse’ to simultaneously describe the behaviour of a dog and a child. While the former is usually criticized as a sign of anthropomorphism, the latter remains unproblematic. However, Wynne argues that “[t]here is no science of “remorse” to which we have appealed. Even as an explanation of human behaviour, “remorse” is vacuous; it lacks any power to predict or control future behaviour” (p. 133). If Wynne is correct, then the question is not whether we are being anthropomorphic when attributing remorse to the dog compared to the human child, but whether the attribution is explanatorily vacuous in both cases.

Therefore, instead of simply denying the use of folk-psychological terms in comparative cognition, a better strategy to avoid anthropomorphism would be to formulate good, non-idiosyncratic, operationalized definitions of our psychological terms (see Andrews & Huss, 2014, p. 726). Once we have reached an operationalized definition of, for example, remorse (or friendship, or fear, and so on) we can ask whether the behaviour of the dog and the human child qualify as instances of it, and we can proceed to compare the species-specific cognitive mechanisms that underly remorse in each species.

One problem here, however, is that we still run the risk of simply re-describing behaviour (albeit in operational terms) rather than specifying the nature of the cognitive mechanism that supposedly underlies and produces the behaviour—which is, after all, the ostensible goal of much cognitivist comparative cognition (see Penn 2011). That is, most researchers are not looking for evidence of ‘mindedness’ or ‘understanding’ construed as an ability, but for evidence of particular kinds of information-processing mechanisms that can be inferred from observed behaviour. Moreover, this strategy accepts a premise that we, personally, would reject: namely, the entire concept of anthropomorphism implies that it is possible to demarcate *a priori* those traits that belong solely to humans, something that is untenable in an evolutionary framework where at least some traits must be shared by descent. In this sense, anthropomorphism is simply a red-herring, and it is actually anthropocentrism—the practice of holding the cognitive capacities of human beings as the “gold standard” against which other species’ cognitive abilities are judged—that is the real problem we should tackle (Barrett 2015; Van Woerkum & Barrett 2024).

Recognizing these issues thus helps us avoid the opposite tendency to anthropomorphism: anthropectomy or anthropodenial (de Waal, 1999; Andrews & Huss, 2014; Andrews, 2020a). This is the inverse of the point we make above: the *a priori* rejection of a cognitive trait in some non-human species, based on the unproven assumption that the ability is uniquely human. Adopting an eliminativist stance towards non-human animals while we keep describing human cognitive processes in folk-psychological terms uncritically is, we hold, a clear sign of anthropectomy.

Similarly, taking on the above points helps us recognize that another bias, anthropofabulation, is clearly a particular flavour of anthropocentrism. Anthropofabulation occurs when we characterize some cognitive capacity by reference to some artificially inflated account of human performance and apply these competence criteria to questions about other species’ cognitive abilities. According to Buckner (2013), we clearly see anthropofabulation in comparative studies about social cognition which assume that our capacity to understand

and predict others' behaviour requires mindreading capabilities. This view exemplifies anthropofabulation because it uncritically assumes mindreading to be a *sine-qua-non* condition for social cognition, overlooking that other simpler yet functionally similar cognitive mechanisms may be in place both for human and non-human species (see Lurz, 2011; Andrews, 2020b, Chapter 7; Barrett et al., 2022). The same occurs, for instance, when Adams (2018) dismisses cognitive abilities in plants and bacteria, arguing that cognition requires higher-order mental representations with semantic contents. Remarkably, the example of Adams shows how anthropocentrism is often a consequence of adopting an anthropofabulatory attitude in the first place (see Segundo-Ortín & Calvo, 2019).

