

Bas van Woerkum-Rooker



Ecologies of Animal Minds

An Ecological Approach to Comparative Cognition

Research Institute for Philosophy,
Theology and Religious Studies

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Ecologies of Animal Minds

An Ecological Approach to Comparative Cognition

Bas van Woerkum-Rooker

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Ecologies of Animal Minds

An Ecological Approach to Comparative Cognition

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Ecologies of Animal Minds

IN THE REALM of comparative cognition, researchers often aim to discover specific cognitive abilities in other species without questioning the validity of such pursuits. Many of the abilities we explore in nonhuman animals stem from a view of human cognition that neglects the influence of our unique environments and bodies on our cognitive abilities. This framework not only centres on humans but also disregards how the bodies and environments of other animals shape their abilities. This dual oversight leads to “anthropofabrication”, the inclination to make animals appear similar to us by selectively emphasizing allegedly human-like features while disregarding species-specific variations. Considering debates on episodic memory, theory of mind and cognitive maps, Van Woerkum-Rooker introduces an approach that avoids anthropofabrication, by viewing abilities as skilful behaviours within an environment consisting of nested affordances—opportunities for action interconnected across multiple levels and in various ways.

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Chapter 3: Van Woerkum, B. and Barrett, L. (2024) Anthropofabrication and the redressing of memory: an embodied approach to comparative cognition. *Philosophical Transactions of the Royal Society B*. 3792023014520230145. <http://doi.org/10.1098/rstb.2023.0145>*

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Chapter 6: Van Woerkum, B. (2023) Animal navigation without mental representation. *Phenomenology and the Cognitive Sciences*. <https://doi.org/10.1007/s11097-023-09940-z>

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Minding ecologies

There's a half-eaten tuna sandwich left on the park bench and an abandoned bowl of soggy fries near the garbage bin. Both are excellent treats for the crow perched atop the lamppost. This intelligent bird is scanning the surroundings, waiting for an opportunity to dive in between the humans passing by. A keen memorizer, this clever bird knows that people often leave tasty leftovers here and at other spots. But he must remain alert—other crows share his knack for remembering these hidden treasures. As I observe, a fellow crow seizes the sandwich, while a busy flow of runners and pedestrians continues. Undeterred, the clever crow takes flight, using the environment to navigate to a quieter location.

It's sophisticated behaviours such as these—remembering numerous places, understanding others, navigating towards locations far away—that researchers interested in animal minds attempt to grasp. In particular, these researchers usually try to get a handle on the cognitive processes “underlying” these behaviours. Do crows and other animals possess episodic memory, the ability to relive personal past events? Are they capable of mindreading? That is, can they infer the thoughts, feelings, and perspectives of conspecifics? Do they rely on spatial representations of relations among landmarks, known as cognitive maps?

Such questions demand empirical and conceptual scrutiny. Roughly speaking, comparative psychologists are concerned with empirical work, while philosophers of animal minds discuss the validity of concepts, methods, and interpretations employed in empirical work (and ideally offer alternative methodological tools, concepts, and ideas for experimental set-ups).¹ Generally speaking, animal cognition researchers try to uncover similarities and differences compared to humans from evolutionary and developmental perspectives, in order to reveal new insights about the cognitive processes of each (see Andrews 2020a; 2020b; Andrews & Beck 2019; MacLean et al. 2012; Hall & Brosnan 2016). Studying and pondering the abilities other animals can teach us a lot about the similarities and differences among species, including ourselves. Accordingly, it gives us a different angle to see where we humans fit in among all these creatures.

But we aren't able to comprehend our spot among the kinds of minds in the animal kingdom yet, because evolutionary thinking hasn't really trickled down into comparative psychology. That is, even though Darwin dethroned humans from their once-privileged status a long time ago, ideas about human cognition still determine most cross-species comparisons. A significant reason for this is that we assume

1. Obviously, comparative psychologists can engage in philosophy and vice versa. The division of labour is not as clear-cut in reality.

that the ideas we have about human cognition provide a neutral starting point for a systematic, hierarchical way of understanding cognition across the animal kingdom, with our capacities at the top.

In the realm of psychology, cognitive abilities are viewed as evolved functions residing within the brain, largely detached from the body and environment. The rise of modern computing reinforced this idea, likening cognitive processes to the information-processing operations of computers. Applied to cognition, this understanding narrowed our focus to “hidden” cognitive processes—mental representations—in the brain, overlooking the diverse ways in which the bodies, senses, and environments of animals (including those of humans) shape their abilities. Essentially, we have neglected all species-specific modes of action and perception in order to compare “cognitive abilities”, despite the inherent problematic nature of excluding these species-specific components, in both humans and other animals. If so, the hierarchical understanding of cognition becomes untenable, and we’ll need to reacknowledge the contributions of the body and environment to the cognitive abilities of animals, including humans.

To alleviate the problem of comparing animals against human standards, a species-specific view is required: a view that allows us to understand and compare the cognitive abilities of animals, detached from our notions about humans. But *how*? How can we understand and study the abilities of animals in *species-specific ways*? I’ll argue that our focus should shift away from assumed underlying capacities for behaviour. Instead, we should view complex behaviours as organized processes involving active organisms within richly structured ecological niches. This perspective grounds cognitive abilities in observable relations between organisms and their environments, establishing a framework that is both species-specific and broadly applicable, to human and nonhuman animals alike.

In what follows, I will focus specifically on so-called *representation-hungry* abilities (Clark & Toribio 1994). Representation-hungry abilities are abilities that appear more complex than simple actions, such as those that have to do with imagining the future or remembering the past. Addressing representation-hungry cognition is a complex issue within the philosophy of the human mind (see Kiverstein & Rietveld 2018) and the challenge may even be larger when considering animal minds. Even so, representation-hungry cases provide the clearest example of how we rather uncritically and problematically incorporate human-like representational capacities into the study of animal cognition, while at the same time demonstrating the scope and power of my alternative approach.

In the remainder of the introduction, I'll provide a concise conceptual background of the prevailing anthropocentric model in comparative psychology, and introduce my ecological alternative. I will first show how evolutionary and psychological conceptions of *human* cognition in terms of distinct cognitive capacities (i.e., only loosely connected to the body and environment of the animal), have impeded the development of a more species-specific approach (sect. 1.1.). Next, I will present an alternative, ecological framework (sect. 1.2.). I will end with the plan for the rest of this dissertation (sect 1.3.).

The anthropocentric framework

Although Charles Darwin's *The Origin of Species* had been published in 1859 and his *The Descent of Man* in 1871, evolutionary thinking didn't take hold in psychology until the 1980s (see Reed 1996; Heft 2001). It wasn't until then that evolutionary psychology emerged as a distinct field, with pioneers like Tooby and Cosmides (1992; 1990) playing crucial roles. Tooby and Cosmides, along with other early proponents, shifted the focus of psychology towards understanding human cognition as a product of natural selection. They emphasized domain-specific cognitive mechanisms or modules, suggesting that our minds comprise an “evolutionary toolkit” adapted to solve specific challenges faced by our ancestors.

Tooby and Cosmides (1990) write that, “variable manifest psychologies, traits, or behaviors between and across cultures [are viewed as] the product of a common, underlying evolved innate psychology, operating under different circumstances” (p. 23). They assumed a set of common cognitive capacities underlying the various behaviours and traits of humans. The adaptationist perspective became a cornerstone of evolutionary psychology, positing that many aspects of human cognition and behaviour are evolved responses to ancestral problems. Moreover, this perspective led to the identification of cognitive adaptations, or evolved modules, designed to address survival, reproduction, and social interaction. As Withagen and Chemero (2009) put it, “The human mind, they [Tooby and Cosmides] surmised, can be conceived as a Swiss army knife with different modules, each of which performs a particular function. And this cognitive architecture is basically the same for each and every human being. Individual differences, then, spring from this architecture and can be explained primarily in terms of phenotypic plasticity—that is, they are generally the result of different environmental factors operating on the same cognitive architecture.” (p.373)

At a psychological and neurobiological level, these cognitive modules or capacities were understood to rely on mental representations (or representations, for short): processes occurring between sensory input and motor output, that enrich or supplement action and perception.² The central assumption here is that information provided by incoming stimuli to the sensory receptors is deemed too poor to account for complex behaviours. Hence, mediating mental representations—such as representations about the past, about what others think and feel, or about the layout of the environment—are needed to explain such behaviours. Even though mental representations are not directly observable, we can (so the reasoning goes) deduce them from behaviour by using strict, controlled experiments. Indeed, inferring the presence of these representations and representation-based capacities in other animals is one of the primary endeavours of comparative psychologists.

Besides cognitive adaptation, the evolutionary concepts of convergence and ancestry underpin much comparative research pursuits. These foundational concepts find their origins in comparative anatomy, in cases such as the convergent evolution of wings in bats and birds, or the shared ancestry reflected in the limb structures of chimpanzees and humans. In comparative psychology, the term “convergence” denotes that the same cognitive capacity has independently evolved in different species, despite distinct underlying structures. For instance, the ability for episodic memory, present in humans, may also have evolved in food-caching corvids, even though the last common ancestors of corvids and humans lived over 300 million years ago and was neither bird nor human. Both species could have faced comparable selection pressures, such as the necessity to remember widely dispersed food sources. Episodic memory could have evolved as an adaptive solution to this ecological demand. Humans and corvids endowed with a genetic inclination that allowed them to better remember what, where and when food resources were available gained a survival advantage. These animals would find more food and thrive, passing these advantageous genes to their offspring (see e.g. Griffiths, Dickinson & Clayton 1999; Clayton & Russell 2009).

“Ancestry” highlights a similar capacity shared by two species, attributable to a common evolutionary lineage. For instance, some authors claim that chimpanzees have the ability to infer mental states akin to humans (Call & Tomasello 2008). Chimpanzees are our close evolutionary relatives: the last common ancestor of humans and chimpanzees lived around 6 to 7 million years ago. This animal would

2. I won't dive into the varieties or types of mental representations. Relevant to comparative psychology is how internal process supposedly “enrich” perception and action and are “decoupled” from the environment. This idea, *of enrichment*, will be my target.

have lived in complex social groups, creating selection pressure to track relationships, build connections, and anticipate the actions of others. These selection pressures favoured those with an emerging “theory of mind”, an ability to infer mental states and understand the perspectives of fellow group members. This advantage would have bolstered their chances of survival and increased their opportunities to pass on their genetic legacy by leaving more offspring. Accordingly, both chimpanzees and humans, when their lineages diverged, may have already possessed a (primitive) theory of mind (Dunbar 1998).

These evolutionary hypotheses provide the rationale to search for these psychological capacities, such as episodic memory in corvids or theory of mind in apes. Since these capacities can only be inferred from behaviour, researchers must deal with any confounding variables to deduce the presence of that capacity. Consider this example: researchers observe that some ravens seem to cache food in specific locations and retrieve it later, suggesting a capacity for future-oriented behaviour. A confounding variable could be associative learning, though, where ravens remember specific landmarks or cues near their food caches. In this scenario, the ravens might not be planning for the future but relying on associations with their surroundings. To address this, comparative psychologists might conduct experiments where familiar landmarks are altered or removed. By doing so, they aim to determine whether ravens can “genuinely” plan for the future, independent of associative cues, and thus uncover the cognitive processes underlying their apparent ability to engage in future-oriented behaviour.³

The concept of associative learning finds its roots in the late 19th century, credited mainly to Ivan Pavlov, a Russian physiologist. Pavlov experimented with classical conditioning in dogs, showcasing how animals associate a neutral stimulus (like a bell) with a significant event (such as food) and start responding to the neutral stimulus as they would to the significant event itself (Pavlov 1927). Meanwhile, Edward Thorndike, an American psychologist, delved into instrumental or operant conditioning. He introduced the Law of Effect, suggesting that behaviours with pleasant outcomes are more likely to recur, while those followed by unpleasant consequences tend to diminish (Thorndike 1898). These foundational studies shaped our understanding of associative learning, illustrating how organisms form connections between stimuli or between actions and their outcomes, shaping their behaviour. Today, comparative psychologists often embrace associative learning processes, adopting it as a “simpler” explanation in their methodology.

3. Note that learning itself is not excluded, if that would even be possible. It's only the learning of rules that researchers try to disarm, because animals would simply be following these rules instead of exercising the capacity that the researchers are interested in.

Initially, the insistence on excluding confounding explanations was driven by a concern about anthropomorphizing nonhuman animals (Boakes 1984/2008). Anthropomorphism means endowing another species—wrongfully—with internal thoughts, feelings, abilities and other characteristics that only humans are thought to have (see also Costall 2007). I say thought to have, because the nature and mechanisms of our human abilities are still debated, and whether only humans have a particular capacity is often the heart of the matter (Buckner 2013; Andrews 2016). To limit this bias, Conway Lloyd Morgan formulated what became known as “Morgan’s canon”, which reads: “In no case is an animal activity to be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development” (Morgan 1903). The canon has basically been interpreted as: if a simpler explanation is available, prefer that one.⁴ A modern rationale behind this dictum is that complex abilities require a complex brain (such as the one humans have), which is energetically expensive, and evolution tends to opt for “good enough” strategies. Today, the Canon is deeply engrained in routinized experimental procedures, and any form of associative learning is usually considered as the “simpler” explanation.

Both the adaptationist model of cognition and representationalism emerged as theories for comprehending the human mind. This is clearly discernible in the prevailing anthropocentric model of comparative psychology (see also Lyon & Keijzer 2007, see fig. 1 below). Whether it makes sense to even *look for* certain representational concepts originating in a human context to other animals, is a question that gets very rarely asked. These theories are uncritically accepted as “species-neutral” and generally applicable across the animal kingdom. Accordingly, the assumption that “there is a single, systematic, hierarchical way of understanding cognition (with our capacities placed somewhere near the top)” sneaks into comparative psychology (Currie 2021, 49). What’s more, *evolutionary* continuity—something few researchers would reject—doesn’t dictate *psychological* continuity, and arguments for mental continuity often tend to portray nonhuman animals as “watered-down humans, not-quite-finished children” (Povinelli 2004, p.32; see also Barrett & Würsig 2014; Barrett 2015b).

4. As a side note, according to Costall (1993; see also Barrett 2011) Morgan has been heavily misinterpreted. In the same work, Morgan (1903) wrote that “the Canon by no means excludes the interpretation of a particular activity in terms of higher processes, if we already have independent evidence of the occurrence of these higher processes in the animal under investigation.” (p.59) and that “surely the simplicity of an explanation is no criterion of its truth” (p.54). This context sheds doubt on the way Morgan’s canon is nowadays employed. Very often, experimenters predetermine two potential explanations for the cause behind a behaviour (the complex cognitive explanation and the simple association-based explanation) and then attempt to find out which of the two it is.

This “infiltration” of an anthropocentric outlook into comparative psychology is troubling, all the more, because this modular, representationalist view of the human mind itself is under pressure (Lyon & Keijzer 2007; Kelty-Stephen et al. 2022). The ideas of cognitive modules or mechanisms that are “decoupled” and “enrich” action and perception do not align with evolutionary thinking, as brains, bodies and environments evolved together to enable the abilities of animals (see Keijzer 2015; Barrett, Henzi & Barton 2022). In other words, human abilities, and the abilities of other animals, are much more entangled with their bodies and environments than we usually assume. Now, if we are mistaken about how humans achieve their feats and use such a mistaken image of our abilities as a baseline for cross-species comparisons, we’ll obviously run into some major problems. Buckner (2013) called this error “anthropofabulation” and argues that it occurs in the case of episodic memory and theory of mind, among others.

From an evolutionary perspective, we should expect “cognition” to be much more integrated with the body and the environment, just like eyes and flippers and trunks are. As the ecological psychologist Edward Reed (1996) writes in the broader context of cognitive psychology:

The emphasis on keeping cognition distinct from other aspects of an animal’s encountering its surroundings has meant that cognitivists have often studied what animals and people do when they are not in adequate contact with their environments. How do observers cope with a lack of information? [...] Evidence about how animals are disjoint from their environment forms the basis of most modern theories of cognition. Much of cognitive psychology has become the study of how animals and people manage under unnatural conditions.
(170, box 23)

Reed’s point is apparent in comparative psychology too, where clever ways to exploit environmental processes are recognized as “confounding” variables and disarmed, such as the reliance on solar cycles or scent in corvid caching behaviour (Clayton & Dickinson 1998) or the use of learnt generalizations of behaviour in social interaction (Lurz 2011).

Many researchers will think that Reed’s remark sounds nice, but that we simply *need* mental representations to account for a host of behaviours. However, it’s exactly this assumption, that the information in the environment is too poor to account for complex behaviours, that can be challenged. On my view, it’s not the *information* from the environment that’s impoverished, but the *theory* about the environment. With

a solid theory of the environment, the need to posit mental representations falls away, allowing for more comprehensive, species-specific interpretations of human and nonhuman abilities. To get at such a theory, I will primarily draw from the resources of ecological psychology (Gibson 1979/2015; Heft 2001), ecological-enactive approaches (e.g. Kiverstein & Rietveld 2018), and the biogenic approach (Lyon & Keijzer 2007). While a combination of these resources may not be the only alternative to the anthropocentric framework, it offers a unique view of the environment that is particularly suited to provide a species-specific perspective of animal's abilities.

An ecological framework

Ecological psychology, which emerged in the 1950s through the pioneering efforts of James J. Gibson and Eleanor J. Gibson, represented a significant departure from the prevailing “enrichment” theories of perception in their time (Gibson & Gibson 1955). Ecological psychologists reject the view that information from the environment received by the senses is “too poor” and hence, too, the need for enrichment—that is, mediating mental representations. Ecological psychology stands out, in particular, for its alternative theory of the environment, which allows us to explain even complex abilities without reference to enrichment processes. I will return to this in the next chapter.

The foundational ideas of *enactivism* trace back to seminal work by Varela, Thompson & Rosch (1991). Enactivists, generally speaking, emphasize that our cognitive processes are not merely reactions to the environment but are actively constructed through our interactions with it. They argue that cognition is not a separate process but is intricately tied to the body and our engagements with the environment. Enactivists usually describe living systems as self-organizing, self-maintaining entities. These ideas—the constructive role of active organisms in shaping perception, and the organization of behaviour—play a pivotal role in my approach to comparative cognition.

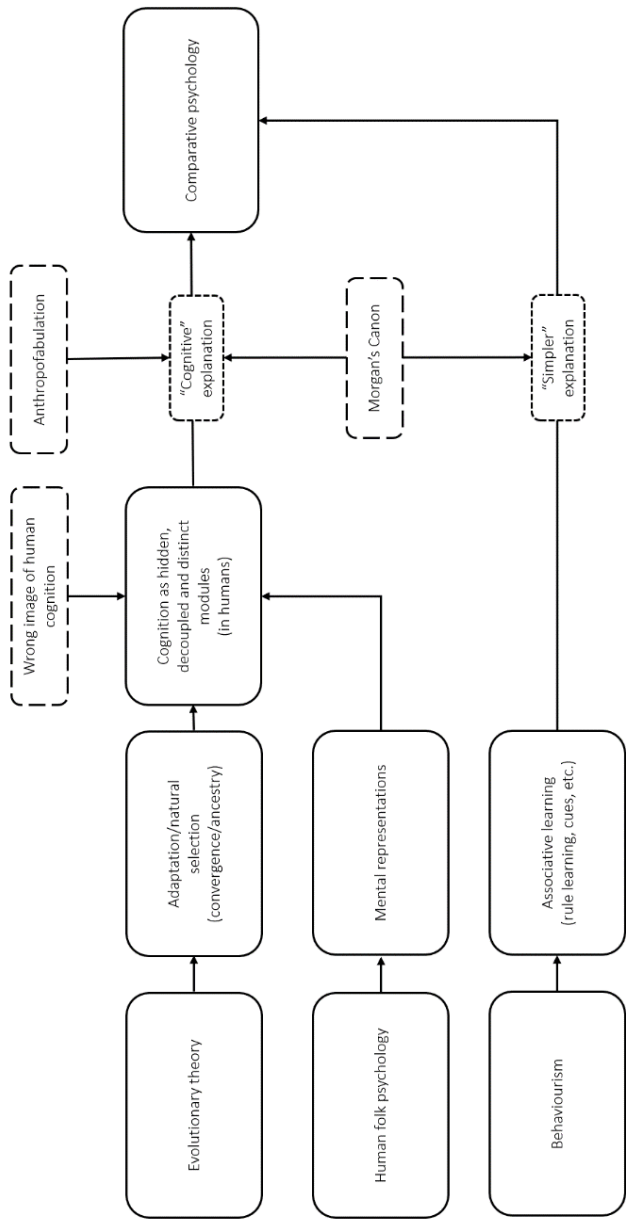


Figure 1. Prevailing anthropocentric framework of comparative psychology. In comparative psychology, cognitive abilities are understood as evolved capacities, loosely connected to the rest of the body and the environment—like a “mental toolbox”. This view on cognition originates from the adaptationist view on the evolution of cognition, alongside the proximate explanation of these capacities in representational terms. While these explanations of human cognition are often misguided, they are taken over into comparative psychology, inviting anthropofabulation (Buckner 2013). The idea of learning through associations, borrowed from behaviourism, operates as a simpler, non-cognitive explanation. To prevent overestimating animal cognition, Morgan’s canon steps in, favouring simpler explanations over complex cognitive ones. Consequently, we may either elevate animals to the misguided image we hold of ourselves or depict them as lacking in comparison to our abilities entirely.

Not all authors view the engagement between enactivism and ecological psychology as a harmonious one, arguing that some of the main assumptions are incommensurable (e.g. Heft 2020, see also Read & Szokolszky 2020; Van Dijk, Withagen & Bongers 2015), but the combination and integration of ecological and enactive ideas has yielded fruitful insights in recent years (e.g. Kiverstein & Rietveld 2018; Bruineberg, Chemero & Rietveld 2019; Gallagher 2017; Chemero 2009; Barrett 2018). Both approaches challenge conventional cognitive assumptions by putting action in complex environments at the forefront, shifting the focus from internal processes to the interplay between animals' abilities and their surroundings, emphasizing active engagement, and conceiving of perception and action as two sides of the same coin. Not trying to faithfully adhere to the core tenets of any of these original programs (or specifics strands thereof), then, a growing number of researchers seek to develop theoretical and methodological perspectives inspired by both. The enactivist influences on my ecological approach stem primarily from such efforts. By bringing ecological and enactive ideas into the realms of comparative psychology and the philosophy of animal minds, I hope to expand these programs in novel ways. That being said, with the bulk of the theoretical foundation resting on ecological principles, I have predominantly labelled my approach in the coming chapters as an "ecological" one.

In addition to ecological and enactive resources, I also embrace a biogenic perspective. In contrast with ecological psychology and enactivism, the biogenic approach is not a theory, but a methodological starting point (Lyon & Keijzer 2007). Biogenic approaches assume that "the properties and principles of biological organization present the most productive route to a general understanding of the properties and principles of [...] cognition". "Cognition" is here defined as "the processes by which humans and presumably other biological systems come to know the world" (Lyon & Keijzer 2007, p.141). Biogenic approaches think of cognition as that which allows animals to effectively navigate their ecological niche. Rejecting human-centric notions as a point of departure, they highlight basic biological capacities, such as perception, action and learning. Though ecological psychology and enactivism are not necessarily biogenic, they are an obvious match.

Another feat of the biogenic approach is that complex abilities—or cognition, if you will—develop as slight modifications or expansions of pre-existing abilities (see also Cisek 2019). More "complex" feats are therefore enabled and constrained

by animals' perceptual systems⁵ and ecological processes. This bottom-up view, which foregoes essentialism and takes biological constraints on complex feats into account, is better equipped to provide a truly evolutionary account of what cognition is. "Bottom-up" doesn't mean that humans can be found at the "top", however. Life increases in complexity from the simplest organisms (those with simple body plans and perceptual systems) in various directions to animals with elaborate bodies and perceptual systems. Humans are among them, clearly, but they are not the ultimate benchmark, nor the most advanced or perfected form. Like other complex life forms, humans are biological systems situated in a specific—and surely very interesting—ecological context (Lyon & Keijzer 2007; Reed 1996).

By combining and integrating ideas from these perspectives, we can construct an alternative—ecological—model (see fig. 2 below). Within this framework, cognitive abilities or capacities do not sit *behind* actions, in the head. Instead, they indicate a particular way of doing things (Reed 1996; cf. Wittgenstein 1953/2009), of exploiting the resources of the environment. They are particular ways in which behaviour is *organized* (Noë 2010). A crow can *remember* where people leave tuna sandwiches without *having a memory*—a mental representation—of where people leave tuna sandwiches. In other words, "remembering" is not a process taking place in the brain, but an acquired or developed way of acting, shaped by routines and environmental influences. Using "remembering" and other cognitive terms to describe ways of acting is not a silly attempt to alter the meaning of these terms. Instead, it is an attempt to offer a more accurate, more realistic, and more evolutionarily grounded account of what these terms entail.⁶

These ecological, enactive and biogenic ideas align more naturally with evolutionary thinking, in particular with the idea that brains evolve together with bodies in specific environments. While the adaptationist perspective on cognition relies heavily on the idea that animals become "adapted" to the environment through the process of natural selection, the viewpoint that I support aligns with an evolutionary understanding

-
5. In anticipation of the next chapter: Gibson (1966; 1979) used the term "perceptual systems" to signify that perception is a situated, active process. The sensory organs are involved, but these are just one aspect of the dynamic involvement of the entire body in a specific environment. For human vision, for example, the eyes are located in the head which sits on a turn-able neck, attached to a moveable body moving in an environment (Gibson 1966).
 6. As Darwin attempted according to Costall (1993). Wittgenstein shared this project, too (see Moyal-Sharrock (2009). Note that, rather than starting an argument over the meaning of "cognition", I set out to explain certain behaviours that fall well under the header of "cognition" in a representationalist paradigm, in terms of how animals exploit structure in the environment using their unique perceptual systems.

where organisms and environments co-evolve.⁷ Rather than considering cognitive abilities as adaptations to specific challenges within an animal's environment, I view those abilities as rooted in the refinement and expansion upon pre-existing perceptual systems in specific niches.

As the perceptual systems of animals become more elaborate, animals can act and perceive in more differentiated manners, and more complex behaviours can emerge. The alterations of these systems thus change how animals engage with, sustain and change their environments (which includes social practices) and later generations come to develop within this altered environment—possibly leading to more fine-grained forms of action and perception. On this view, organisms throughout their lives take up an active role in shaping the evolution of their evolutionary lineage, as “past generations structure and scaffold the developmental context of those that succeed them, providing resources that are essential to the production of species-typical behavior” (Barrett 2011, p.205). Accordingly, a rich, supporting environment is just as indispensable to species-specific abilities as the body (including the brain)—hence the idea of co-evolution of organism and environment.⁸

From this viewpoint, discussing the convergence and ancestry of cognitive capacities becomes less sensible as well. Still, that doesn't mean we should completely abandon comparisons between species. Regarding similarity, we can start to look at the ways that animals exploit stable environmental structures and regularities, given their species-specific perception and action systems. Equally crucial, though, is acknowledging and giving due consideration to the diversity among species. Variation and diversity, of course, have always been a key facet of evolutionary thinking, too—it's just that continuity has received a disproportionate amount of our attention. In the upcoming chapters, I'll explore the implications for cross-species comparison within this ecological framework in more detail.

An ecological outlook is valuable because it grounds the examination of cognition in principles of biological organization, observable behaviour, and the complexity

-
7. For discussions on the role and emergence of affordances in the evolutionary process, see Heras-Escribano (2019), Withagen & Chemero (2009), Heft (2014). Evolutionary perspectives related to my view but do not directly refer to the concept of affordances can be found in Cisek (2019), Keijzer (2017), Ingold (2006; 2007), and developmental systems theory (Oyama 2000).
 8. To anticipate the coming chapters: affordances, on my view, are tied to the abilities available in a “form of life”—a term coined by Wittgenstein which denotes a population of animals with specific behaviours and shared practices (Rietveld, Denys & Van Westen 2018). Actual engagement with affordances—using tools, building burrows, climbing trees—therefore, also sustains and shapes the availability of certain affordances and abilities in a form of life over generations (see also Costall 1995).

of ecological niches, rather than in preconceived notions of human cognition. It offers a perspective on which the unique bodies of animals, equipped with unique perceptual systems, and occupying unique niches, constitute the cognitive abilities of animals. On such a perspective, we must focus on observable, situated performances, rather than on hidden capacities that underlie those performances—even in cases of perceived complexity. Accordingly, it offers constraints for understanding those abilities and keeps our intuitions about human cognition at bay.

Following this strategy, the clear distinction between cognition, action, and perception will blur, and hence I will use terms such as *processes*, *abilities*, and *capacities* as well as *actions*, *activities*, and *behaviour* (with or without cognitive, complex, higher-order, skilful, etc. attached) interchangeably (as I have done up to this point). Different choice of words doesn't reflect any deep theoretical commitments, but I do tend to use "cognitive" to clarify my explananda, which is not "mere behaviour" but a new perspective on what's traditionally been called "cognition (see Lyon & Keijzer 2007). What's more, folding the term "cognition" into a biological framework is also an attempt to reclaim this famously vague term from representationalists, who sometimes appear to have claimed ownership of it (see also Costall 2007; Penn 2011). Ultimately, I just want to provide a framework for understanding how animals do what they do when they do it, while avoiding, as much as possible, undue attributions of allegedly human-like abilities to these animals.

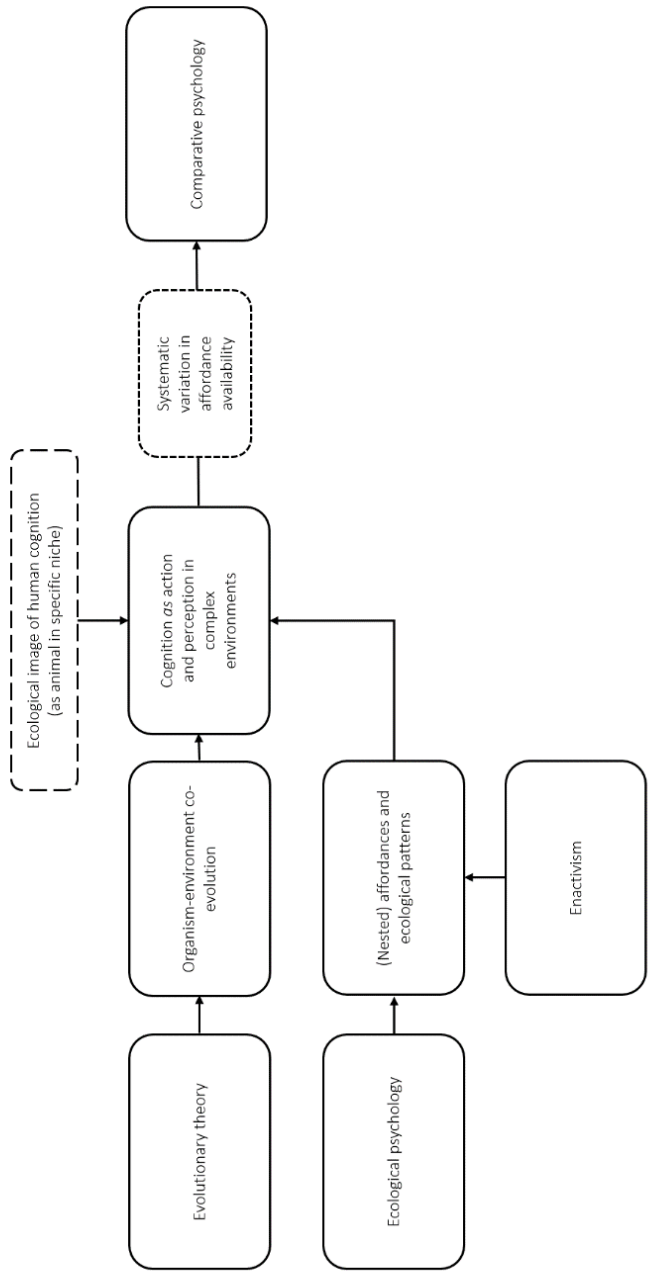


Figure 2. An ecological framework for comparative psychology. Evolutionarily speaking, my view aligns with those who emphasize co-evolution of organisms and environments. Combined with ecological and enactive ideas, “cognitive abilities” refers to the ways that animals learn to exploit and change their environments given their perceptual systems. Methodologically speaking, systematic variation in the availability of affordances—opportunities for action offered by the environment—takes the place of Morgan’s canon (that stacks anthropofabulated explanations against associative learning explanations).

Plan for the thesis

Of all the creeping, swimming, flying, galloping, slithering and walking creatures on this earth, I will focus mostly on birds, although various animals will be discussed. Even so, my points are meant to generalize: the way of thinking I will put forward is applicable across the animal kingdom. In this sense, I offer a *species-specific* approach that is *generally applicable*. I defend a way of thinking about and studying animal behaviour, but don't aim for exhaustive explanations of any animal or any animal behaviour specifically. Drawing upon a wealth of existing empirical information, I have hopefully done what philosophy can do at its best: offer concrete tools to advance the empirical work, and offer fresh and surprising perspectives on the “minds” of our fellow earthlings.

One other species is at the same time peripheral and central to everything in this dissertation: us. Humans are peripheral, given that I will not provide a full-blown positive account of human cognition from an ecological perspective.⁹ Humans are central to the extent that I'm trying to remove them from the centre of comparison, where they currently linger. Quite simply, it's impossible to talk about other animals without talking about humans, given that we are humans. To understand the abilities of other animals as intricate behaviours in complex niches, we also need to comprehend our own niches—how our abilities have been shaped and organized by the environments that we have built around ourselves. For instance, our ability to remember and to think in a map-like fashion may be completely “entangled” with our sociomaterial practices of drawing and using maps, to such an extent that it doesn't even make sense to look for such abilities in other animals. As Reed (1996) put it, “we are unique in that we have our own distinctive way of life—our own ecological niche, if you will—but every animal species has its own unique way of life as well.” (p.97)

Here's the plan. Chapter 2 will provide background for my view, introducing the ecological tools to be wielded in later chapters (as well as, in doing so, how I incorporate biogenic and the enactive ideas in there). The central concept running throughout the coming chapters is that of *nested affordances*. Broadly speaking, affordances (Gibson 1979/2015) are opportunities for action that the environment offers to an animal, and so to say that affordances are *nested* means that affordances are interrelated in various ways. Nested affordances elucidate how animals harness environmental structures to accomplish intricate behaviours. I will explain why and how it is pivotal in my approach.

9. Indeed, there are numerous authors who do this wonderfully already, and they will recur throughout this work.

Chapter 3 will introduce the notion of “anthropofabrication”. Anthropofabrication entails the fabrication of a sense of similarity by ignoring, as a matter of experimental routine, species-specific differences in humans and the animal that is being studied alike. The basic idea is that, in a quest to find “universal mechanisms” of memory, planning, and so on, species-specific bodily and environmental factors that contribute to how humans achieve certain feats are ignored—basically bracketing the variation away until a commonality is discovered, which is deemed to be a (hidden) representation. This then provides a justification for ignoring body and environment in the study of animal cognition, looking for similar representational capacities. Similarity is thus often constructed within experiments, rather than discovered. We *make* animals more similar by focusing only on a specific, select set of details, neglecting the sources of *variation* that also exists and could also be studied. I will also highlight how we can “redress” cognition, arguing that we should embrace variation and complexity. This chapter will set the stage for three case studies that will follow, in which anthropofabrication will continue to be discernible.

Chapters 4 to 6 serve as case studies. Moving away from a predominantly human-centric perspective, I will consider cognitive abilities as intricate forms of action and perception in complex environments. Each of these chapters shows how work that is commonly attributed to complex internal representations is carried out by active engagement with nested affordances.

Chapter 4 is about episodic memory. Episodic memory, the ability to relive personal past events, is often seen as a capacity that is largely or completely detached from the environment. That is, regardless of their current location or activity, people seem to be able to re-experience events such as their last year’s birthday. Researchers are exploring the possibility of animals having episodic memories as well. In this chapter, however, I challenge the notion of episodic memory as being decoupled from the environment. Instead, I draw attention to how animals can use environmental structure and regularities to exhibit behaviours that we commonly associate with episodic memory—that is, behaviours involving events that occurred in the past and in a different location than the current one.

Social cognition is the topic of chapter 5. Many animals engage in intricate interactions and anticipate the actions of their conspecifics. Within the study of animal minds, a major debate revolves around whether animals can deduce mental states from behaviour or if they predict actions based on generalizations about behaviour. I aim to expand this discussion by placing it within a broader ecological context. I argue that social interactions unfold within rich environments, which

encompass the behaviours of other animals. The regularities in these behaviours—what, where, when, and how actions occur—enable animals to grasp how affordances are embedded or nested within a socio-material context.

Chapter 6 explores animal navigation or wayfinding. The complexity of animal navigation is typically described using a range of representational tools, from basic to sophisticated. On these theories, as navigational complexity increases, the importance of the animal's body, senses, and environmental structure tends to decrease. In other words, the animal seems to become more detached from the environment. My argument takes the opposite stance: animals, guided by their perceptual systems, become more finely attuned to the environment, specifically to its nested structure.

As you can see, a recurring structure and method to my analyses will be discernible: how can animals' perception and motor systems, attuned to environmental structure, do the work typically attributed to mental representations? In other words, instead of asking, "given that the information in the environment is too poor to account for the complexity of this behaviour, what kind of representation does the animal need?" I will ask, "given what the animal can do, what's the structure of the environment like?" Recall the navigating, remembering, interacting crow from the beginning of this chapter. How can and does he use his environment, with his unique body and perceptual systems, to do what we typically associate with human-like thinking?

I end with some general lessons, implications and future research avenues in chapter 7. All in all, I aim to offer another way of thinking about animal cognition, human cognition, and the relation between them—about the ecologies of minds. Exciting new avenues in this direction are emerging at full pace, like the creation of well-trodden desire paths through constant use. I hope that the pages of this dissertation will help expand and solidify these trails into a major network.



2

Nesting

Armed with a beak, feet and a set of wings, a young bird is busy gathering materials. She's trying to build a nest, arranging twigs, branches and other materials into some kind of configuration. She's still learning how the size and shape of branches and their placement and arrangement afford the creation of a sturdy nest. But year by year, nest-building becomes easier, until she can effortlessly gather the best materials and place each twig carefully to construct a secure home.

As Van Dijk and Rietveld (2018) highlight, any activity that seems like a completed action is often part of a larger, ongoing sequence of actions. In other words, activities often have a *nested* structure. Nest-building is a case in point. To build a durable nest, birds must learn how various materials fit into the whole and how the nest should be organized. In other words, they need to know what those materials afford in relation to the larger-scale activity. Each *addition* to the nest, such as fitting in a twig, shapes and constrains the selection of subsequent materials, as the nest takes shape over time. With increasing experience, the ability to construct a sturdy nest becomes more refined, and the bird can start to *foresee* the completed nest when she *sees* the bare beginnings.¹

Nest-building serves as a compelling image for the idea of *nested affordances* that's central in this dissertation. Recognizing that affordances are nested is crucial for elevating engagement with affordances beyond immediate contexts. We need this concept to attain a species-specific perspective on the representation-hungry abilities of other animals—which again, are activities having to do with absent or abstract states of affairs, such as imagining the future or remembering the past. Such explanations have been developed over the last years for human activities (see e.g. Van Dijk & Rietveld 2018; 2020; Kiverstein & Rietveld 2021) but not, in a similar way, for other species.