Although the biases described above were developed in isolation, as we have seen they are all grounded ultimately in anthropocentrism, and this represents the real barrier to a genuinely comparative science of cognition (see de Waal, 1999; Buckner, 2013; Barrett, 2015, 2016). By placing human beings at the top of a *scala naturae* and using human cognitive abilities to set the agenda for comparative cognitive science, we inadvertently privilege evolutionary continuity at the expense of acknowledging that evolution is also a diversity-generating process. Other organisms are likely to have evolved their own unique, species-specific mechanisms to navigate the complexities of their environment. This can affect negatively our capacity to formulate hypotheses regarding non-human species' behaviours and perceptual experiences (see Brebner et al., 2024), and steer us toward unjustified conclusions, such as assuming that chimpanzees cannot learn by imitation (Andrews, 2020b, p. 213).²

Such anthropocentrism is, we hold, further reinforced by the previously mentioned marriage between comparative cognitive science and computationalism (see Barrett, 2016). After the fall of behaviourism, comparative psychologists found refuge in the computer metaphor, and came to understand cognition as “the mechanisms by which animals acquire, process, store, and act on information from the environment” (Shettleworth, 2010, p. 4).

Unlike folk-psychology, descriptions of cognitive abilities in computational terms (e.g., “information-processing,” “encoding,” “retrieving,” “storing,” and so on) offer an appearance of abstraction and neutrality. However, this appearance vanishes as soon as we remind ourselves that cognitive computational notions originated in human technological artifacts rather than in observations of behaviour or physiological records (Brooks, 1991).

² Other accusations of anthropocentrism concern, for example, the use of the mirror self-recognition task as a test for self-consciousness (see Andrews, 2020b, pp. 96-98; Barrett, 2016, p. 11), or the use of monitors to present visual stimuli (Brebner et al., 2024).

Hence, computational concepts and models retain a “human stain” (Lyon & Keijzer, 2007), as they were created to mirror human capabilities—most notably, symbol manipulation, linguistic reasoning, and mathematical calculation—in the first place (see also Brooks, 1991, p. 139). Echoing this suspicion, Van Woerkum & Barrett (2024) refer to the uncritical adoption of computationalism in comparative psychology as part of a process of “anthropofabrication,” whereby we assume computational approaches are entirely species-neutral, rather than heavily anthropocentric, and artificially generate more similarity between human and non-human cognition than is warranted.

Moreover, mainstream approaches in comparative psychology are not only computational, but neurocentric too. For instance, after characterizing cognition in terms of information-processing, Olmstead and Kuhlmeier claim that “[a]ny cognitive process, therefore, is internal: it happens inside the organism’s brain” (Olmstead & Kuhlmeier, 2015, p. 3), thus rejecting any possibility that bodily and environmental resources can contribute to the successful task performance, and so immediately biasing the kinds of studies that will be designed and conducted. Consequently, it is assumed that similar cognitive abilities will therefore require only the presence of the same (or functionally analogous) brain areas, and other species can therefore be judged depending on how similar their neural makeups are to ours.

Taking this into account, we hypothesize that adopting non-neurocentric and non-computational theories of cognition, such as Gibsonian ecological psychology, is a potentially fruitful step to building a non-anthropocentric comparative psychology. It is only by abandoning the view that cognition is brain-bound information processing that we can get a sense of how different species with different bodies, perceiving different affordances, can solve cognitive tasks in potentially unique ways. A recognition of natural cognitive diversity must begin with a recognition of the diversity of organism-environment systems and perceptual capabilities.

To illustrate this point, we will mention some empirical research projects that already point in this direction. For starters, let us consider Barbara Webb’s (1995) studies of cricket phonotaxis.³ To attract mates, male crickets emit species-specific acoustic signals (‘songs’), composed of ‘syllables’ with species-specific patterns. Females can distinguish these songs from background noise and from other heterospecific male calls and use them to steer

³ Webb (2009) recognized ecological psychology as an inspiration for her approach (see also Wilson & Golonka, 2013).

towards calling males and find suitable mates. Yet, how does this process unfold? How do female crickets successfully find their mates? Webb provided an elegant explanation of this phenomenon, focusing on the morphology of the female cricket's auditory system and the structure of the acoustic signals.

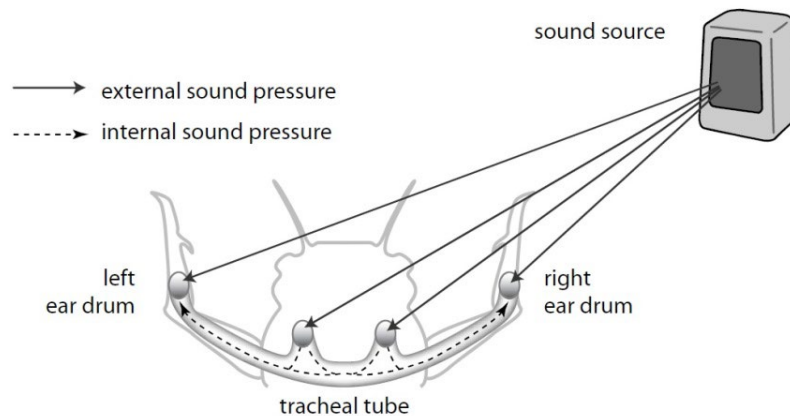


Figure 2: Illustration of the structure of the female cricket's auditory system. Continuous arrows represent external sound waves. Discontinuous arrows represent the internal sound waves (from Barrett 2015a, Fig. 3.1, p. 52, with permission)

The auditory system of female crickets includes two eardrums located on the tibiae of their front legs, which are linked to a tracheal tube that connects to openings on the thorax (Fig. 2). This configuration allows sound to reach the eardrums both externally (directly from the source) and internally (through the tracheal tube). As a result of this configuration, a female cricket's auditory system is inherently directional: on the side closest to the sound source, the external sound travels a shorter distance than the internal sound, while on the side further from the source, the sounds travel nearly identical distances. This means that the sound will be out of phase on the nearer side and in phase on the farther side, resulting in greater eardrum vibration on the side closer to the sound. In addition, the eardrums are connected to a pair of dedicated inter-neurons that activate once the intensity of the vibration crosses a certain threshold. The interneuron on the side with stronger vibrations therefore fires first, causing the female to steer in that direction.

Additionally, the male's song—its rhythm and frequency—has co-evolved with the female auditory system, meaning that the patterning of syllables is attuned to the activation profiles of the females' inter-neurons, ensuring that the rate of neuronal activation is neither too fast (which would make it less clear which neuron fired first) nor too slow (which would cause the female to drift off course). The trachea is also involved here, as its physical structure evolved to transmit sounds of the frequency produced by conspecific males. The structure

of the male's call is therefore just right in terms of enabling the female to both steer accurately toward the male and to pick out his song, because the steering and "discrimination" mechanisms are one and the same. This co-adaptation enables the female to be more responsive to these signals while filtering out background noise, detecting the relevant information that affords locating the mate. Additionally, by responding to the vibrations' amplitude, the female is guided toward the loudest song, ensuring she finds the best possible mate—one likely to pass on the most advantageous genes.

The appeal of this hypothesis was that a single, very simple, rule of thumb—turn in the direction of the neuron that fires first—could account for the female's ability to (a) detect conspecific male song, (b) discriminate them from the songs of other species and background noises, and (c) select a good quality male. This simplicity was also its weakness, however, as the "onset hypothesis," as it was known, seemed just too simple to account for such complex behaviour.

This is where Webb and her robotic crickets played a central role. Webb tested her hypothesis using robotic models, which "performed like the crickets, effectively and consistently finding the specific sound source under various conditions" (1995, p. 132). Interestingly, Webb's robots had "no pre-stored information about the male cricket's songs and acted purely based on their physical configuration" (Wilson & Golonka, 2013, p. 4). This suggests that cricket sound-seeking and tracking behaviour similarly relies on the scaling of perception-action loops to the available affordance-specifying information, rather than stored data and inference mechanisms. In the words of Barrett:

the females' "mate-choice" behaviour was a truly emergent property; that is, there was no "choice" mechanism explicitly programmed into the robot; it showed this behaviour purely as a consequence of the way its internal mechanism interacted with the environment. (2011, p. 54)

Thus, instead of assuming that crickets generate sophisticated models of the environment based on their perception and conclude that phonotaxis requires considerable computational complexity, Webb decided to start from studying the morphology of the crickets' auditory system in relation to the environment. The 'choice' behaviour comes about through the interaction of the female's body (the configuration of eardrums and trachea), brain (the activity profiles of the inter-neurons), and the environment (the structure of the male's song). As such, cricket phonotaxis capitalizes on the structure and resources of the entire organism-environment system, and cannot be understood by investigating any of these elements in isolation. These pioneering studies further suggest that the complexity of

behaviour need not bear any relationship to the complexity of the mechanism(s) that produce it.