Rather than providing a comprehensive overview of these explanations, I'll offer a selective discussion merely to introduce the concept of “nested affordances” as I will use it. I start off by discussing some key ideas: ecological information, affordances and the distinction between enrichment and differentiation. Then, I'll elaborate on the view of perception as an active process, geared toward possibilities that are often removed in space and time, using the example of object permanence (sect. 2). I'll continue with the pivotal notion of affordances as nested processes, or nested affordances for short (sect. 3) and end with some general remarks (sect. 4). The notions of affordances, information and nested affordances will be explained and expanded upon in all of the later chapters, too. The purpose of this chapter is to provide an initial, systematic overview of the concepts that I will employ.

1. To use a phrase used by Gibson (1979/2015, p.94) in a different context.

Ecological equipment

“To see is to see how to get about among things.”

~ J.J. Gibson (1979/2015, p.213)

James J. Gibson (1979) claimed that we do not perceive stimuli or even objects. Rather, we directly perceive *what we can do*. In other words, we perceive *affordances*—opportunities for action offered by the environment. Complementing James Gibson's work, his wife Eleanor J. Gibson, formulated a developmental theory that elucidates how children acquire the ability to perceive the affordances of their surroundings. This theory, known as perceptual learning, constitutes an integral component of the ecological approach, introducing a critical distinction between enrichment and differentiation (Gibson & Gibson 1955). In what follows, I'll explain these ideas in more detail.

A fundamental tenet of ecological psychology is the rejection of so-called “enrichment” processes. Enrichment accounts assume that the information available in the environment is insufficient to account for the intricate and adaptable behaviours observed in humans and other animals. As a result, sensory stimuli must be “enhanced” by internal processes of enrichment, such as categorizing, combining, updating or abstracting. Enrichment processes align with prevailing theories in comparative psychology that posit mental representations between action and perception. Indeed, mental representations are models of the outside world constructed from *limited* information provided by sensory stimuli. Consequently, representations can be said to “enrich” sensory input (see chapter 1). Researchers following these approaches often explicitly aim to demonstrate animals' capacity for specific forms of enrichment.

Ecological psychologists replace enrichment with differentiation in their theory of perception and its workings. A differentiation-based view starts with the premise that the environment teems with a wealth of information—though “information” in this context takes on a distinct meaning compared to enrichment theories. From an ecological perspective, perception does not begin with “sensory input” stimulating the sensory receptors, and sensory input is not believed to contain “information” that requires interpretation by the brain. Instead, ecological psychologists describe how electromagnetic waves move through the environment, reflecting off surfaces and other features.² This continuous and boundless flow of energy in the environment

2. In *The Ecological Approach*, Gibson is concerned with visual perception (Gibson 1979/2015).

settles into a relatively stable state, forming what they call an ambient optic array. Now, when an animal moves within this array, patterns of energetic stimulation are generated from the organism's perspective, providing that organism with information about its surroundings. Initially, Gibson (1979/2015) coined the term “stimulus information” for these movement-generated patterns (in contrast with “stimulation”, understood as “sensory input”), though nowadays the term “ecological information” is common. In turn, I will often employ the term “ecological patterns” to underscore that information is detected in movement over time. In their original conception, ecological information is described as *lawfully specifying* features of the environment.

To illustrate the idea of lawful specification, think about a bird looking for nesting materials. As she flies through the environment, certain optic flow patterns are generated. Optical expansion patterns specify approaching objects, whereas contraction patterns specify receding ones (Niehorster 2021). Optic flow patterns thus specify distance (i.e., the rate of expansion), but also size (e.g. relative proportion in the array), and the bird's own velocity (e.g. rate of optic flow surrounding the organism), among others. The perception of speed, distance and size through optic flow arises from the consistent relationship between the bird's movement and the corresponding changes in optic flow patterns. These relationships itself are *invariant*, despite the dynamic nature of the ambient array (Gibson 1979/2015; Smart, Hassebrock & Teaford 2020). Now, as discussed above, patterns in the array are itself specified by the structure of the environment, which is why ecological information specifies environmental features for an organism. In other words, there is a one-to-one mapping between information in the array and features in the environment.

This view on information emphasizes the direct coupling between the organism and its environment, with perception being an active engagement with the ambient energy flow rather than a passive reception of sensory data (Gibson 1979/2015; Gibson & Pick 2000; see also Jacobs & Michaels 2007). Accordingly, there's no necessity for “enriching” sensory input in the bird's brain, such as computing distances based on “cues” about depth and size. Instead, the bird develops the ability to *differentiate* patterns within the abundance of perceptual information available. Gibson and Pick (2000) explain that “Perceptual differentiation can be characterized as a narrowing down from a vast manifold of information to the minimal, optimal information that *specifies* the affordance of an event, object, or layout” (p.149). This learning process allows them to adapt and refine their understanding of the visual cues provided by optic flow, enhancing their ability to navigate and fly through their surroundings.

In addition, animals learn to selectively attune to relevant ecological information, depending on the circumstances and task at hand (Szokolsky et al. 2019; Gibson & Pick 2000). Consider the bird currently engaged in nest building. Depending on the stage of construction—whether just beginning or nearing completion—the bird must selectively tune into relevant ecological patterns while disregarding those presently irrelevant. For instance, she may concentrate on assessing the flexibility of materials by bending and twisting them, or perhaps on discerning texture by handling them with her beak. These actions allow her to gather crucial information about how these materials can be utilized—that is, what they *afford*.

As mentioned, ecological psychologists argue that animals directly perceive what they can do. That is, they perceive affordances or opportunities for action. For instance, humans perceive level floors as *walkable*, doors as *passable*, small gaps as *bridgeable* and low-hanging branches as *pass-under-able*. A bird perceives the branches of trees as *landable* and a twig on the ground as *grabbable*. As Alan Costall (1995) writes, “What, fundamentally, we attend to in our surrounding are not the shapes, colours and orientations of surfaces in our surroundings, but rather the meaning of things for action”. Gibson originally introduced the notion of affordances as follows:

The *affordances* of the environment are what it *offers* the animal, what it *provides* or *furnishes*, either for good or ill. The verb to *afford* is found in the dictionary, but the noun *affordance* is not. I have made it up. I mean by it something that refers to both the environment and the animal in a way that no existing term does. It implies the complementarity of the animal and the environment (Gibson 1979/2015, p.119)

Affordances are intricately linked to the unique characteristics of animals’ bodies. Consider perceiving a gap as *bridgeable*. For humans, perceiving this affordance depends on factors such as the height of our eyes, the length of our legs, and the pivotal function of our knees in mobility. When a human approaches a gap, that gap seems to expand optically at a certain pace (optical variation) while its fixed width remains evident too (optical invariant). These generated patterns are ecological information, and they specify the affordance of “bridgeable” for humans. Of course, humans’ body characteristics and skills vary, but that’s beside the point. It’s not the properties and dimensions of the gap, but the *relation* between leg length and gap width that constitute the perceived bridgeability (see Wagman & Blau 2020; Burton 1992). In a similar way, rats and hamsters perceive a lever to be reachable, based on the same height-to-forepaw-rearing-height ratio, despite the fact that rats are larger than hamsters (see Cabrera et al. 2013; Wagman et al 2019). This organism-environment relation is invariant. As a third example, consider how, for a bird, the

flexibility of a particular twig is an invariant feature that can be discovered by bending (that is, varying) it in multiple ways. Hence, what the twig affords is constituted by the material composition and discovered in use, given the bird's action capabilities, such as how she can use her beak and feet to bend and twist these materials. In fact, I already touched upon the relation between ecological information and affordances when explaining how invariant features within optic flow patterns allow birds to navigate their landscape. It's these invariant features that allow animals to navigate and dodge objects as they fly.

Now, bridging, grabbing, bending and dodging are all relatively simple cases of engagement with affordances, and I've used these to explain the basics of ecological psychology. These actions involve immediate, tangible interactions with the environment. Thus far, the animal behaviors that an ecological framework can explain without resorting to enrichment processes may appear somewhat limited. However, one of the primary objectives of this dissertation is to illustrate that the scope of an ecological approach is extensive, encompassing complex representation-hungry abilities.

Perceiving beyond the here and now

In the previous section, I focused on actions that involve environmental features within the animal's field of view. But again, perception does not start with sensory input from the environment. It starts with an active organism seeking for ecological information that allows it to engage with future possibilities or affordances. A consequence of this view is that animals can engage with the affordances of the environment even if they can't directly see, feel, smell, hear the environmental features that afford this engagement.

In fact, as Van Dijk & Rietveld (2018) remark, "Even in their most intuitive rendering—as possibilities for action—affordances already imply anticipation [...] That is, although they are available in the current environment, they pertain to that which the environment offers a skilled individual to do in the future (p.3). Similarly, Reed (1996) a student of Gibson who was particularly engaged with Darwin's evolutionary theory, writes that "All experience, even that of newborns and animals like spiders and flies, is prospective [...] once perceiving is tied up to acting, it is less helpful to represent the world as it is than to anticipate imminent changes in one's surroundings." (Reed 1996, p.144).

To illustrate the prospective character of perception, let's consider a very basic and fundamental capacity: object permanence. Object permanence is the capacity to determine whether an object continues to exist when it has gone out of view. Enrichment thinkers believe that grasping continued existence involves the construction of a mental representation of the vanished object. After all, the senses are no longer directly stimulated by the object. Gibson (1979/2015) opposed this reasoning. He claimed, instead, that grasping the continued existence of objects requires a sensitivity to the “occluding edge”. The occluding edge is the optical boundary between an occluding surface and an occluded surface. Gibson's discussion of the occluding edge illuminates how we can start to “scale up” engagement with affordances beyond the here and now (see also Heft 2020).

To illustrate the concept of the occluding edge, take the admittedly somewhat abstract example of one surface (surface B) gradually moving to the left behind another one (surface A) as depicted in figure 3. You can think of someone moving one piece of paper behind another:

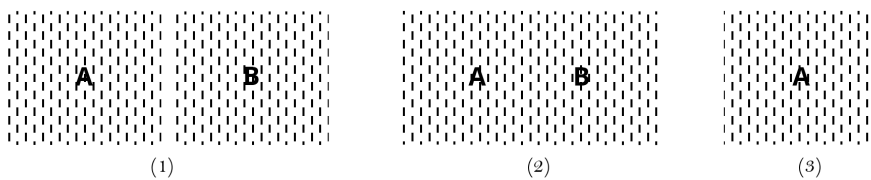


Figure 3. Perception of the occluding edge. An optical edge is generated within motion, while that edge isn't detectable without motion. The occluding edge specifies the persistence of surface B.

In still images, explaining this concept is a bit tricky.³ It revolves around the optical phenomenon where an edge is formed, due to a decrease in surface area B while the surface area of A is preserved. Gibson (1979/2015) called this optical edge the *occluding edge*. In the environment, occluding edges may occur when you move from left to right or front to back. For example, if you were to move to the left or right at this moment, the area behind your screen or paper would become visible. The optical boundary where this occurs is known as the occluding edge. Now, the exact opposite movement, from 3 to 2 to 1, results in the accumulation of surface at the occluding edge of surface B, while surface A remains preserved. Gibson termed this symmetry in movement the principle of reversible occlusion. Because the event is reversible, we perceive the continued existence of surface B. In contrast, an irreversible event, which lacks an occluding edge, implies that an object has ceased to exist (see Gibson 1979, p.181).

3. For an actual video of the effect, see: <https://www.youtube.com/watch?v=1qQLtIICXoE>.

The crucial point here is that animals don't require the construction of a mental representation of occluded objects or features to comprehend their persistence. The purported necessity for these mental representations to enrich perception arises from the absence of sensory stimulation when that object has moved behind a barrier. However, these enrichment processes are unnecessary once we recognize the presence of ecological information over time, such as reversible occlusion at the occluding edge, which specifies the persistence of the occluded surface. An organism perceives, literally, that an occluded object continues to exist even when light bouncing off that surface does not reach its eyes (see also Heft 2019). In a natural environment, such as when advancing in a certain direction and a building is concealed by another building (see fig. 4), one perceives that it's still possible to return to that building, even though it's currently hidden from view. Perception is active and forward-looking.

Let's turn to another animal, one that will return throughout this dissertation: the scrub jay. Scrub jays, like other corvids, store nuts and other food items. Object permanence appears to be a vital capacity for this behaviour. Salwiczek et al. (2009) demonstrated that young scrub jays undergo four phases of learning to cache. Initially, they begin by simply picking and dropping items. Subsequently, they progress to placing items in specific locations, such as corners and edges, sometimes in the presence of other jays. In the third phase, they begin "inserting" these items, pecking them until they vanish beneath the surface. Interestingly, in the study, the young birds never retrieved these items themselves but consistently relied on fellow jays. Fourthly, the jays will engage in tentative caching; they will cache items and retrieve them right away.



Figure 4. A jay learning about the occluding edge in caching. As they learn to cache, scrub jays become attuned to the patterns of optic and haptic flow that specify the occlusion of the peanut. It is the information detected in movement that specifies the persistence of the peanut.

Scrub jays eventually come to grasp that objects continue to exist even when they disappear from their field of view. Object permanence, according to Salwiczek et al. (2009) is a *cognitive* skill, and they conclude that "it is important to study cognitive development (e.g., object permanence) separately from behavioral development." (p.302) However, an ecological interpretation of this developmental trajectory offers

a different perspective: the jays are acquainting themselves with transformations in the ambient optic (and haptic) array during these developmental phases. Behavioral development and cognitive development intertwine seamlessly, blurring the distinction between the two. Their attunement to ecological information, including occluding edges, enables them to understand the persistence of the cached item—or rather, that the cached item affords retrieval even though it's currently out of view (see fig. 4).

These two views diverge significantly, not only in their interpretations of the phenomenon but also in their research goals and methods. To paraphrase Guthrie (1935), as far as the theory of object permanence is concerned, animals (including humans) are “left buried in thought”, and whether they will retrieve an occluded object, that would be “[the animal’s] concern, not the concern of the theory” (p.143).⁴ On enrichment accounts, what the animals *do* is only a gateway into their “minds”. From an ecological perspective, it matters not only *that* an object has disappeared, but also *what* disappears, *how* it disappears, *where* it disappears and perhaps even *when* it disappears. These differences generate different optical patterns that specify different affordances— determining whether an animal perceives something as recoverable or retrievable. An animal can perform poorly on an object permanence test, then, not because that animal lacks a notion of object permanence, but because the animal wasn’t afforded the relevant action—retrievability. In cases of failure, the experimental set-up may simply not have furnished the ecological information for perceiving the affordance of retrievability, given the animal’s body and perceptual systems.

Engaging with affordances that can’t be directly seen, felt, heard or smelled, then, is possible because there is ecological information in the environment that indicates what animals can do. As Heft (2019) summarizes: “Dynamic occlusion reveals perceptual awareness to be extended beyond a momentary slice of time, and critically, features of the environment are experienced as persisting even when they are not in the immediate field of view.” (p.189) But now the question becomes: how prospective is perception? What is the reach of explaining behaviours in terms of engagement with affordances?

4. Guthrie (1935) made this claim about rats who should try to find the exit of mazes in order to study whether they used spatial representations.

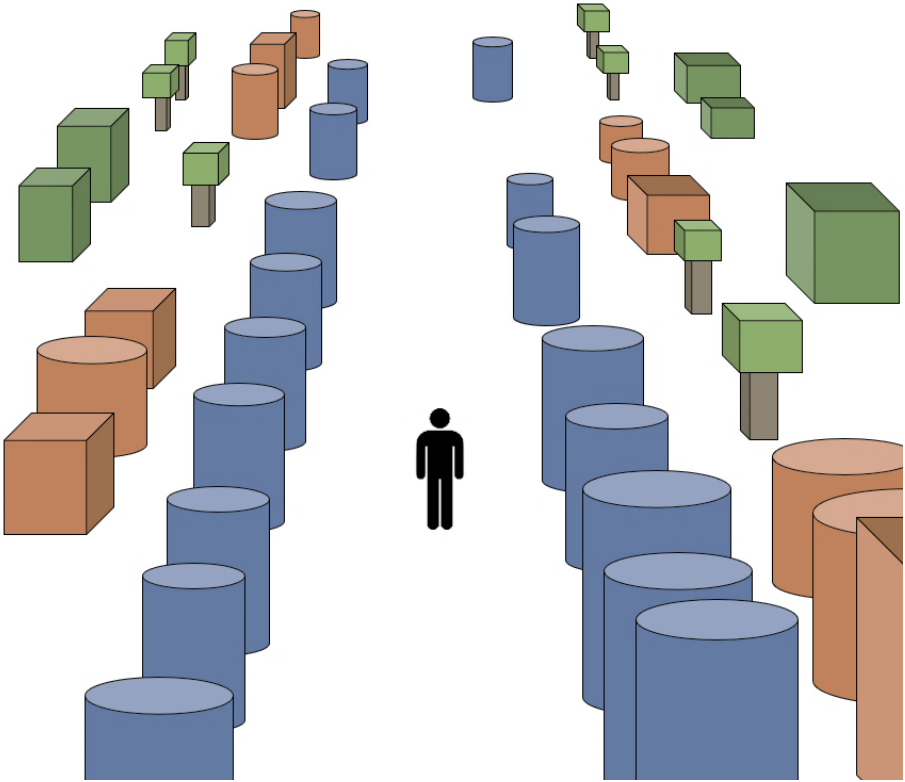


Figure 5. Occluding edges in an everyday human situation with buildings and trees. As a person moves forward, the persistence of buildings and trees are specified by occluding edges.

Nested affordances

While I have discussed affordances in relative isolation so far, they rarely occur as such in reality. Affordances are embedded in rich sociomaterial contexts. Accordingly, while affordances, in their most basic formulation, depend on the composition of the environment and the action capabilities of the individual, there is a growing recognition that affordances must be understood as depending on abilities available in a niche, or more specifically, in a *form of life*. A form of life refers to “the regular ways of doing things and steady ways of living that can be observed in groups of animals” (Kiverstein & Rietveld 2018). Affordances, in this sense, pre-exist any *specific* individual; they are *anticipated* in a form of life for its individual members, who learn to engage with them as they become participants in that form of life (see also Gibson & Pick 2000, p.16; see also chapter 5).

But there's more: recognizing how affordances are nested in sociomaterial practices, allows us to extend the reach of an ecological approach (Bruineberg, Chemero & Rietveld 2019; Kiverstein & Rietveld 2018). This expansion is possible due to the existence of sufficiently stable higher-order regularities in the environment—regularities that are shaped by our social practices. Exploiting these regularities offers the potential to engage with affordances beyond the here and now.

To better elucidate this concept, consider the scenario outlined by Bruineberg, Chemero & Rietveld (2019). Imagine a person with a craving for a banana. Despite occasional instances where bananas are temporarily out of stock, the person can still engage in banana-buying behavior (Bruineberg, Chemero & Rietveld 2019, p.5236). This is possible due to the reliable and relatively stable relationship that has developed between the local supermarket and the availability of bananas (see also Rietveld, Denys & Van Westen 2018). In other words, the person's decision to enter the store and purchase a banana is not determined by the immediate visual presence of the fruit. As Bruineberg, Chemero & Rietveld (2019) put it, “there is no light bouncing off the future” (p.5244). Rather, it is informed by the consistent restocking practices of the supermarket, which create an expectation of bananas being available, and which themselves stem from people's tendency to replenish their supply of bananas whenever they are running low.

Bruineberg, Chemero and Rietveld (2019) introduce the notion of “general ecological information” to capture these stabilized relations. General ecological information *indicates* or *constrains* engagement with affordances, due to relatively stable and reliable patterns or regularities in the environment (see also Chemero 2009). This notion of information is contrasted with the specifying ecological information that we can find, for example, in the optic flow patterns specifying distance and speed. The latter are determined by lawful, rather than merely sufficiently stable, regularities between the perceiving organism and the environment. As Withagen (2004; see also Withagen & Chemero 2009) have argued, however, while specifying information may be available, it's not imperative for organisms to detect it in order to directly perceive and navigate their surroundings effectively. For instance, in a forest, hearing a rustling noise isn't always a sure sign of danger for a prey animal. The sound could be muffled by other noises, and harmless creatures can also cause rustling. So, while rustling can signal potential danger, it doesn't always specify the threat. Nonetheless, the sound constrains or indicates the presence of a danger.

Now, in terms of affordances, leaving your home, walking to the supermarket, passing through the door, and grabbing bananas may each be seen as engagement

with a distinct affordance. However, crucially, humans do not engage with these affordances individually, as isolated units, but rather as a “complex particular” (Turvey 2015; Wagman, Cialdella & Stoffregen 2019; Wagman et al. 2019). Even though these affordances may be initially learnt separately, they are eventually perceived as affordances themselves, as the relations among them are grasped. As Gibson & Pick (2000) describe, “Achievement of a primary affordance, the function of the task overall, is accomplished with greater complexity as subunits that involve use of varied means begin to be nested within the task as a whole. The means for accomplishing a task is learned as an affordance itself, but it can later develop into a subunit embedded in the larger and longer task structure” (p.151). The possibility of engaging with “higher-order” or “distal” affordances, arises precisely due to the stable relationships—that is, nesting—among these affordances.

Van Dijk & Rietveld (2018; see also Van Dijk & Withagen 2016) concur that affordances are nested in various ways. However, they believe that in order to explain how animals can directly engage with higher-order affordances by leveraging how affordances are nested, we must reconsider the basic notion of affordances. In their *process-based* account of affordances, they argue that even engagement with simple affordances such as grasping, climbing, bending, sheltering and retrieving can’t be understood in isolation. For example, describing how humans perceive a stick based on its physical properties in relation to our action capabilities as solely for “grasping” means that we ignore the concrete situation in which this affordance occurs. Simple actions are always already part of larger-scale activities, and should be understood within that larger context. It’s this intertwinement that allows for a “scalable” notion of affordances, they argue:

By developing a process-based account of affordances in which affordances are determined in activity and intertwine across timescales we thus aim to provide a scalable notion of affordances that allows any aspect of human involvement, from quickly unfolding “simple” grasping, to “complex” architectural making unfolding over a larger timescale to be understood in equal terms (Van Dijk & Rietveld 2018, p.3)

To say that affordances are *processes*, is to say that they are, in a sense, never fixed or specified in advance, but always *in formation*. Here, ecological psychology meets enactivism, as engagements with affordances are now conceptualized as “*continuations* of real-life ongoing practices in terms of unfolding activities of individuals rather than as *realizations* of possibilities pre-existing *in abstracto*.” (p.6) That is, affordances do not exist in any abstract sense; they are continued or shaped, or *enacted*, within real-life situations. What an environmental feature affords is not

solely determined by the abilities of the organism and the properties of the feature, but also by the specific activity the animal is involved in. This activity, in turn, plays a role in defining what the environment affords.

For instance, because we routinely use chairs to sit on, perceiving them as affording sitting is salient, despite the fact that they could also serve as leg rests or stepping stones (Costall 2012). Or consider how, after a storm in a forest, many tree branches break, forming new paths. When squirrels start using these paths, they make them more noticeable—the affordances of using them become more salient. As the squirrels keep using these branches, it makes these affordances more stable for them. Each situation is unique, and affordances continue to take shape over time, and become stable, through the activities of organisms themselves. So, although we could describe the affordance of using these pathways as relations between abilities available in squirrel forms of life and the properties of the trees, that would be an abstraction from the concrete circumstances. Viewing affordances as processes, as being in formation, then, does not imply that they are no longer directly perceived. It simply entails that the ease with which animals perceive and engage with affordances itself depends on regular and stable practices. Recognizing the active role of organisms in shaping what the environment affords is a distinct influence from enactivist thought on the concept of affordances.

Van Dijk and Rietveld (2018) continue that “On the basis of this process-based notion of affordances, we can show how affordances like activities, become nested and hang together.” (p.4) Nesting and the process-based view of affordances go hand-in-hand. Van Dijk and Rietveld (2018) illustrate how affordances become nested by showing how architects can anticipate a grand art installation by engaging with concrete materials under specific circumstances that, on their turn, invite and constrain further actions, in an ongoing fashion, as the large-scale affordance of building the art installation is slowly determined (see also Van Dijk & Rietveld 2020). In a case like this, the “buildability” of the art installation, is enacted over longer timescales as an affordance itself. It is precisely because affordances are not predetermined but rather enacted that it becomes possible to directly engage with more abstract affordances like this. Van Dijk & Rietveld (2018) add that, “It is not necessary to know all the steps to be taken in advance, nor to have a ‘final state’ of the process specified in order to engage the possibility (nor indeed, need there be such a state). Openness to the process to which the participants contribute as they act is all that is required of the skilled individual” (p. 14/15).

To explain this a little further within a nonhuman context, I'll return again to the example of a bird building a nest. To build a durable nest, birds must learn how various materials fit into the whole and how the nest should be organized. In other words, they need to know what those materials afford in relation to the larger-scale activity—to perceive how they are nested. Each addition to the nest, such as putting in a twig, shapes and constrains the selection of subsequent materials, as the nest takes shape over time. The affordances here thus are not realizations of pre-given possibilities, but shifting and taking shape over time, depending on the current state of the nest. What individual nesting materials afford can't be separated from the activity of nest-building as a whole.

What's more, by engaging in the activity of nest-building—making certain choices in a specific order—birds are actively stabilizing the relationships among affordances, essentially contributing to how these affordances become nested over time, for themselves and other birds. As experience grows, the capacity to anticipate and execute the larger-scale affordance of nest-building become easier and more refined, as the bird can now exploit the nested structure of affordances in the activity of nest-building. And like the architects, there's no need for the bird to have a pre-formed image of what the nest is going to look like. Anticipating a nest is not the execution of a predetermined plan, but an ongoing activity in which the bird depends on the stabilized relationships among affordances in its environment (see Guillette & Healy 2015).

Nest-building and other activities remain open-ended. Behaviour does not become fixed or stereotyped with repetition and experience. Nothing exemplifies this more than the creation of novel and unique nests that we witness today: animals now use anthropogenic materials in the construction of their nests, such as plastics and cigarette buds (Mainwaring et al. 2023) and even anti-bird spikes (Hiemstra et al. 2023). In doing so, they continue the practice of nest-building while also adjusting the possibilities for nest-building using novel materials that will afford the creation of new kinds of nests (cf. Van Dijk & Rietveld 2018, p.4).

Conclusion

When animals act, they are engaging with the affordances—opportunities for action—of the environment. These affordances are perceived through ecological information, the optical, acoustic, haptic and other patterns generated by moving around and interacting with environmental features. These two components (affordances and

ecological information) entail a major rethinking of animal perception. Instead of a linear path from sensing to enrichment processes to action, we must understand their abilities in a more dynamic manner, viewing them as actively exploiting environmental patterns to interact with affordances beyond the here and now. This, then, allows us to explain certain representational capacities—recall the discussion on object permanence—in terms of action, perception and the exploitation of environmental patterns. Instead of enrichment, this is achieved by differentiating the wealth of informational patterns that exist within the environment.

Critically, affordances don't occur in isolation from other affordances, and this fact is crucial for upscaling engagement with affordances beyond immediate contexts. What the immediate environment affords is inseparable from the larger-scale activity the animal is engaged in (or the larger-scale affordance the animal is enacting). This intertwining constitutes the central idea of *nested affordances* that I will employ in the upcoming chapters. By exploring nested affordances, we can start to elucidate how the representation-hungry behaviours of animals depends on their actions within intricately structured environments. The learning process in more complex activities, such as nest-building, still relies on differentiation rather than enrichment. Animals must differentiate and become attuned to the relevant features of the environment, such as the size, shape, and consistency of twigs, and learn how engaging with one particular affordance prompts the engagement with another—for example, understanding the type of material required and where to find it—based on the overarching task at hand.

A major advantage of an ecological perspective in general, and of nested affordances in particular, is that we can experimentally observe all aspects of complex activities, without having to appeal to hidden enrichment processes. As Louise Barrett (2015a) writes: “If we continue to observe behavior over an extended duration, the necessity to postulate private events diminishes, as we can then sufficiently describe the history of interactions with the environment” (p. 33). Consider the nest-building bird. After extensive observation, we would learn about the twigs and branches a bird selects, given the current stage of her nest and given the environmental conditions, such as weather conditions. That is, we will find recurring patterns.

The application of nesting or nested affordances in comparative psychology and the philosophy of animal minds is rare (but see Wagman et al. 2019). Yet, this approach could offer solutions to significant challenges in comparative cognition, including anthropomorphism, its relation to evolutionary theory, and empirical obstacles. These will be highlighted in the upcoming chapters. A potential barrier to its

adoption is the entrenched methodology of comparative psychology: animals' access to certain immediate affordances is typically restricted, while the possible species-specific reliance on the nesting of affordances is overlooked. This approach, fuelled by an enrichment-based perspective, distorts our understanding of other animals, either portraying them erroneously as "human-like" or unfairly as falling short of human capabilities.



3

Anthropofabrication and the redressing of cognition

“And what the computer people don’t realize, or they don’t care, is we’re dancing animals. You know, we love to move around. And it’s like we’re not supposed to dance at all anymore.”

~ Kurt Vonnegut (2005)

Abstract

On what basis do researchers posit that humans and other animals share cognitive capacities? A common answer is that such claims are based on inherent, pre-existing similarities. Here, I will argue that they emerge through a two-step process that I call “anthropofabrication”. In the initial stage, embodied action-based strategies and environmental context in human studies are ignored due to the need for measurement and quantification. Consequently, cognitive terms become disconnected from the context to which we apply them, and human classificatory cognitive terms are transformed into broad explanatory terms, assumed to be “species-neutral”. The second phase entails translating and applying these generalized explanatory terms to specific nonverbal animals. Here, again, researchers selectively discard contextual information to facilitate the comparison with humans. To limit anthropofabrication, we should reacknowledge that cognitive abilities are not species-neutral and cannot be detached from embodied action, perception and their context of occurrence. These points about anthropofabrication will be illustrated using the example of memory research.

One size doesn't fit all

Darwin's assertion that "[t]he difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" (p.105) continues to loom large in comparative psychology (Darwin 1871). This statement encourages the search for cognitive abilities that humans *share* with other animals. Differences, if discussed at all, typically appear as a *lack of*, or at best a precursor to, "full-blown" human abilities, and there is little recognition of the fact that Darwin also was at pains to emphasize that evolution is a diversity-generating process. Such an anthropocentric goal is not wrong *per se*. As MacLean et al. (2012) write, "if we understand how cognition evolves in nonhumans, this knowledge may in turn inform our understanding of how our own species' cognitive abilities have evolved" (p.224). But what if our dominant idea of similarity is built on shaky grounds?

Many comparative psychologists endorse a universal language of cognitive mechanisms and processes, despite considerable variation in the morphology and ecological niches of animals. They regard cognitive processes as brain-based, species-neutral, and universally applicable across organisms. In order to make comparisons, researchers translate concepts from human psychology to concepts that apply to nonhuman animals. They deem this process of translation as a straightforward and harmless practice of generating effective experimental designs, but we think that "[t]he decisive moment in the conjuring track has been made, and it was the very one that we thought quite innocent." (Wittgenstein 1953/2009, p.308). That "decisive moment" was assuming that cognitive abilities can be treated as species-neutral.

As Sandis (2012) showed in his analysis of Wittgenstein's famous statement about a talking lion¹, transposing concepts from human to nonhuman contexts is different from transposing concepts between two human cultures. Understanding other humans, whose language we don't understand, and whose customs differ "does not require us to learn a new ability; we may currently lack their ways and concepts but already possess the ability to master them" (Sandis 2012, p.149). For instance, a Danish person visiting Japan might not speak the language, but they share a biological structure and sensory and bodily abilities, and the Dane will notice similarities in their ways of living and will have some idea of how to go about learning Japanese. But to make sense of a lion, an elephant, a baboon, a raven or any other animal, we will need to acquire a whole new ability: we have to immerse ourselves in an utterly

1. Wittgenstein (1953/2009) wrote that "Wenn ein Löwe sprechen könnte, wir könnten ihn nicht verstehen" (p.223e). This statement is commonly translated to English as "If a lion could talk, we could not understand him".

different “form of life”, to use Wittgenstein’s term. Other animals have unique sensory and bodily abilities, and all live in very different niches compared to humans.

Where immersion embraces complexity, translation is a process of pruning. In translation, human concepts are stripped down, with various aspects of those concepts—related to perception, action, environmental context and experience—adapted, bracketed, or left out altogether. These stripped-down concepts are adopted by comparative psychologist who, as a consequence, also gather limited data about what their animals do, as well as where, when and how. Stripping away the situational and embodied aspects of cognition makes it seem like we are stripping away superficial layers of difference to uncover deeply rooted similarities. Actually, we may be actively manufacturing superficially similar cognitive concepts, by replacing embodied, situated elements—which are constitutive of “cognition”—by an abstract, intellectualized view of these processes, so that they can be made to apply generally. The term “anthropofabrication” will be used to refer to this two-pronged process of making animals appear “human-like” by fabricating similarity and cloaking differences.

Anthropofabrication is related to Buckner’s (2013) notion of anthropofabulation. Researchers engage in anthropofabulation when they define particular psychological capacities by reference to an exaggerated sense of human performance, and only count performance at this level as “genuine” possession of the skill by non-human animals. In other words, we are often wrong about our own cognitive prowess, and we judge animals according to these inflated standards in a way that serves to compound the problem. Anthropofabrication precedes anthropofabulation, however, because debates about the definition and criteria for possession of certain abilities depend on the initial assumption that cognitive processes can be regarded as wholly species-neutral.²

To mitigate anthropofabrication will require us to redress—that is, re-situate and re-embody—cognitive abilities. The concept of anthropofabrication will be illustrated, by discussing the history of the concept of memory and how it has been studied in humans (sect. 2) and, as a consequence, in other animals (sect. 3). This serves to illuminate how “artificial” our current scientific notion of biological memory really is, in the sense of being both produced and constituted by human artifice and artifacts. Finally, a discussion follows of how we can limit anthropofabrication by

2. See also Andrews & Huss (2014), who problematize the assumption that “special human properties can be unproblematically identified” (p.714) and that our cognitive concepts should not be reserved for humans *a priori* (see also Keeley 2004; De Waal 1999; Andrews 2011)

embracing within-species and between-species variation in morphology, sensory modalities and sociomaterial processes (sect. 4).

Step one: fashioning memory

If you asked a comparative psychologist “what is memory?” they would probably bring up something about storage and retrieval—much like putting your winter jacket in a box during summer and fetching it when winter returns. For instance, Shettleworth (2011) broadly defines memory as a cognitive ability that “deals with how information is stored, retained and retrieved” (p.210). Given developments in memory research over the last three decades or so, researchers would concede that your jacket may not be the colour you anticipated, or it looks different from how you imagined it. That is, our memories are known to be susceptible to distortion, alteration and inaccuracy (Loftus, 1997; Brainerd & Reyna 2005; Cleary & Schwartz 2020). Even so, memory is strongly regarded as a means by which humans and other animals store a record of past events, albeit an imperfect and revisable one.³

As Danzinger has (2008) has argued, we tend to presume that our current scientific notion of memory, of (imperfect) storage and retrieval, points to what memory “naturally” is, and that it evolved through natural selection as it provided an adaptive advantage. However, consider an example that challenges this presumption: in Ancient Greek cultures, stories and poems were transmitted orally. Recitation was a performative activity enriched with rhythm, intonation, gestures, and bodily movements. These elements played a crucial role in aiding memorization. Through these expressive means, the storyteller reconstructed the narrative with each telling. Today, we recast these embodied techniques in terms of *scaffolding* for memory, as if the bodily techniques serve only to elicit the recall of memory in the head.⁴ Such a view is at odds with the view of memory at the time. The storyteller’s gestures and actions were not considered mere by-products of memories; rather, they actively constituted the process of remembering. The strict separation between body and

3. They would also say that memory comes in many shapes and forms. Just as pants can be jeans, chinos and slacks, there are different types of memory, such as episodic, semantic, procedural and autobiographical memory. The increasing differentiation of concepts withdraw attention further away from situated activities, but here it will not be detailed *how they do so—I’ll stick with the fact that the storehouse formulation of memory diminishes attention to environmental structures and embodiment.*
4. More recent memory research has demonstrated that recollection is enhanced when the movements that participants make during recall align with their movements during the initial learning process (Tversky 2019). However, in such cases our actions are exactly understood as “scaffolding”—self-imposed embodied cues for retrieving stored memories. This is a slow reintroduction of the body into an activity that is and always has been fully embodied and situated.

mind, and between past and present, did not hold up: “[N]o distinction between reproduction and composition can be detected in the earliest Greek literature that refers to Mnemosyne [meaning: ‘remembrance’], the exercise of memory as an activity. [...] Early on, remembering means listening to a voice.” (Danziger 2008, p.29) The isolation of memory as a distinct (cognitive) process—as a thing that we possess, rather than an activity in which we engage—occurred much later with the invention of writing.

By writing down words, the act of speaking and its “content” are separated, and written words therefore take on a quasi-permanent existence, subject to inspection by numerous individuals (Danziger 2008, p.33). Consequently, as humans embraced writing, they gained the ability to compare recollections of people with recorded events, which allowed them to assess how accurate these recollections were (Danziger 2008, p.50). Interestingly, writing became a metaphor for memory itself, leading people to believe that memory resembled the storage of words (Danziger 2008, p.50). With the advent of computer technology, computers and the language of information-processing also became memory metaphors. However, these metaphors slowly lost their metaphorical ring and became accepted as ordinary descriptive terms (Danziger 2008, p.44). Examples of such “dead metaphors” are information, input, output, encoding, decoding, and content. This information-processing language has led to “a closed conceptual world in which anything that was not expressible in the language of information processing remained unseen, unrecognized and unexplored” (Danziger 2008, p.53). These terms, and the experiments they give rise to, thus warranted the omission of the contextual, performative elements that for the Ancient Greeks were very much part of remembering.

The prevailing image of memory as the storage and retrieval of “information” was further substantiated by Hermann Ebbinghaus, the renowned psychologist, who brought memory into the lab in an attempt to quantify it. He asked research subjects (often just himself) to learn nonsense syllables and word lists and then to recall them later. Because he could compare these syllables and words in his lists, he could establish whether the participants’ memories were accurate and how much information was retained over a given time frame. However, “Without the use of fixed, recorded materials neither the measurement of memory performance nor the standardization of experimental conditions would be possible” (Danziger 2008, p.174). The use of nonsense syllables, moreover, suggested that the “contents” of memories were isolated “snapshots” of the environment. This content was thought of as passive “input” to the senses, and the performative side of remembering was left

out “by simply not collecting such information” (Danziger 2008, p.131) in order to get to “memory proper, defined as ‘mere retention’” (Danziger 2008, p.128).

Ebbinghaus’ participants were not really passively taking in information. Their urge for action, even if minimal, and for discovering meaning within apparent nonsense, could not be suppressed. Drawing from their prior experiences, they added rhythm or sought meaningful patterns anyway. As Danziger (2008) puts it, “Ebbinghaus and those who followed in his footsteps had chosen material with poor intrinsic organization that could be remembered only by intentionally imposing some organization of one’s own” (p.135). While later research replaced nonsense syllables with words and word pairs, the foundational premise of memory research has remained intact (Danziger 2008, p.256). At the time, Ebbinghaus’s findings were interpreted to reveal the cognitive mechanisms that underpin every instance of what we call “remembering”.⁵

What Danziger’s (2008) detailed historical perspective highlights, then, is that we have come to think of remembering as storage and recollection in our heads, because we’ve been studying and talking about remembering *as if it were*—and so increasingly confining them within our skulls along the way. Danziger (2008) has rightfully questioned whether twenty-first-century laboratories are investigating a universally shared and generic “human memory” or rather a socially influenced manner of functioning that evolved over time due to the gradual development of literacy (p.5).