This is something that can also be seen in the behaviour of salticid spiders belonging to the taxon *Portia*. These are predatory species that hunt other spiders, using a range of sophisticated tactics that, at first glance, seem astonishing for an organism with a brain no larger than a poppy seed. Most notably, *Portia* spiders take detours through the environment when on the hunt for prey. Taking a detour is regarded as cognitively demanding because it seemingly requires the spider to retain a representation of the prey's location once it is out of sight, combined with the ability to plan a route that will take the spider to the prey. However, a more detailed knowledge of the *Portia* spider's visual system, along with close attention to the exploratory behaviour shown by the spiders suggests an equally plausible, but more ecological, explanation for this conduct (Barrett, 2011).

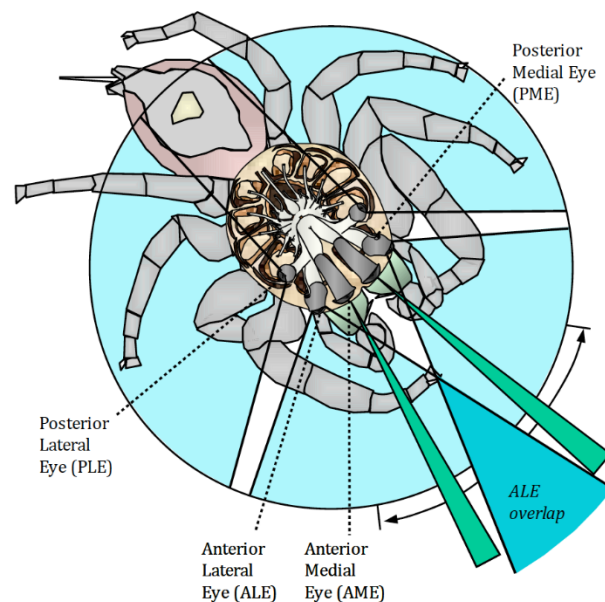


Figure 3: Diagram of the visual field of the *Portia* spider as viewed from above. The secondary eyes (posterior lateral, anterior lateral and anterior medial) specialize in detecting movement and provide the *equivalent of peripheral vision shown by mammalian eyes*. The anterior medial eyes, in turn, can be moved independently, and are specialized in detecting fine details of objects. (From: Hill, D. M. (2010), Fig 16, p. 14). Image used under a Creative Commons Attribution 3.0.

Salticid spiders have six secondary eyes arranged around the sides and two larger anterior-medial (AM) eyes at the front (Fig 3). The AM eyes are tube-like structures with the retina positioned at the end of the tube. Whereas the secondary eyes specialize in detecting movement, offering the equivalent of peripheral vision shown by mammalian eyes, the AM eyes enable the spider to detect fine detail and colour. In addition, the AM eyes are “active,” meaning that the spider can move them to bring different parts of the visual scene into focus on the retina. The eye-tubes are therefore functionally equivalent to fovea of the mammalian

eye. Moreover, it has been suggested that the complex patterns of movement shown by the AM eyes are specific to certain objects, enabling the detection and discrimination of relevant features in the spiders' environment. That is, the AM eye acts as a filter that detects relevant affordances for moving through the dense vegetation of their natural habitats. This arrangement, with a division of labour between secondary and AM eyes, means that salticid spiders possess amazingly good vision for such a small creature with a very limited number of photoreceptors. For instance, they can detect movement from any angle and then, via a servomotor mechanism that turns position of stimulation on their retina into steps taken by the legs (reminiscent the female crickets steering mechanism), they are able to turn and orient their AM eyes toward the object, which enables them to pick up fine details.