We can go further, and bring in Noë’s (2023) argument that, as human beings, we are not merely integrated with our cultural products but are deeply entangled with them. Using the examples of dancing, seeing and speaking, Noë argues that the ways in which we have been organized and reorganized by our cultural practices—choreography, pictorial art, writing—have been going on for so long that any attempt to investigate our “natural” impulses to dance, see and speak, our unadulterated “human nature”, would require the impossible: we would need to “go back to Eden, that is, go back to a make-believe prehistory” (Noë 2023; p.31, see also Barrett 2017; Dupré 2018; Ingold 2006). Memory can be seen as an entangled concept in this sense, too. The material and social practices that we have used to support and engage with memory—literacy, external storage devices, our scientific methods for studying memory, depictions of memory in oral story-telling, written fiction and other forms of representational and visual art—have now become so fused together with whatever biological capacities we possess that this “entangled creature”, to use Noë’s words,

5. As Hutchins (1995) has pointed out, when we are studying what “really happened”, we are actually studying our sociocultural tools rather than our cognitive processes.

now just is the human form of memory that we study scientifically: we *are* creatures capable of storing and producing accurate recollections of the past, and for whom a more abstract, disembodied form of memory is part and parcel of human life.

In short, this form of human memory—the storage and recollection of past events—is an entangled skill, subject to further entanglement. It is not a fixed and general biological function. However, the view that psychological studies of memory are geared toward probing a universal and general biological function is widely accepted and has seeped into other fields, including comparative psychology. Generic *human* memory has become generic *animal* memory; as such, it has been transformed from a typically human process into a species-neutral process. To illustrate this latter point, we'll have a look at a specific type of memory that researchers have explored extensively in Western scrub jays, among other animals: episodic memory.

Step two: sustaining a sense of similarity

In 1972, Endel Tulving wrote that “[o]ne of the unmistakable characteristics of an immature science is the looseness of definition and use of its major concepts” (p.381). Dissatisfied, he took steps to resolve this and made the now-famous distinction between *episodic* memory (memory for personal experiences) and *semantic* memory (memory for generalized facts).⁶ Tulving (1985) attached the term *autonoetic consciousness* to episodic remembering. This term indicates *conscious* recollection of a past event, an ability for “mental time travel”. Although by this time “[t]he lesson was taken that distinctions among memory systems were conceptual and classificatory, not causal and explanatory, [...] in practice they were never treated as mere heuristics” (Danziger 2008, p.175). Attempts to empirically isolate *episodic* memory in nonhuman animals ensued. Moreover, while conscious experience and contextual variables of the *remembered* event were explicitly integrated into the definition of episodic memory, the dynamic, context-dependant behaviours exhibited during remembering were still overlooked.

Taking on Tulving's distinction, Clayton and Dickinson (1998) wanted to test whether Western scrub jays, a North American bird known to cache various food items

6. If we take the historical perspective from the previous section again, we can see how the term semantic memory also reflects the ideas of Ebbinghaus, where the world is thought of as a vast array of “isolated facts” that animals can learn to retain and is devoid of experiential aspects—an image that is very much shaped by experimental practices and storage technology (see Danziger 2008, p.174). However, the focus here is on episodic memory, as this was the capacity Clayton and Dickinson (1998) were primarily interested in.

that vary in decay rate, also possessed episodic memory—or rather, episodic-like memory (the suffix was added to evade questions about auto-noetic consciousness, which, understood as a *private* experience, could not be assessed empirically).⁷ Episodic-like memory was thus defined as “what-where-when-memory”: memory for *what* happened, *where* it happened and *when* it happened. Clayton and Dickinson hypothesized that episodic-like memory may have evolved in this species, not only to enable birds to retrieve caches effectively, but also avoid those caches that were “past their sell-by date”.

The birds were placed in an experimental set-up that allowed them to cache both meal worms, a highly preferred but also highly perishable food, and less preferred but longer-lasting peanuts. Crucially, after a 7-day delay the birds recovered the peanuts right away, despite these being less preferred as food, and avoided the preferred meal worms. As the meal worms but not the peanuts would decay over a 7-day period, the authors inferred that the birds remembered not only *what* they had cached and *where*, but also *when* they had done so, such that they recovered only the non-spoiled food. The authors concluded: “[T]he cache recovery pattern of scrub jays fulfils the three, ‘what’, ‘where’ and ‘when’ criteria for episodic recall and thus provides, to our knowledge, the first conclusive behavioral evidence of episodic-like memory in animals other than humans.” (Clayton & Dickinson 1998, p.274).

The design of the study itself was elegant and clever. However, the researchers were engaging in anthropofabrication even *before* their experiments had started. They didn’t question whether episodic memory in humans *can be translated* to nonhuman animals. Episodic memory, for them, was a generalizable, species-neutral process, and could be stripped of the features they deemed mere “add-ons” in order to isolate the “core” features of episodic memory. But take the “auto-noetic” component of episodic memory, the ability to relive a past moment. As with memory in general, our notion of episodic memory may be entangled—that is, intertwined with sociomaterial practices and technologies, such as our reliance on clocks, calendars, and other time-keeping methods, that together with our communicative abilities, enable a sense of past events *as past events*, independent of our current goals or engagements. In other words, these technological and linguistic means enable us to separate time neatly into the past, present and future and to locate personally experienced events on a timeline. Does this neat separation also exist for animals that lack these means? If we answer “yes” to this question, then we seem to be making the same mistake as claiming that the Greek storyteller was retrieving pre-existing information, rather

7. On my approach it won’t make sense to distinguish between a genuine episodic and a mere episodic-like capacity, so I will use these terms interchangeably in this chapter and the next.

than engaging in a reconstructive performance in which the distinction between past, present and future made little sense.

On an “entangled” view of episodic memory, our sociomaterial environment cannot be taken out of the equation if we want to understand human episodic memory. However, on the dominant cognitivist view, situational cues or sensory-motor strategies are considered to be confounding factors (see sect. 2). Much like Ebbinghaus considered memory to be a purely “cognitive” internal process, comparative psychologists consider episodic memory as a purely brain-bound internal phenomenon. In order to establish episodic memory in their study animals, they therefore have to exclude alternative explanations by which animals are able to solve a memory task using occurrent cues. To this end, environmental features that animals can smell, see, feel, hear or even taste are treated as confounding variables that can be neutralized through experimental routine and standardization.

Because the jays passed the experiment, and the experiment was set up in such a way that passing indicated the possession of episodic-like memory, the researchers claimed to have found a similarity between humans and scrub jays. We suggest, in contrast, that by *first* ignoring the impact of the human environment on episodic memory (thus seeing it as species-neutral capacity) and *then* accounting for “confounds” in the animal’s environment (e.g., olfactory of visual cues, solar cycles, circadian rhythms), the researchers are actually generating a sense of similarity as the experiment proceeds. Put differently, while it seems as though we are uncovering a similarity, a case of evolutionary convergence, we are actually selectively ignoring or “cloaking” species-specific, situational influences on the capacities of both humans and jays—all due to cognitivist assumptions about species-neutrality. Species-specific “solutions” to these experimental tasks are discussed in the next section.

These scrub jays are one specific and well-known case, but this is not an isolated incident: the species-neutral assumption about episodic memory still permeates research on episodic memory in nonhuman animals, including cuttlefish and bottlenose dolphins (see e.g. Martin-Ordas & Call 2013; Crystal 2018; Schnell et al. 2021; Davies et al. 2022) As long as we treat human forms of memory as species-neutral capacities, we’ll continue to anthropofabricate. So, what’s the solution?

A solution: redressing memory

“Insights about and analyses of the behavior of worms need to be developed with the same methods and concepts used to understand human beings—without attempting to reduce humans to worms, or turns worms into miniature cylindrical human beings.”

~ Edward S. Reed (1996, p.96)

3

To tackle anthropofabrication, we need a notion of memory that *embraces*, rather than *masks*, embodied action-based strategies and between-environment variation, and accordingly, acknowledges species-specific differences—that is, we need an approach that welcomes those aspects of memory that are currently cloaked by our species-neutral view and our dominant research practices.

Such an approach can be found in ecological psychology, where the term memory captures the altered relationship between an animal and its environment, without the need for “storing” information. Put differently, remembering is a generic term for the things that organisms do at an earlier time to facilitate their future encounters at a later time.⁸ As Michaels & Palatinus (2014) put it, “the consequence of personal experience is not that the old animal has new knowledge, but that it is a new animal that knows better” (p.25). Or as Danziger (2008) says, remembering results in “some ‘tuning’, in our disposition to see things in a particular way when encountered in a certain kind of context.” (p.258). In what follows, we’ll discuss how this ecological notion of memory allows for better comparative memory research, by highlighting two elements: the wealth of the stimulus and cognitive structuring, respectively. Note that these elements cannot really be separated: identifying the cognitively relevant environment hinges on considering the animal’s embodiment. That is, our task here is to understand more fully the opportunities that the environment is likely to offer an animal possessing those specific attributes. We can use these to categorize similarities and differences between species, as well as between individuals within a species.

Patterns everywhere

The term “wealth of the stimulus” signifies that the environment provides far more and richer information than usually assumed. Comparative psychologist typically accept that animals only receive direct information from proximal sources.

8. We could call this “remembering” but also “perceptual learning”. We stick with the former here to highlight anthropofabrication in cross-species comparisons.

Everything *beyond* proximate sources, on this view, demands “cognitive” processing. As previously mentioned, comparative psychologists strive to uncover “cognitive” capacities that are independent of perception and context, and for that reason they mask immediate cues as a part of the experimental procedure. However, the wealth of information available to animals in experiments is rarely recognized. For instance, covering up the smells emanating from a peanut and a decaying worm does not yield a room void of scent. If anything, experimenters smell, and they tend to visit regularly, though the word “presence” often obscures these facts, as Despret (2013) observes:

[I]f the scientist's body is evoked, it is never for itself nor is it named as such: when seeking the body, we are offered a surprisingly abstract concept: the 'presence'. This abstract term—most of the time under the guise of the 'presence of the observer'—while referring to the body, actually conceals it. It conceals what the actual and concrete 'presence' is for the animals: the space the so-called observer's body occupies, the body which moves, which walks, bears and diffuses smells, makes noise, follows, and does everything a body may do – including what we don't know our body may do since we are so unaware about what it is capable of, but which animals may nevertheless perceive. (p.52)

So, for example, and similar to the case of Clever Hans⁹, the experiments described above could well involve unconscious cueing, despite efforts to remove such “confounding” variables. The bird may become sensitive to the correlation between certain smells (or other sights and sounds) in the room—be they of the experimenters or something else—and the decay rate of worms, during initial phases of the experiments (see also next chapter). In other words, the ability to remember *when* something happened could be tied to events in the experimental room. Experience would teach the birds such relations, similar to the way that dogs can learn to perceive “the passage of time” by the decrease of scents in the environment (Horowitz 2016).

Animals in experiments have plenty of time to familiarize themselves with the smells, sights and sounds in the room and learn to focus on the relevant environmental contingencies. The behaviours that might indicate this process of perceptual learning—such as the animals' movements between trials, their observations, and interactions with their surroundings—can all be systematically and rigorously collected during experiments. However, such elements are not collected as data because they are considered irrelevant to episodic memory, which is defined in isolation from the body and environment.

9. Clever Hans was a horse that appeared to be capable of performing arithmetic; his abilities were later shown to rely on his trainer, who was unintentionally cueing the correct responses.

Humans also exploit relations among events. Such events may include self-induced ones, such as adding rhythm, chunking variables, or entering variables into some other kind of meaningful organization based on the person's past experience. These human strategies, like the jay's potentially relying on higher-order olfactory patterns, are ways to connect past experience to the task at hand. When researchers attempt to exclude certain perceptual and motor "cues" in order to more effectively infer the structure of internal cognitive processes, they are actually cloaking the environmental patterns that animals' perceptual systems can exploit to solve the experimental task. Rather than figuring out how, where and when animals do what they do, they need the animals to act in a certain way, so that they accord with the way experiments in comparative psychology are carried out.

In addition, while psychologists tend to throw all caching behaviour on the same pile—given that a specific memory capacity is thought to underly these behaviours—caching and retrieving worms and peanuts may involve different processes of perceptual learning. Jays potentially learn to perceive relations between the edibility of worms and other opportunities for action that are available over similar timescales. The same could be true for the retrievability of peanuts, which may become associated with affordances that are available over relatively longer time-scales than affordances associated with edible worms (see fig. 6). These relations can be studied systematically by varying (rather than excluding) availability of information, in the way Reed (1996) has suggested: "Does the animal behave differently with respect to that thing under circumstances in which it is likely to have access to information about it, and does it behave in an undifferentiated manner when such information is unavailable?" (p.25).¹⁰ By systematically varying what affordances the animals have access to, researchers can determine the relations or higher-order patterns jays rely on for specific tasks. Put differently, it is an effort to fill in the spaces currently occupied by question marks in figure 6. These could be affordances related to mould growth or plant growth, specific lingering smells, temperature or humidity changes, behaviours of conspecifics, and so on and so forth. Unless animals are placed inside a sterile room, there will be "indicators of time"—but of course, actually placing animals in sterile rooms undercuts the precise point made here, that we can't separate abilities from their context of occurrence.

10. This systematic variation approach was also employed, for instance, by Darwin in his analysis of earthworms. Earthworms plug up their burrows with leaves to keep warm. Darwin manipulated, among other variables, the shape and thickness of the leaves, the structure of the soil, and the size of the burrow (Darwin 1881; Reed 1982).

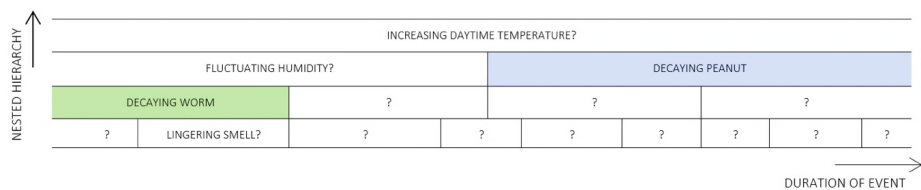


Figure 6. Nested organization of affordances in scrub jay caching experiment. On top are regular events or patterns that take relatively longer, and towards the bottom, events take shorter—they are “nested”. While these describe ecological patterns, they may encompass several affordances. Roughly speaking, a peanut is edible or inedible, and this changes over time. Perhaps we could also specify affordances in between, as the peanut may have an optimal edibility, and many variations in between. Temperature may afford various behaviours, in isolation but also in relation to other processes. Through all these behaviours, life becomes one big nested organized activity.

Such a research paradigm would grant animals some agency to solve the problems on their own accord, allowing genuine similarities and differences between humans and other animals to manifest. For instance, we can ask if and how a jay and a human are able to recover something they hid a week ago. We can look at the way they potentially exploit higher-order (visual, olfactory) relations in their environment in order to achieve this. That is, we can see how animals (including humans) solve actually *similar* tasks, and incorporate differences and similarities in sensorimotor strategies into our data collection protocols. If this seems far-fetched, researchers have found that humans are actually much better at tracing scent trails than expected, when pressed to the ground. They will even automatically employ the characteristic “zigzagging” patterns also found in rats, dogs, cockroaches and honeybees, among others (see, Porter et al. 2007; Khan, Sarangi & Bhalla 2012). In some human cultures, moreover, smell trails are very much an integral part of hunting (Low 2008; Ingold 2011, p.121). This counterintuitive point illustrates that our image of ourselves should not be used to guide our research practices.

To be sure, the suggestion here is not that animals (and sometimes, humans too) are employing “simpler” strategies than researchers currently claim—that is, we should reject the false dichotomy drawn between “mere” associative learning or some other “non-cognitive” interpretation and those attributed to more complex “cognitive” processes.¹¹ Rather, it’s a proposal for a more evolutionarily appropriate, embodied,

11. This, incidentally, is itself an incoherent distinction, given that according to Shettleworth (2010), association-based processes fall under the definition of cognitive—and both kinds of explanations ignore important variables that make up the wider organism-environment system.

embedded notion of what cognition is (and in this case, what memory is), and how it operates in the natural world. So, instead of assuming that animals can reason in a “human-like” way (full-blown or otherwise) whenever they display a capacity that we think humans possess, we should consider that we are more “animal-like” than we like to think, in the sense that our own capacities incorporate our own unique bodily and environmental resources. Of course, this was exactly the point about the entangled nature of human memory in the first place.

Stretching memory

Besides relying on the wealth of available information, animals also actively structure their environment in order to remember. Recall how Ebbinghaus confined his participants to experimental rooms, and shrank their world to a table, chair and some nonsense syllables. The possibility of using sensorimotor and situated strategies for remembering was almost impossible (although as noted above many subjects tried their best), and it is no surprise that a particular form of memory was made manifest. Most (if not all) experimental studies take place in such confined settings, and so the ability to remember of the animal in question—whether human or nonhuman—is also necessarily limited. The “real world” is nothing like this, and given our perspective that remembering is tied to its present context, findings in experimental settings will not, therefore, easily translate to “the wild”—remembering in the laboratory is a different species of remembering to that which occurs in richly stimulating environments that afford free movement. Although, critically, we could exploit the experimental situation in ways that would point to the strategies likely to be employed in the wild.

Before discussing nonhuman animals, let us look at some of the things that humans do “naturally” to remember, because humans organize their surroundings in the service of remembering constantly. We keep things in particular places as an integral part of memory—we distribute the process into the environment (Kirsch 1995). Putting objects in specific places turns “conceptual” tasks into more effective, and easier, perceptual ones: if we wish to remind ourselves to eat more fruit, we’ll place the bowl on the tabletop, not in a kitchen cupboard. If we always put our keys in a specific place, we can more easily remember them on our way out of the door. We charge our phone every evening, in the same place, so that we don’t forget to do so, and so we know where it is when we need to take it with us. As Kirsch (1995) argues, “Experts find sufficient cues in the situation to trigger a known rule without halting the activity in order to consciously and analytically take stock of the situation and reason or deliberate about a solution.” (p.37) These strategies aren’t necessarily deliberate, and “even though we often do not realize that we are structuring our

workplace to help us keep track of processes and a host of other useful functions [...] we should not assume that such cognitive or informational structuring is not taking place all the time” (Kirsch 1995, p.33).

Why wouldn't animals employ similar strategies if given the leeway to do so? Like humans in memory experiments, the scrub jays in the episodic memory experiments are confined to a particular (and impoverished) space, so their opportunities for action are limited, just as the laboratory limits human remembering. In many cases, such impoverishment can reveal animals' resourcefulness, or indicate that particular information is not essential for the task in hand. For example, since jays will return to the correct caching sites, despite the removal of mealworms and peanuts, we know that their cache-recovering abilities are not dependent on the smell of the cached food. However, this finding does not imply that, under normal circumstances, the birds do not use the smell of cached food as a cue, nor does it rule out the possibility that they are using other environmental scents to register the state of cached food (as detailed above).

Whatever way we slice it, the fact remains that animals' action opportunities are restricted in an experimental context, and we have no means of discovering whether remembering involves action-based strategies for creating a more cognitively conducive environment. In the wild, jays are able to cache in particular places, that maintain particular relations to each other, perhaps at particular times, and which are close to landmarks or other meaningful places, and so on. Such behaviour is often seen as a means of “off-loading” the cognitive burden onto the environment—that is, as scaffolding for internal memory. However, a different view is that such behaviours are the parts of memory that get masked in the experimental context by designating them as “confounds” that obscure the operation of “pure” memory.

Navigation studies in rats offer a similar example. Rats leave odour trails as a way to recall places they have visited before. Relying on scent is often opposed to the use of memory, and researchers that are interested in the “minds” of animals will see the use of odour trails as akin to “cheating”. Leaning on the environment in this way obviates the need for brain-based representational processes to solve the problem, and indicates that the animal is somehow solving a given task in “non-cognitive” fashion (e.g. Means, Alexander & O'Neal 1992). In other words, occurrent perceptual cues of any kind are viewed as potentially *interfering* with the research goal—that is, they obscure our ability to get at how animals *really* think (see also Healy and Rowe 2014, and comment by Barrett 2014).

From a cognitive structuring perspective, on the other hand, scent trails are a means of rendering a wholly unnatural environment—one that appears similar in every direction—easier to navigate in the future. As humans, we are inclined to see space as an empty container, so that leaving behind an olfactory cue represents an *addition* to that environment. But the world of rats (their *Umwelt*, see Von Uexküll 1934) is always, already a scent-world, and rats, by leaving scent cues for themselves, are simply remembering in the way that rats remember. That is, leaving scents is the way in which they come to know, to cognize, their environments. Researchers see these scent-based strategies as non-cognitive, we think, because they're unaware of the perceptual strategies that humans also use (often unknowingly) to recall locations at later times. Our use of trails is more often visual (a well-trodden path, a sequence of post-it notes and book-marks pasted into a book) but trails they are, and they are integral to our ability to remember and allow the past to influence the present.

Memory in full regalia

While necessarily brief due to space limitations, these comments on cognitive structuring, and exploiting the wealth of information (e.g. exploiting higher-order patterns) in the environment reinforce some points about Ebbinghaus's participants and the episodic memory studies on jays: you cannot take movement or context out of memory (at least you cannot do so without generating a distinct form of "scientific" memory found only in the laboratory). Situated, sensory-motor strategies have been set apart as somehow "not memory" to justify the search for "species-neutral" cognitive mechanisms, on the model of what literate humans can achieve under highly specific conditions. The sense of similarity that we have fabricated by cloaking the differences, thus starts with the faulty image we have of ourselves: by choosing to focus on only a narrow aspect of what humans are capable of doing within an overtly scientific context, and *a priori* excluding several active, perceptual strategies that, even if we try to get rid of them, we can't but help employ.¹² In all cases, we *do something* to remember something later. In this sense, there is no "passive" sensory input that is stored and later recalled. All remembering is *active* and memory is therefore an activity—it's just that sometimes we don't know the things that we do.

Finally, although I couched discussion here in terms of "memory" as a distinct faculty, my approach is much more task- or action-oriented—remembering where we left our

12. If you still wonder whether the perceptual and motor aspects I think of as being part and parcel of memory are genuinely memory, let me emphasize that my goal is not to start a semantic discussion over what counts as "memory", but to draw attention to these perceptual skills that are at least strongly related to memory and that comparative psychologists haven't given much attention, though they will allow for a less anthropocentric comparative psychology by limiting anthropofabrication.

keys is a different task from remembering how to make an omelette, or remembering the lyrics to a favourite song. The same goes for the activity of animal memory. This means that each task will require several classificatory types to describe, and it is impossible to “isolate” any of these capacities, to show that animals *really* possess it.

Conclusion

Our scientific interest in what occurs “*in the mind*” of humans and animals has yielded a long-standing neglect of what occurs “*outside the mind*”—or rather, with the idea that mind could be more broadly conceived, and regarded as something that animals do (they engage in “minding”) rather than something they possess. I recognize the complexity entailed by working with nonhuman animals, however, and by no means wish to deny it. Rather, I wish to encourage researchers to acknowledge this complexity, rather than selectively ignore it; to embrace variability, rather than trying to iron it out.

The way that most experiments are currently set up is not helpful. These setups usually attempt to distinguish “cognitive” from “association-based” explanations. Experimental rigidity and standardized controls are usually undertaken to reduce “irrelevant” variability and the influence of so-called confounding variables, or at least diminish them. In doing so, we are trying to wrangle resistant animals into ill-fitting clothes. Avoiding anthropofabrication, however, does not mean simply making alterations in the clothes themselves so they fit better—taking them in here, adding extra material there. We simply cannot assume that all variability is eradicated once we put controls in place; variability will still be present, and ignoring it doesn’t solve the problem. A larger organism-environment system is always, already in place.

Rather than excluding certain parts of the environment *a priori* because they are generators of “noise”, we argue that researchers should attempt to *discover cognitively-relevant environments* through their experiments by systematically varying the availability of affordances. These environments, and the distinctive manner in which animals can act on and enact strategies within them, must play an integral role in the generation and testing of novel hypotheses. For instance, researchers could actually create higher-order patterns between certain smells and the decay rate of worms, and later remove this olfactory pattern. By measuring response latency, for instance, they could then uncover whether animals are sensitive to these higher-order patterns. In addition, constructing ethograms could enable researchers to find patterns in the alternative strategies employed by jays when certain higher-order patterns suddenly

become unavailable to them. To stick to the same set of metaphors: we should let the animals show us what clothes they like to wear. This approach will also allow genuine similarities to manifest in how animals exploit environmental features to solve tasks. The idea of “trails” (see sect. 4) is one example. Whether by vision or scent, laying down a trail is a way to make homogenous environments more unique and recognizable. Whether these trails are “natural kinds”—whether they “really” exist—is not important. What is important is that our terms allow us to ask *new questions*, to see things that we could not or did not see before. Rather than masking species-specific strategies, they offer a level playing field for comparison, one that doesn’t privilege humans.

The difference in mind between man and all (not just the “higher”) other animals, ultimately, is both a difference in degree and a difference in kind. All remembering is about improving engagement with available affordances. However, each animal relies on different affordances, given the differences in their bodies, senses and niches, making every instance of remembering species-specific. Even the entangled skill of storing and recalling “information”, unique to humans, remains a fully embodied, situated way to improve how we encounter the world



4

Ecologies of memory

Abstract

In this chapter, I will delve further into the enduring debate surrounding episodic memory (EM) in comparative cognition. A persisting question in this field is which, if any, nonhuman animals share our capacity for episodic memory. Many authors address this question by primarily defining EM, trying to capture its seemingly unconstrained flexibility and independence from environmental and bodily constraints. EM is often opposed to clearly context-bound capacities like tracking environmental regularities and forming associations. The problem, though, is that conceptualizing EM in humans first, and then reconstructing how humans evolved this capacity, provides little constraints for understanding the evolution of memory abilities in other species. “Genuine” EM is defined independently from animals’ evolved sensorimotor setup and learning abilities. In this chapter, I define memory in terms of perceptual learning: remembering means “knowing (better) what to do in later situations because of past experience in similar earlier situations”. After that, I explain how episodic memory can likewise be explained in terms of perceptual learning. To achieve this, we should consider that the information in animals’ ecological niches is much richer than has hitherto been presumed. Accordingly, instead of asking “given that environmental stimuli provide insufficient information about the cache, what kind of representation does the jay need?” we should ask “given that the animal performs in this way, what kind of information is available in the environment?”

Introduction

At first glance—and probably a couple more—cuttlefish, dogs, bees, chimpanzees, mice and rats, pigeons, scrub jays, crows and a lot more species seem to have little in common. Concerning their mental lives, however, at least one striking similarity is purported: a capacity for episodic (or episodic-like) memory (see Dere et al. 2008; Van Horik, Clayton & Emery 2012; Martin-Ordas & Call 2013; and Templer & Hampton 2013; Clayton, Salwiczek & Dickinson 2007 for overviews). The evolutionary function of episodic memory (EM), plausibly, is remembering past situations to anticipate future situations (Suddendorf & Corballis 2007). While anticipation is probably useful for any animal, debate ensues about whether animals' anticipatory behaviour genuinely relies on episodic memory as opposed to some simpler capacity. Despite diverging claims, then, is episodic memory widespread across the animal kingdom? Do only humans and a handful of other animals have it? Or is it uniquely human?

Most authors have tried to answer this question by primarily defining what episodic memory is in humans and what representational capacities are required for it (Clayton & Dickinson 1998; Dally, Clayton & Emery 2006; Suddendorf & Corballis 2007). Subsequently, they aim to determine whether these representational capacities are present in nonhuman animals. Though major disagreement exists, most authors try to capture the intuitive fact that episodic memories seem *decoupled* from the environment and can be conjured up at will. EM is therefore often opposed to tracking environmental regularities—a capacity that seems clearly context-dependent and stimulus-bound. This approach—defining EM in humans first, consequently reconstructing how humans evolved this capacity, and to what extent animals did (if at all)—is an anthropogenic method (Keijzer 2017; Keijzer & Lyon 2007; Lyon 2006). Anthropogenic methods are non-ideal for a rich understanding of the evolution of memory abilities, because they define memory independently from animals' evolved biological (i.e. sensorimotor) constitution and their ecological niches. These methods therefore lack the tools to arrive at a fuller picture of what species share concerning (episodic-like) memory and what is species-specific (see Osvath, Kabadayi & Jacobs 2014; Barton 2012; Keijzer 2017). It is no coincidence, then, that most comparisons have been narrowly concerned with answering the question of whether any nonhuman animal has EM either positively or negatively.

The opposite of an anthropogenic approach is a biogenic one. As mentioned earlier, a biogenic approach assumes that “the properties and principles of biological organization present the most productive route to a general understanding of the properties and principles of [...] cognition” and “Cognition” is defined as “the

processes by which humans and presumably other biological systems come to know the world” (Keijzer & Lyon 2007, p.141). I contend that a consistently evolutionary explanation of EM requires a biogenic method. Accordingly, I define memory in terms of perceptual learning. This entails that remembering means “knowing (better) what to do in later situations because of past experience in similar earlier situations”. After that, I explain how EM—which can be loosely defined as memory of situations *seemingly* independent from the present context, and that improves one’s dealings with future situations—must likewise be understood in terms of perceptual learning.

Sceptics might object that a perceptual learning account is not an account of EM (which must by definition be decoupled). My point is precisely that such an “unconstrained” view of EM is hard to defend within an evolutionary framework. That is, accounts of EM have been conceived of independently from animals’ biological, sensorimotor organization and ecological niches. I will argue that while episodic memory may *seem* unconstrained to us, this does not imply that it actually *is*. To make sense of this view, we need to consider that structure and regularity in the environment are indispensable aspects of what makes episodic remembering possible. While regularity already plays a role in the episodic memory debate, it has been part of the “simpler” explanations. This is because EM seems inexplicable without positing persistent mental representations that mediate between past, present and future. Once representations come into play, the debate shifts towards the nature of these representations: whether they are akin to those of a human in complexity, or different and simpler. The challenge for a biogenic approach, then, is to identify non-trivial environmental regularities that could render mental representations superfluous.

The biogenic method to be defended here will be developed in terms of affordances and ecological information (Gibson 1979/2015, see chapter 2). Affordances are opportunities for action provided by the environment, given the animal’s perceptual systems. Ecological information refers to patterns of energetic stimulation—for instance, in light waves and air pressure—which allow animals to engage with affordances.¹ Remembering something, accordingly, means that one has become successful in engaging with specific affordances because prior situations have attuned one’s perceptual systems to the relevant ecological information making this engagement possible.

1. Since ecological information is only available over time, I will use the term “(ecological) patterns” as well as “regularities” or “regular patterns” as a synonym for “ecological information” to emphasize this temporal dimension (in this and subsequent chapters).

This chapter is structured as follows. First, I will briefly describe the evolutionary debate about episodic memory—whether any nonhuman animal has acquired an episodic-like capacity for mental time travel similar to humans (sect. 2). In section 3, I will develop my biogenic, ecological approach to memory. In section 4, I will argue that remembering distal places and things is possible while staying true to this biogenic, ecological outlook. To manage this, I will explain how regularity and structure in the environment allows animals to engage with “distal affordances”. Regularity and structure in the environment, effectively, take over the work that cognitivists attribute to representations. I will conclude with a discussion of evolutionary convergence (sect. 5). My goal is not to comprehensively address all the intricacies encompassed by the term “episodic memory”. Instead, I offer a conceptual analysis in order to contribute to a more detailed understanding of the similarities and differences between EM in various animals.

Did episodic memory evolve only in humans?

Did the capacity to anticipate future events by considering past events evolve in any nonhuman animal, or is this capacity uniquely human? The question has generated a lot of debate. In this section, I will paint a general picture of the dialectic at work in the evolutionary debate (for more elaborate discussions, see Dere et al. 2008; Van Horik; Clayton & Emery 2012; Templer & Hampton 2013; Martin-Ordas & Call 2013).

Remember from the previous chapter that the term “episodic-like” memory—prevalent in comparative psychology—denotes uncertainty about whether nonhuman animals have the distinctive phenomenology of reliving personal past episodes that is characteristic of human EM (Clayton & Dickinson 1998; also called “autonoetic consciousness”, see Tulving 1972; 2002). As several authors have suggested, autonoetic consciousness should not be a central part of episodic memory’s definition. Including autonoetic consciousness may be anthropocentric and problematizes the empirical study of EM in nonhuman species (Barrett, Drew & Rendall 2007; Van Horik, Emery & Clayton 2012; Buckner 2013). Functional and behavioural aspects of EM have, therefore, guided most of the research.

An early functional definition of EM was applied to the caching behaviour of scrub jays. Scrub jays can cache and recover hundreds of items of food, which they make use of in times of food scarcity (Dally et al. 2006). These foods are often widely distributed and fluctuate in availability. The scrub jay’s caching behaviour is a solution to this problem. Comparative psychologists have investigated whether scrub

jays may have evolved an ability to flexibly remember the locations of their caches (Clayton, Yu & Dickson 2003; Van Horik, Clayton & Emery 2012).² The authors of these studies defined EM originally in terms of memory for what, where and when: the difference between foods, the different places or locations where they cached the foods, and the different times they buried the foods, respectively (Clayton & Dickson 1998, see fig. 7).

Several studies seem to support the presence of episodic-like memory—understood as *www-memory*—in scrub jays. In well-known studies, this capacity in jays has been examined by making reliance on direct perceptual cues (such as visual or olfactory ones) and association (based on prior learning) impossible. These experiments show that after a couple of hours have passed, scrub jays will first recover worms—their preferred food—but opt to collect peanuts right away after a couple of days, when the worms will have gone bad (Clayton & Dickinson 1998). The researchers altered time intervals between caching and recovery, so that the jays could not learn to rely on a temporal regularity. Other studies ruled out tracking of larger-scale environmental cycles. Scrub jays would still recover only the edible foods at several intervals while reliance on astrophysical or geophysical cycles was impossible (Clayton et al. 2001, see also previous chapter).

Internal cues in the form of “memory traces”—neural changes representing associations between stimuli—(see Roberts 2002) have also been examined, and discredited. The idea of memory traces is that jays would first recover worms if the memory trace is strong and opt for peanuts if the trace is weak. However, the jays selectively recovered peanuts and worms they cached earlier respectively from two different trays, both of which contained peanuts and worms, but cached at different times (Clayton et al. 2001). Later studies even showed that jays are also capable of taking future motivational states into account by caching more food in the places where they are likely to be hungry (Raby et al. 2007).³

Despite the authors’ elaborate efforts to prove the contrary, a common response is that simpler explanations are still available to explain the jays’ feats. These explanations frequently rely on the identification of internal or external patterns that the researchers may have overlooked. They also, often, call for additional criteria for genuine episodic memory, thus challenging both the interpretation of the experiments and the definition of episodic memory used.

2. Something that may also have been true for other species, such as certain cetaceans (Marino 2002).

3. A related, interesting case is the chimpanzee Panzee, who could indicate the place where food was hidden outside her enclosure (Menzel 2005; see also Bobrowicz, Johansson & Osvath 2020).

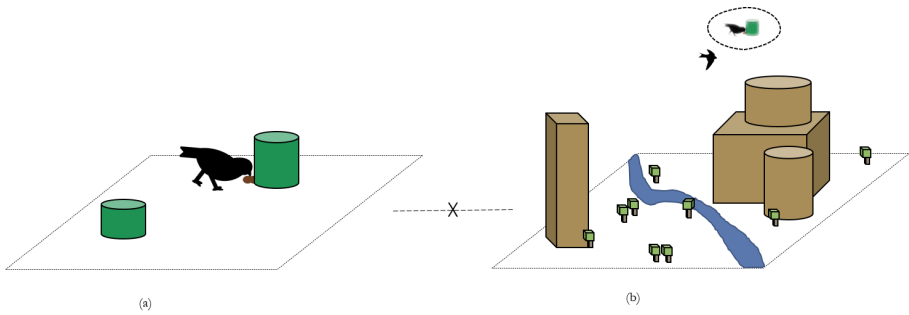


Figure 7. The representational view of episodic memory. (a) A scrub jay hides a peanut at a certain time. (b) Later, the jay remembers at least the details of where, when, and what she cached, without being able to perceive the peanut or depend on learnt associations. While episodic memory typically involves a re-experiencing of the initial event in great detail, in episodic-like memory, this experiential aspect is bracketed.

Suddendorf and Corballis (1997; 2007) are well-known opponents of the view that nonhuman animals have EM. They argue that there are various types of memory with differing levels of flexibility, with episodic memory being the most flexible because it is not limited by current circumstances. They also contend that episodic memory (EM) is a component of a broader cognitive system known as mental time travel (MTT), which serves the adaptive purpose of anticipating future events (see also Dudai & Carruthers 2005; Suddendorf & Busby 2005). While anticipation seems like an adaptive capacity for any species, Suddendorf & Corballis (2007) think that relatively inflexible ones often suffice. What-where-when memory, for instance, is not as flexible as MTT: the past could influence the animal's present state and hence a later state, without an intervening episodic memory that is *about* the past. As the authors themselves put it, very often "flexibility extends only to learning to respond to current indicators of upcoming events; behavior is stimulus-bound, or better, bound to perceptual tracking of stimuli" (p.3). But their most important claim, perhaps, is that, EM and MTT are not about tracking *regularities* but about constructing *particularities*. Particularity relates to singular episodes of experience, whereas regularities relate to recurring events. Episodic memories, they write, are "decoupled representations" no longer tied to perceptual systems. Such a level of flexibility requires a range of complex capacities, such as metacognition, mental rehearsal, inhibition, recursion and declarative knowledge that no species has of yet convincingly demonstrated. Hence, MTT sets humans apart from nonhuman animals (Suddendorf & Corballis 2007).

A recent, similar defence of the uniqueness of human episodic memory comes from Hoerl and McCormack (2018; 2019). They argue that nonhuman animals could act based on a model of the present that is currently updated in a way sensitive to the passing of time (by systemic use of an “interval timer”), but that is not itself about the past. Being capable of making past events *objects of thought*, or put differently, having the ability to *locate particular events in objective time*, signifies the detachment from the present required for remembering past experiences, according to them. This feat requires “temporal *reasoning* abilities” (Hoerl & McCormack 2019). Humans can objectively recall specific past events without apparent restrictions, while animal behaviour, for now, can be explained by their use of models of environmental patterns and the constant updating of these models. Thus, Hoerl and McCormack draw a similar conclusion to Suddendorf and Corballis (2007): EM or MTT sets humans apart from other animals. Humans are temporal beings free to navigate through time, while other animals are stuck in the present.

Despite reaching different conclusions, both proponents and opponents of EM in animals employ a similar anthropogenic approach (Keijzer & Lyon 2007; Keijzer 2020). That is, first they conceptualize a specific type of capacity in humans, by offering necessary and/or sufficient representational criteria and behavioural indications for this capacity. Secondly, they evaluate to what extent (if at all) nonhuman animals share this capacity with us. Shettleworth (2007) expresses the problems with anthropogenic approaches strikingly. The question “What is mental time travel, and is it unique to humans?”, she writes, “leads to a quest for an existence proof (just one animal with ‘it’ is enough), followed by endless disputes over whether ‘it’ really was demonstrated” (p.332).