In experiments designed to investigate the detouring behaviour of spiders, researchers presented the spiders with a choice between two rampways leading to prey positioned atop a connected pole: one ramp was complete, providing a path to the prey, while the other had an unbridgeable gap (Tarsitano, 2006; Tarsitano & Andrew, 1999; Tarsitano & Jackson, 1997). In addition, the spiders were allowed to see the entire apparatus and would show their characteristic turning and scanning movements. This stationary scanning before choosing a route creates the impression that the spiders are planning their path in advance. However, detailed analysis of scanning patterns suggests a more ecological explanation.

Importantly, the spiders displayed distinctive variations in their turning directions as they scanned complete versus incomplete routes. In both cases, they would begin to scan at the prey item and then backtrack away from it till the beginning of the rampway. In the case of complete routes, they would complete the scanning; on incomplete routes, however, they reversed direction upon encountering the gap, scanning back toward the prey. This variation across the two conditions suggests that the spiders' behaviour depends on whether they detect an unbroken horizontal line in their field of view: If the line remains unbroken, they continue to scan and fixate in the same direction; if, on the other hand, they detect the end of a horizontal line specifying an impassable gap, they turn back until it once again detects the horizontal line and the prey. That is, rather than engaging in some high-level planning of their routes, the spider seems to be using a simple feedback mechanism to detect the relevant affordances of its environment, and this enables it to abandon incomplete routes and move toward those that ultimately lead to prey. Crucially, this behaviour does not require the spiders to perceive poles, rampways, or gaps as distinct objects. Instead, they perceive the horizontal features that afford movement toward prey. This in turn reflects the functioning

of the AM eyes, which move in ways that are attuned to the detection of these invariants and so automatically filter out irrelevant features.

Paying greater attention both to embodiment and the specifics of how animals behave when confronted with a problem (that is, how they regulate their behaviour with respect to the affordances offered to them) is, in our view, a richer and more satisfying way to understand other organisms on their own terms, as opposed to theorizing about what may or may not be going on in their heads alone. Consider, too, New Caledonian crows (NCC). Although other avian species like jays or ravens are known for using tools, NCC stand out due to the remarkable diversity and inventiveness of their tool use. However, NCC do not outperform said species in non-tool using tasks (Teschke et al., 2013). This seemingly paradoxical finding is usually explained by assuming that the NCC's competence is highly domain specific, and that they have evolved brain-based cognitive mechanisms specific for tool-using. An alternative explanation, however, suggests that the exceptional tool-using abilities of NCC are closely linked to their unique anatomical features, particularly the structure of their bills and the positioning of their eyes (Troscianko et al., 2012). Unlike other corvids, NCC have straight bills and a higher degree of binocular convergence in their vision (i.e., more forward-facing eyes). These adaptations enable NCC to securely hold a tool while visually tracking its length during use. As a result, NCC demonstrate superior tool-using performance compared to other species with similar cognitive capabilities.

Thus, even among larger-brained species, where it is often assumed that cognitive solutions are purely brain-based, paying closer attention to bodies and how these afford certain actions that are constitutive of the cognitive solutions they employ may yield significant insights. Accordingly, ecological and embodied approaches can be applied profitably to non-human primates too (Barrett et al., 2022). Due to their relatively large brain size, much research on primate social cognition has focused on identifying the brain-based correlates of the cognitive mechanisms that enable anthropoid primates to interpret the behaviour of their group members (Dunbar, 2024). This approach, however, tends to reflect a heavily anthropocentric bias stemming from the earliest incarnations of the "social intelligence" hypothesis (Humphrey, 1976).