Anthropogenic accounts of EM in humans are formulated independently from biological constraints (evolved sensorimotor setup) and ecological constraints (contextual conditions enabling cognitive performances) (see Osvath, Kabadayi & Jacobs 2014; Barton 2012; Keijzer 2017; see also Withagen & Van Wermeskerken 2018). As mentioned, the fact that a capacity *appears* unbounded does not imply that *is*—why and when we have (and don’t have) certain episodic memories is at bottom an empirical question that has not been addressed so far. What’s more, any theory consistent with evolutionary theory should acknowledge constraints on cognition given the body and niche of the animal just as we acknowledge constraints on simple behaviour given the body and niche of the animal.

Remembering as knowing better what to do

Biogenic approaches offer an alternative to anthropogenic ones, providing the foundational tools for constructing a theory of episodic memory that aligns with biological and evolutionary perspectives. Biogenic approaches consider cognition as an extension of more “basic” sensorimotor behaviour. That is, basic material structures, such as the bodily and sensory components of perceptual systems, become more and more elaborate over time (Keijzer & Lyon 2007). To elucidate “cognitive abilities” from an evolutionary perspective, then, we should focus on the progressive refinement and elaboration of these systems. To do this for *memory*—to keep the capacity to remember firmly grounded in the biological constitution of the animal—we should begin with a basic biological understanding of memory, and then expand it to explain the memory abilities of animals with more advanced perceptual systems and neural organizations (see Barrett 2015a). My approach to smoothly make this transition from “basic” to more “advanced” memory abilities relies on principles of ecological psychology (Gibson 1979/2015).

Ecological psychologists steer clear of postulating mental representations in their definition of memory. Instead, they conceptualize memory as a form of perceptual learning. Memory means knowing better what to do in later situations due to past experience in similar earlier situations given similar goals (Gibson 1979/2015, p.242; Barrett 2011, p.214; Michaels & Palatinus 2014; see previous chapter). Remember Michaels & Palatinus’ (2014) helpful analogy between memory and adaptation: “[T]he consequence of personal experience is not that the old animal has new knowledge, but that it is a new animal that knows better” (p.25). Put differently, earlier experiences do not “accumulate” somewhere and somehow so that they can be conjured up later, but “calibrate” animals’ perceptual systems directly, improving their ability to deal adaptively with future situations (see Michaels & Palatinus 2014, p.25, see also Moyal-Sharrock 2009; 2013).

This description of memory in terms of perceptual learning can be refined by rephrasing it in terms of affordances and ecological information. Recall that affordances are opportunities for action in the environment, while ecological information refers to regularities or patterns in the environment that “allow an animal to engage with affordances” (Bruineberg, Chemero & Rietveld 2019, p.5232). Now, what do affordances and ecological information have to do with remembering? Recall that affordances, as part of their definition, refer both to animals’ *past* abilities and learning trajectories as well as to their *future* possibilities (Van Dijk & Withagen 2016; Van Dijk & Rietveld 2018; see chapter 2). Hence, if an animal perceives a

particular affordance, similar situations in the past have attuned that animal's perceptual systems to regularities in the environment that indicate that affordance.

A simple example: a jay knows how to efficiently bury a peanut because she has done so before (see Salwiczek et al. 2009). The activity of caching makes the jay's perceptual systems increasingly sensitive to the patterns that specify how to do this. Among the informational variables involved in effective caching are optical flow patterns generated by moving the head towards the surface and optical patterns generated by surface transformation as the peanut is inserted. Generating this pattern is being able to successfully bury a peanut. Hence, we have a minimal form of memory, often called procedural memory (Suddendorf & Corballis 2007, p.3): we can say that the jay *remembers* how to bury the peanut in that later situation if her perceptual systems are attuned to the relevant optical (and haptic) patterns.

Now consider a slightly more complex example: contemplating a hike in the woods. For this case, it helps to understand ecological information in terms of ecological *constraints*: if ecological constraints hold between two situations or events in a niche, instances of the former situation or event are informative about instances of the latter (see Chemero 2009). A forest affords hiking (or not) in virtue of the constraints holding between rainfall and the forest paths' condition. For instance, heavy rain will make forest paths more swampy—this is a higher-order pattern in the environment. As excessively waterlogged forest trails don't afford hiking for humans, heavy rain is indicative about the trail's hike-ability. Noticing the rain thus allows you to *perceive* that the forest paths are not hike-able.⁴

Remember, though, that animals, including humans, primarily perceive *affordances*. So, when you look out the window, what you see from a non-scientist, “animal” perspective, is how the streets become less “walkable” as the rain continues. In the ambient perceptual array, there's *ecological information* in optical patterns, olfactory patterns and auditory patterns. But in terms of *affordances*, there's a transition from a walkable to a non-walkable street (and probably some more affordances “in between”).⁵ What you learn, primarily, is how one affordance in your immediate surroundings (the walkability of the streets just outside your house) is related to another affordance outside your field of view (i.e., the hikeability of the forest trails). You don't have to *infer in your head* whether the woodland is hikeable. Instead, you

4. Recall that the word “perception” for ecological psychologists is different than for representationalists. Because for ecological psychologists perception is of affordances, and affordances can be distal, one can *perceive* what is distal (see the discussion of object permanence in chapter 2).

5. I'm concerned here with how affordances are *perceived*, not with their “ontological” status.

exploit a stable relationship in the *environment*. What's more, because affordances are *opportunities* for action, they imply an anticipatory capacity. I perceive that the forest is not hike-able, but I am simultaneously engaging with a future possibility: whether to go for a hike or not. This indication is less reliable than when I would be standing in the forest—as there could be other processes that keep the forest path hike-able—but it does to a certain extent.⁶ Accordingly, I know better what to do in this situation now based on similar situations in the past, which allows me to make an adaptive decision and stay inside.

This ability to remember will further improve with experience, as you will learn to detect more fine-grained relations between these events—that is, how the duration of rainfall relates to the condition of the trails. Jacobs and Michaels (2007) make a helpful analogy with measuring instruments: if you want to measure a certain environmental property (say air pressure) a barometer will initially be influenced by temperature and humidity, and must consequently be “calibrated” to more reliably track air pressure. Similarly, animals' perceptual systems “tune in” on more subtle regularities or patterns in the environment.

Before continuing, a few critical remarks are in place. First, for an ecological psychologist, memory, perception and anticipation shade off into each other. Perceiving is both a kind of remembering and a kind of anticipating—or conversely, both remembering and anticipating are kinds of perceiving (Gibson 1979/2015, p.242). Secondly, on an ecological approach “tracking regularities” in the environment and “remembering” are not understood as different, competing explanations, but as different levels of explanation: we use the term “remembering” to explain how an animal's engagement with affordances improves through previous experiences in comparable situations. We speak of “tracking or attuning to environmental regularities” to describe how animal's perceptual systems are changed by experience (see Heft 2010, p.170). In short, tracking regularities is an *explanation* for how animals remember.

6. Recall that when ecological information fully specifies or completely reliably indicates an affordances based on ecological laws (e.g. of ecological optics), some authors speak of “lawful ecological information” or just “ecological information” (Gibson 1979; Stepp & Turvey 2015). When we detect information that reliably indicates, but does not fully specify affordances, the term “general ecological information” is sometimes used (Bruineberg, Chemero & Rietveld 2019). However, in this context, the difference is not crucial, so I will use “ecological information” or simply “information” and speak of more or less reliable information for affordances (see also chapter 2).

This ecological definition of memory already entails a rather different perspective on the evolution of memory abilities. To illustrate, Pahl et al. (2007) found that bees can remember what, where and when, but that this ability is circadian-timed, meaning that there is a direct cue available. For a representationalist, the question of whether we should call this episodic-like memory—or memory at all—is a real issue. Is the bee really remembering or just acting based on processes in the environment? For an ecological approach, on the contrary, memory is always based on coupling with regularities. There is no question of whether the bee is “genuinely” remembering. Circadian rhythm plays a role in what the environment affords for bees, and hence is simply one of the regularities that allows bees to remember.

Now, how does remembering as I have characterized it so far “scale up” to episodic-like memory abilities—abilities that are seemingly “decoupled” from such regularities? The hiking example is concerned with a situation beyond the field of view, but the rainfall could be seen as a perceptual cue, and associative processes could explain my decision to stay inside. Accordingly, does episodic memory not require representations after all, setting it apart as a unique form of memory distinct from those based on recognizing environmental regularities? Unsurprisingly, I will suggest “no” for an answer. The framework for memory I have presented so far can account for episodic memory. We only need to acknowledge that the information in the environment is much richer than we commonly assume

Remembering and anticipating distal situations

How can we explain episodic-like memory abilities by considering the wealth of information in the environment? Like procedural memory, episodic memory (i.e., remembering situations seemingly independent from the present context, and that improve one’s dealings with future situations) can be construed in terms of *perceptual learning*. The difference between remembering the hike-ability of a trail and cases of episodic remembering, I will argue, doesn’t hinge on the availability of environmental cues—as if environmental cues would be present in the former case and not in the latter. Both situations involve the environment. Crucially, however, episodic or episodic-like remembering, I suggest, involve sensitivity to temporal regularities—that is, to relations among affordances and when they are available for an organism—that are not readily apparent to researchers. In this section I will elaborate on this idea, again based on the scrub jay case.

The ecological niches of animals consist of events taking place on multiple spatial and temporal scales. Gibson (1979/2015) wrote that such events are “nested” within one another (see chapter 2). (p.5). Metaphorically, we could speak of a “clockwork” in the environment, with events taking place on larger and smaller scales, bearing specific relations to each other. Some events take place over long periods of time, extending over years or months. Some take days. Some take mere hours, minutes, seconds, or microseconds. Shorter events are nested within longer ones, and multiple shorter events can occur during a single longer one. These events can be environmental (e.g. solar cycles) as well as bodily events (e.g. fluctuations in body temperature). For scrub jays, the decaying of food items like wax worms, taking about 124 hours, is also a vital event (cf. fig. 6 in the previous chapter).

Because of this nesting, particular constraints hold between multiple events in scrub jay life. Identifying these events is an empirical task. The philosophical point is that due to nesting, events within the direct field of view, due to what they afford, allow animals to engage with distal affordances. Similar to constraints between rainfall and forest trail conditions, certain constraints hold between certain events in scrub jay life and the decay rate of wax worms. Accordingly, observing what those immediate events afford (whatever those may be) is indicative about the recoverability of the worms—even if a jay is spatially and temporally removed from the wax worm. In other words, these constraints indicate a *temporal invariant*: the worm’s decay rate. Unlike the relation between rainfall and forest trails, events don’t need to be *causally* related to indicate something about each other. In other words, one event doesn’t need to *change* another event. It only needs to bear a relatively stable temporal relation to it. For reliable indication, multiple events in time and space can and likely do allow animals to engage with distal affordances.

Note, again, that while human scientists can specify the relations between the decaying wax worm event and other events, the jay is not perceiving these relations when she is trying to recover a worm. The jay is perceiving or engaging with affordances. This parallels the hiking scenario, where the walkability of the streets outside allows me to directly perceive, too, whether the forest trails are suitable for hiking. Similarly, certain affordances for the jay in their immediate surroundings are coupled to the “edibility” of wax worms. Such stable relations among affordances allow the jay to remember when she buried the worm. Put differently, the jay doesn’t need to “track and match” the duration of these events *first*, so that she can *then* remember that the worm is still edible. Rather, remembering that the worm is still edible (or not) is being appropriately attuned to the relevant relations among affordances, due to a relevant history of interactions.

Now, how does this work? How does a jay become attuned to the relevant affordances through a history of interactions? The answer involves both evolution and development. Given the irregular distribution of food items in scrub jays' niches and the importance of relying on caches in times of food scarcity, over evolutionary time scrub jays' perceptual systems could have become disposed to learn to detect ecological patterns that are relevant in relation to caching and recovery of various essential food items. This predisposition ensures that non-edible foods are avoided most of the time and no useful energy is wasted. Put differently, given the goal of recovering, the jays perceptual systems tune in on the information that makes those affordances inviting for the jay that are actually recoverable (see Rietveld & Kiverstein 2014; Rietveld, Denys & Van Westen 2018).

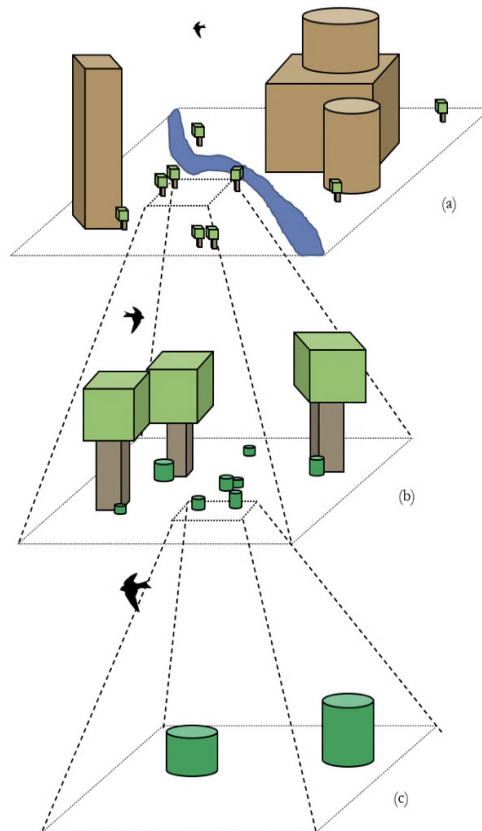


Figure 8. Nested structure of the natural environment in caching and recovery. (a), (b) and (c) describe different ecological scales of the environment, which teem with ecological information. Due to stable spatial and temporal relationships in the environment among these nested places, the jay can learn how to retrieve the peanut while it is still edible.

Developmentally speaking, jays become attuned to higher-order ecological patterns that indicate the affordances of caches in increasingly reliable ways. When behaviour turns out to be adaptive—that is, when it leads to successful recovery—animals will become attuned to the ecological patterns that have enabled this feat. So, if a jay recovers a worm while it has gone bad, the perceptual systems are not sufficiently attuned to the patterns that are related to, or constrain, the perishing rate of worms. What a jay learns, accordingly, is not *that* a worm perishes in 124 hours, but *how* the worm-perishing event is related to other events that allows the jay to recover the worm when it is still palatable. We should understand what happens in between the moment of caching and recovery, then, not as the retention of the caching episode, but the detection of information—of (higher-order) patterns—by the jay’s perceptual systems that in earlier situations have proved to be reliable indicators for the most relevant affordances, given the need for the most valuable food.⁷

Would we call the capacity we discussed “episodic-like memory”? Certainly, the capacity here described is not “decoupled” from the environment, nor is it “no longer tied to perceptual systems” (Suddendorf & Corballis 2007). However, it should be clear by now that an ecological account dismisses the possibility of such decoupling, because it ignores biological and ecological constraints. Our memories may *seem* decoupled, but this does not imply that they *are*. It is just that the information on which they rely is perhaps less evident and direct and has thus far received little to no attention. Detecting information in the environment about a past caching episode in order to make an adaptive decision (even if that information is non-trivially related to the affordance) is undeniably reminiscent of what we commonly gather under “episodic-like memory”. The point here is that detecting information in the environment should not be seen as evidence against episodic-like memory, but rather as a methodological principle: we should aim to discover such regularities, for instance through systematic variation (see Reed 1982, see previous chapter) in order to understand *how* and *why* and *when* animals are able to remember (and fail to remember) situations from the past and how this leads them to make adaptive (or non-adaptive) decisions with respect to the future: it is because ecological information is either available or unavailable to the animals’ perceptual systems. In this way, an ecological approach could help to account for memory abilities, including EM-like abilities, without starting from the human case that ignores species-specific

7. In the wild, this information is obviously much richer than in experimental contexts, but if the present account is right, we should find such events also in experimental contexts.

biological and ecological constraints.⁸ Consequently, we no longer need to discuss whether something counts as “genuine” episodic memory.

Two final points that are crucial to evolutionary theory—points that anthropogenic, representationalist approaches have trouble accommodating—follow naturally from the ecological approach to memory: individual variation and suboptimality. A first point is about the distinction between the ecological information available in principle and the information an individual animal picks up at any particular moment. Most of the time, it is not possible to detect *all* information that a situation can potentially provide. Often, the optimal information is unavailable because environmental conditions are not optimal, or simply because animals are no optimality machines (Withagen & Chemero 2009). Even though much information may be available, an animal may only be able to detect a portion of this. But neither lead to problems for an ecological approach. As Gibson stressed, “Those features of a thing are noticed which distinguish it from other things that it is not—but not all the features that distinguish from everything that is it not (Gibson 1966b, p.286)” The same applies to memory: what is required is *sufficient* ecological information, information that is reliable enough. However, it is obviously possible that animals *fail* to pick up sufficient information and misremember when they, for instance, cached something. As mentioned, a jay might recover a worm that has gone bad hours before.

A related point concerning the difference between optimal and detected information, is that the possibility that all jays detect the same information in similar situations is small—for two reasons: because of variability in individuals’ perceptual systems, in accord with evolutionary theorizing, and because of different developmental trajectories (Withagen & Chemero 2009). No two animals detect *exactly* the same information. The crux is that, because an ecological account “untangles” memory in terms of action and perception, and perceptual systems differ between individuals, the ecological view can naturally account for the fact that the ability to remember will differ between individuals based on their sensitivity to information.

My aim in this part has not been to provide a complete account of the (EM-like) memory abilities of jays or other animals in terms of ecological information and

8. Eventually the goal is to account for EM-like abilities in humans all the same. This explanation should capture, just as in any other species, what is species-specific and what is shared with other species. This requires considering the regularities in the human niche—regularities that we have substantially constructed ourselves: we have developed a temporal system using calendars, clocks, holidays and many more things—and we have the language to talk about these things. These are essential in understanding our own memory abilities “from the outside” as it were, rather than based on the intuition that they are “unconstrained” by environmental and bodily factors.

affordances. Doing so still requires a lot of empirical and theoretical work, and I am aware that many details have not been offered here simply because we do not know what they are. Nor, in focusing on patterns in the environment, do I want to deny that jays *also* rely on other mechanisms, such as spatial memory and landmark use, which can further constrain what affordances become relevant. Compare it with having an episodic memory of where you left your keys, where once you arrive at that place other spatial cues might be available to indicate the affordance more reliably. Instead, what I tried to do is make steps toward a biogenic method concerning episodic-like memory—especially its temporal component, which is arguably the most contested.

So, instead of asking, “given that environmental stimuli provide insufficient information about the cache, what kind of representation does the jay need?” we should ask “given that the animal performs in this way, what kind of information is available in the environment?” This difference is important: it puts the focus on directly observable aspects of the environment, rather than on internal entities that can only indirectly be inferred from behaviour. An ecological approach provides a means to study memory abilities ranging from simple to complex, while ensuring they remain closely tied to the physical bodies and perceptual systems of animals, which reflect the environmental niches in which species have evolved. Hence, this approach aligns much more closely with biological and evolutionary principles than the “unconstrained” view of EM.⁹

Evolutionary convergence on remembering

When authors believe that species have converged on EM-like abilities, what is it that they recognize as being similar? In the beginning of this chapter, I suggested that it is the intuition that these behaviours *seem* to rely on information that cannot be drawn from perceptual cues within the sensory scope. Experiments are devised and conducted to show that various animals either can or cannot remember in this seemingly unconstrained way that humans seem to do. Accordingly, the point of these comparisons is either to look for similarities between humans and other animals or to show that there is no such similarity, and therefore other animals’ capacities are “lesser” than ours. The question of convergence becomes an all-or-nothing verdict; a one-dimensional hierarchy with a threshold somewhere. This is

9. Note that in no way have I denied that animals have specific phenomenological experiences accompanying their remembering abilities; instead, an explanation in terms of regularities in relation between events is, on an ecological account, perfectly compatible with such experiences. The point here has been to account for the behavioural aspects of such abilities from an evolutionary standpoint.

only possible if cognition and behaviour are viewed independently, if EM is thought to operate independently from biological sensorimotor constraints. Not only is this dichotomy too simplistic, it lacks an explanation of how an “unconstrained” capacity evolves from a simpler “tracking” capacity (see Osvath & Kabadayi 2018). In contrast, if we untangle memory in terms of action and perception (Barrett 2011; Penn 2011) we have a clear method to investigate those differences.