To overcome this biased perspective, Barrett et al. (2022) remind us that social life is, by nature, participatory rather than observational, and that brains primarily evolved to control bodies and facilitate interactions within dynamic environments (Engel et al., 2015). Hence, they propose that researchers pay greater attention to the manner in which primates physically coordinate their behaviour in relation to the affordances of their environments,

including their group mates. This research, in addition, can be related to aspects of primate brain structure and function that are well documented empirically (e.g., areas of visual cortex and the structure of the lateral geniculate nucleus, along with areas of the parietal cortex associated with peripersonal space). As such, a more ecological approach may help us identify those traits that humans share with other species by focusing on the concrete behaviours that help shape and scaffold particular kinds of social interactions, and from which more complex strategies supported by language and culture can emerge (e.g., Van Dijk & Withagen, 2014). This seems more evolutionarily appropriate and less anthropocentric than adopting the current ‘top-down’ approach, which starts with high-level human capacities such as mentalizing and perspective-taking (which may well be entangled with human cultural artifacts, see Noë, 2023), and so ensures that non-human primates can only ever show the ‘pre-cursors’ or ‘primitive’ manifestations of human psychological strategies.

To conclude, we also hold that the adoption of an ecological approach can help us get a better sense of human cognition. For instance, ecological explanations of cognitive tasks, based on the detection of affordance-specifying information in the environment, are less cognitively demanding than computational explanations, thus avoiding the risk of falling into anthropofabulation. As an illustration, consider the ecological explanations of the outfielder problem—the problem of determining where and when a flying baseball will land in order to catch it (Wilson & Golonka, 2013). Ecological explanations rely on the detection of specifying information and ongoing perceptual-motor adjustments at the expense of sophisticated mental calculations of the ball’s trajectory, velocity, and so on. The same occurs with ecological accounts of interpersonal coordination, which can do without positing mental simulations and mindreading capabilities (Marsh et al., 2006, 2009; Segundo-Ortin & Satne, 2022).

In addition, focusing on the organism-environment system as the main explanatory unit can also help us explain some seemingly unique human cognitive capabilities (e.g., linguistic reasoning, symbolic production and manipulation, or mathematical calculation: Barrett, 2015, 2016). The crucial difference between human and non-human species is that the environment in the human organism-environment system is richly saturated with highly sophisticated cultural artifacts, practices and institutions, in which we are trained from birth (Heft, 2020; Segundo-Ortin, 2024). For instance, learning the norms that rule how mathematical symbols must be manipulated makes it possible that a pen and a sheet of paper afford the possibility of solving a mathematical puzzle (Clark, 2008). To be sure, human beings have evolved neural structures that allow us to acquire the capabilities for highly

sophisticated cognition, but an explanation of human cognition, both evolutionary and developmental, must begin by taking seriously that the minimum unit of analysis is the ecological organism-environment system.

Conclusion

This chapter has explored how the principles of ecological psychology provide a compelling framework for comparative cognitive science, offering a robust alternative to the dominant brain-centric, computational models. By focusing on the mutuality of organism and environment, ecological psychology emphasizes the role of perception and action as integrated processes of the organisms' task-oriented cognitive repertoires, and highlights that cognitive solutions are distributed across entire organism-environment systems. Empirical studies discussed in the chapter demonstrate that behaviour previously attributed to complex internal computations can often be explained through embodied perceptual processes attuned to the affordances of an organism's environment. Such findings call for recognizing the unique, adaptive strategies evolved by different species to solve ecological cognitive challenges.

The chapter also highlights the potential for an ecological framework to address anthropocentric biases in comparative cognition. Biases like anthropomorphism, anthropofabulation, anthropodenial, and anthropofabrication arise when researchers fail to account for the specific contexts and embodied constraints of non-human species of interest. By integrating ecological principles, we can move toward a less biased, more inclusive understanding of cognition that honours the diversity of life.

In sum, ecological psychology offers a transformative lens for comparative cognitive science, one that integrates perception, action, and environment into a coherent whole. By adopting this approach, researchers can transcend the limitations of traditional models, fostering a richer, more equitable understanding of cognitive abilities across the biological spectrum. This shift not only deepens our scientific insights but also challenges us to rethink the human place within the continuum of life.

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