There will be species-specific differences in memory abilities based on the differences in the animal’s ecological niche and the perceptual systems that have evolved to detect the ecological information for perceiving the affordances in these niches. This is an important, largely overlooked observation: we can examine the differences and similarities between species *not only* because they either fail or succeed in performing the experimental tasks that comparative psychologists set for them, but also because of their different bodies and ecological niches: different regularities and relations among such regularities exist in different environments, and animals have evolved perceptual systems to deal with those regularities. Species and even individuals live and have evolved in very differently structured worlds—open and cluttered, aquatic, terrestrial and aerial, large and small scales, to mention a few obvious but major differences—and this will have a big impact on the kind of perceptual systems they have evolved to pick up ecological information.

Now, it may be that animals displaying relatively more flexible behaviour have learnt to exploit the nesting of their widely differing niches—the ecological information about distal affordances—in closer-to-optimal ways. It is even possible that many species alive now—even those we commonly dub “simple” such as insects—have evolved the ability to learn to detect information indicating distal affordances, and not only spatially proximate affordances, given that remembering and hence anticipating situations seems useful for most, if not all, species. Nevertheless, this does not undermine the main message that such capacities are still bound to ecological information available within the sensory scope and that there will be species-specific differences in the information that can be and will be detected. Convergence does not have to be all-or-nothing: there can be partial convergence of the perceptual systems to detect particular ecological information in a habitat but also striking differences—differences that could have to do with pre-existing biological constraints (that result from having evolved in different environment) that make “complete” convergence

impossible.¹⁰ In any case, charting both the differences and similarities on the level of ecological information allows for a more detailed taxonomy of the (evolution of) memory abilities than the one we currently employ (see Buckner 2013).

An ecological approach, finally, abandons an anthropocentric perspective in favour of a zoocentric perspective. This approach provides the tools to investigate the differences between two or more *nonhuman* species, regardless of what humans can do. While this is something that behavioural ecologists and zoologists, for instance, routinely do, animal cognition researchers often confine themselves to human-nonhuman comparisons. Those occasional moments when two nonhuman species are compared, this is often because they both share a capacity once thought to be uniquely human (see Barrett 2014). Comparing how bees and ants, or dolphins and whales, or elephants and giraffes, exploit the nesting of their environment to remember situations and anticipate future ones, will lead to a much richer comparative psychology.

Conclusion

In this chapter, I have first provided a brief reconstruction of the evolutionary debate about EM: is EM a uniquely human capacity or do some or even many animals share it with us? Anthropogenic approaches define EM in an unconstrained way: they try to capture the intuitive fact that episodic memories are seemingly unbound by present circumstances and can be conjured up at will. This alleged capacity is consequently contrasted with simpler explanations like tracking environmental or internal regularities. I argued that this method is hard to unite with evolutionary theorizing by making EM-like abilities independent of biological and ecological constraints.

In turn, I offered a biogenic approach grounded in ecological psychology. On this view, memory can be seen as improved engagement with affordances, due to an animal's perceptual systems having become attuned to the relevant ecological

10. One can wonder whether two species can “completely” converge on any ability at all, given their different evolutionary histories and hence different perceptual and motor systems. This is especially true for very distantly related species, like dolphins and ravens whose bodies and perceptual systems could not be more dissimilar. The ecological information in their respective niches is equally different, so can they converge on abilities at all? However, as I have argued, nesting exists in all niches, and it is interesting to see how resourceful animals are in exploiting this. Convergence on EM-like abilities can be sought, for instance, in the sensitivity to nested regularities across a range of contexts. In any case, what will be important is that we clearly define what we mean by “convergence” (see also Osvath, Kabadayi & Jacobs 2014).

information indicating those affordances. Memory is a type of perceptual learning. Moreover, I argued that by considering the nested regularities in the environment, remembering distal affordances—affordances outside the sensory scope—is possible. On this view, EM-like capacities are elaborations and sophistications on basic sensorimotor functioning. Episodic memory, therefore, can also be understood in terms of perceptual learning. In this way, the capacity for episodic memory stays firmly tied to the biological and ecological constraints of animals, as the ability to remember in particular situations will depend on the ecological information about regularities that animals will be able to pick up. Note, however, that rather than having provided a complete alternative to existing theories of EM, I have provided a method I believe to be both useful and necessary to integrate our knowledge about animal biology and ecology with animal cognition.

In the end, I hope to have contributed to a shift from simplistic yes-or-no-perspectives on EM in nonhuman animals as compared to humans, to a definition that allows for more detailed comparisons between any two species—human or nonhuman. This marks a shift from an anthropocentric to a zoocentric perspective. By having “untangled” memory in terms of perception and action, we have a fruitful method for such comparisons. This is an important insight: differences and similarities between species are *not* limited to them either passing or failing certain tests, but due to their different bodies and ecological niches. Accepting this provides a much stabler ground for future studies into comparative thinking about memory abilities in species, both closely and distantly related.



5

Ecologies of social interaction

Abstract

Mirroring the discourse surrounding episodic memory, the debate on theory of mind or mindreading in nonhuman animals revolves around the contrast between a more sophisticated cognitive capacity (namely mindreading), and a simpler alternative (referred to as behaviour-reading). Both approaches depict social cognition as an inferential process, taking place inside the individual. This process consists either of mental state ascription (mindreading) or application of general rules (behaviour-reading). In this chapter, I develop an ecological alternative to both views, which focuses not on the processes in the animal's head, but on the sociomaterial processes that animals are immersed in and that organize their ongoing activities. Instead of an individual trying to predict the behaviour of another individual based on inferential abilities, the animal is responsive to affordances and how they are nested within the sociomaterial processes that make up the environment. I argue that this depiction of animal social cognition is preferable, because it allows us to understand the social abilities of nonhuman animals free from our current understanding of human social cognition.

Introduction

A raven pecks a small piece of meat in the ground, covering it with a branch. Looking up, she notices a set of watchful eyes, takes out the food and hides it a few meters further along under the shade of a tree, facing the other with her back. Does the raven know what the other raven believes, desires or sees? Or does she predict what the other will do based on behavioural rules? Similarly, a chimpanzee notices a banana in clear view of a dominant's view and refrains from taking the banana. Is this because he knows what the dominant thinks and perceives, or does he rely on generalizations about behaviour? The former ability to infer others' mental states is known mindreading or theory of mind¹ (Lurz 2019; Dally, Emery & Clayton 2010; Emery & Clayton 2008). The latter is commonly referred to as behaviour-reading (Povinelli & Vonk 2004; Povinelli 2004).² Lurz (2019) formulates the difference clearly:

In the field of animal social cognition, there are two generally recognized types of strategies that animals are understood to use to make such predictions. Behavior-reading is one type of strategy. This strategy involves predicting the behavior of others on the basis of observable cues that are perceived, believed, or otherwise represented to obtain without interpreting those cues as signs of underlying mental states (Lurz 2009, 2011; Povinelli and Vonk 2003). The observable cues can include bodily appearances (e.g., threatening posture), behaviors (e.g., reaching toward a particular object or place), and environmental relations (e.g., looking in the direction of a particular object or place); and the predictive process itself can be the result of individual learning or innate mechanisms. The other behavior-predicting strategy is mindreading (aka theory of mind). This strategy involves inferring others' mental states, such as sensory experiences, desires, and beliefs, from represented observable cues, and using this information about others' mental states to predict their behavior (Premack and Woodruff 1978). Here, too, the inferential and predictive processes involved may be the result of individual learning or innate mechanisms. (p.229)

1. How mindreading takes place is also a contentious topic. Does it happen by means of "experience projection", i.e., inferring the other's perspective by means of simulation, based on one's own experiences (Clayton, Dally & Emery 2007; Lurz & Krachun 2019) or theoretical inference (Call & Tomasello 2008)? I will not go into this debate, however, since I focus on the assumption of inferential processes in both these accounts of mindreading as well as in behaviour-reading accounts.
2. Behaviour-reading serves mostly as an ad hoc alternative to mindreading however, a description of what the animal could have done, and is rarely if ever studied in its own right as a valid explanation (though there are calls to do so, e.g. Van der Vaart & Hemelrijk 2014).

Despite long-standing debate, the so-called “logical problem” of disentangling these two “generally recognized explanations” remains unsolved (Lurz 2019, see also Buckner 2014). What’s more, within the context of human cognition, the theory of mind or mindreading paradigm has been greatly criticized, especially regarding the mind-body dualism that is visible in the difference between mindreading and behaviour-reading strategies (see e.g. Leudar & Costall 2009; 2004). Accordingly, this chapter does not directly confront the logical problem, but aims to make progress in the debate by contributing to a third alternative: being responsive to affordances. The goal is to show that the work usually ascribed to inferential processes like mindreading and behaviour-reading can be done by responsiveness to affordances—opportunities for action—and how they are nested within sociomaterial processes (which is not to deny that some important internal processes are going on in animals’ nervous systems, just that those internal processes must not be understood as inferential).

The distinction between anthropogenic and biogenic theories (Lyon 2005; Lyon & Keijzer 2007; Lyon & Kuchling 2021) illustrates why an affordance-based approach is worth pursuing. Anthropogenic approaches try to define essential features of abilities in humans and look for similar features in other animals; a style of reasoning that is ubiquitous in the mindreading debate. The result is a bias towards species that intuitively resemble us in some sense—being social, having large brains and behaving flexibly in a general sense—and that will inevitably be viewed as precursors or otherwise lesser versions of ourselves (Barrett 2015a). Perhaps this is no problem if our goal is to see what typically human-like features are present in nonhuman animals (though what is “typically human” it itself contentious, see e.g. Andrews 2016a; Buckner 2013), but what about comparing two or more nonhuman species, or humans and a nonhuman species without departing from ourselves? Anthropogenic approaches seem less useful here.

In contrast to anthropogenic ones, biogenic approaches assume that cognition “is best seen as a biological function” (Keijzer 2020). Understood as a biological function, cognition “contributes to the persistence and wellbeing of an organism embedded in an ecological niche with which it must continually contend” (Lyon & Keijzer 2007, p.137). The ecological approach (Gibson 1979/2015) alludes to the same idea, as affordances are defined in relation to the biological “constitution” of animals and their ecological niche. Hence, the social skills of animals must be explained in terms of animal-environment relations, even in cases that intuitively really do seem to require inference. Such an approach opens up a multitude of questions that address similarities and differences between species, and can help us to see “what it means

to be any kind of animal, and not whether other animals are more or less like us” (Barrett 2011, p.18).

In what follows, I will first discuss some arguments in the animal social cognition literature that invoke affordances, with the aim of highlighting some important differences with inference-based approaches (Sect. 2). Then, the importance of understanding the environment as consisting of nested processes is discussed, to enrich the discussion in the second section (Sect. 3). The next section discusses two examples—humans playing football and ravens re-caching food—as illustrations of individual responsiveness to nested affordances (Sect 4.). After that, I will discuss how social cognition or social interaction can be understood as an individual’s know-how of responding to affordances to make distal affordances available, “playing the role” of a process in which affordances are nested (Sect 5.). I end by arguing how the account outlined here allows us to understand animals’ social skills non-anthropocentrically and by addressing some general implications for future social cognition research in nonhuman animals (Sect. 6)

Affordances and animal social cognition

The ecological approach differs from mindreading and behaviour-reading in its central commitments and general focus. The biggest divergence concerns the role of inference and how perception is characterized. It is helpful to highlight these key differences first.

Mindreading approaches are committed to the idea that something can be inferred from directly perceivable behaviour—namely, mental states such as beliefs, intentions and perspective (Call & Tomasello 2008; Krupenye & Call 2019; Krupenye et al. 2016; see also Andrews 2016b). Mental states are understood as *hidden* causes of behaviour. Behaviour-reading accounts reject this “extra” inference to mental states in the case of nonhuman animals—notably, without denying the existence of mental states as hidden causes as such (for instance, in the case of humans). As an example, Povinelli writes that a behavioural rule such as “Don’t go after the food if the dominant was oriented towards it” is sufficient, and that “One doesn’t need to add the additional ToM clause: ‘because he has seen it, and therefore knows where it is.’” (Gallagher & Povinelli 2012, p.151), even though humans may sometimes use this “additional ToM clause” as well.

Despite these differences in *what* nonhuman animals infer, behaviour-reading accounts are similarly committed to the idea that *something* must be inferred from behaviour—namely, abstract categories or rules. As Povinelli writes, “the behavioral account does require a hidden premise; namely, the behavioral rule, the result of some process of abstraction. In this respect, the behavioral rule hypothesis, as much as the ToM account, understands the process to involve inference.” (p.151). This agreement can be attributed to the assumption that “the information available to sensory systems is impoverished, ambiguous, and otherwise insufficient to support perception” and that therefore “these theories assume construction of representations or inferences to supplement the information.” (Gibson & Pick 2000, p.10).

The ecological approach, as explained in foregoing chapters, rejects this characterization of perception as the passive reception of stimuli and, consequently, the necessity of inference to enrich those stimuli (Gibson 1979/2015; Gibson & Pick 2000). Perception, instead, is understood as an organism’s responsiveness to the environment’s affordances (Gibson 1979/2015; Chemero 2009; Rietveld & Kiverstein 2014). Affordances or opportunities for action are what animals perceive—see, hear, smell, touch, etc.—most fundamentally and what constrains or organizes their actions (Gibson 1979/2015, p.411; Costall 1995, p.470). Additionally, perceiving—in contrast with mindreading and behaviour-reading—is understood as something that takes place over time and goes on. Action and perception are thus inseparable; perception presupposes action and vice versa. In other words, perceiving is continuous, perceptually controlled activity.³ Finally, “perceiving” is not first and foremost consciously attending to something, but often bodily, non-deliberative activity. For instance, instead of seeing something brown-ish, shaped like two connected ovals, roughly textured, and about two centimetres in length which is categorized as “a peanut”, a bird responds to the peanuts “edibility”, which is both “perceiving” it and preparing to pick up and eat the thing. As Costall (1995) has put it, “What, fundamentally, we attend to in our surroundings are not shapes, colours and orientations of surfaces in our surroundings, but rather the meaning of things for action.” (p.470).

Affordance-based accounts are uncommon in the animal cognition literature in general, and in the debate on mindreading and behaviour-reading specifically.

3. A note on terminology: Gibson (1979/2015) used the term “perception” as including action. He also used the term “perceptual systems” to refer to the whole, active and moving animal engaged in, say, grasping or seeing something. Gibson & Pick (2000), on the contrary, also used “action and perception systems”. In any case, since some readers will think of perception as the *beginning* of or input for cognitive processing and for action, I will often refer to “activity” and “responsiveness” as including both the perception and action sides.

Nonetheless, Gallagher and Vincent (2019; see also Gallagher & Povinelli 2012), as well as Barrett and Henzi (2005) and Barrett, Henzi and Rendall (2007) provide several interesting insights into the work that affordances can do specifically in the context of animal cognition, to put mindreading and behaviour-reading out of work. Their accounts overlap in some ways and diverge on others—and do so as well in relation to ecological psychology—but nonetheless provide a good starting point, which I later aim to enrich with a discussion of the nested structure of the environment.

Gallagher & Vincent (2019) give the example of the affordances a subordinate chimpanzee is responsive to in the presence of a dominant in a food-competition false belief task. In such settings, the authors argue, chimpanzees do not infer “hidden mental states”, but rely on “other’s posture, movements, gestures, facial expressions, gaze directions, vocal intonations, etc.” (p.281). This is no behaviour-reading, since it does not require inference: the subordinate does not first consider (either consciously or subconsciously) *that* the dominant is gazing in a particular direction and has an aggressive posture and *then* decides what he should or should not do by relying on behavioural rules. The interaction is better construed in terms of ongoing coordination, where “my perceptions are feeding my responses or potential responses to you, and I perceive your actions in terms of our continuing interactions” (Gallagher & Povinelli 2012, p.162). Social interaction, then, is a matter of “practical or pragmatic (and specifically social) reason—being able to see what is possible in a socially constrained situation.” (Gallagher & Vincent 2019, p.283). Social interaction is guided primarily by situational and developmental constraints, and so does not need to be “supplemented” with inferences. Those constraints pertain to the chimpanzees’ ways of living together—their ways of doing things, of interacting with each other in particular situations (Rietveld & Kiverstein 2014; Andrews 2016a).

A second and related difference with inference-based accounts, is that the chimpanzees “are not primarily observers but rather participants with respect to social cognition” (p.281). Elaborating on their case, Gallagher and Vincent (2019) write that,

Much of what unfolds in this food-competition experiment has to do with the social roles of the chimpanzees, that influence the subordinate chimpanzees’ perception with respect to possibilities for action. [...] From previous interactions with the dominant chimpanzee and other group mates, the subordinate chimpanzees have become just that: subordinate. A subordinate’s perception of the mutually observable food item is already informed by her history of interactions. (p.282/3)

What Gallagher and Vincent (2019) suggest here is that the chimpanzee *becomes* a subordinate through a history of interactions with dominant chimpanzees. Interacting with a dominant increasingly organizes the behaviour of the subordinate, making the subordinate responsive to what to do and what not to do given the situation at hand, including the dominant's posture, gaze, and so on. In *becoming* subordinate, that is, and given particular circumstances, the chimpanzee will continue take advantage of some affordances (such as grabbing food when the dominant's gaze is not turned towards the food) and refrain from taking some affordances in other circumstances (such as grabbing food in plain sight of the dominant). So, although the latter set of affordances continues to be available as well, pre-existing social practices constrain subsequent actions—that is, the actual taking advantage of those affordances.⁴ The fact that the subordinate perceives the world in terms of those rather than other possibilities, because he has his own history, demonstrates also that he cannot simply be regarded as an observant. Ecological psychologists (more so than Gallagher here) also emphasize that being a participant indispensably involves *actual* movement: animals move to change the situation and their relation to others, and this too may avert the need for inferences (Reed 1996; Heft 2001; see also section 5).

These situational constraints on perception and action are similarly emphasized by Barrett, Henzi and Rendall (2007). Writing in the context of monkeys' social interactions, they argue that individual animals “do not need to hold abstract conceptual notions of ‘bonds’ or track others’ relationships because they can gauge circumstances directly by looking at what is happening around them [e.g. distance to others, grooming to get into zone of tolerance of dominant, etc.]: the spatial structuring of the animals in their environment may obviate the need for certain kinds of high-level processing in the animals themselves.” (p.568) Though animals need to develop a sensitivity to how spatial structuring constrains actions within

4. Heras-Escribano (2019) calls such constraints in social situations *normative* constraints and writes that social norms constrain actual *actions*, not affordances or *possibilities* for action. He gives the following example from football: “Sometimes, when the league is already won before the ending of the season and the winning team aims to achieve more records, such as making one of their players the top scorer of the league, the coach tells the players that, if possible, they should pass the ball to the teammate who could become the top scorer (Heras-Escribano and Pinedo 2016: 587). They deliberately avoid seizing the affordance of kickability, and they pass the ball to their teammate.” (p.109). In such cases, it is obvious that it's still possible to aim directly for the goal—the affordance is still available—but that social norms constrain which affordances players will actually make use of. “In this way”, Heras-Escribano (2019) writes “the social environment enters in the picture as a key factor for regulating the taking advantage of affordances”. I recognize these differences, while using these examples primarily to make a point about how sociomaterial processes make inference redundant.

their population, it is the structure of the environment that organizes the actions of individuals, rather than inferences about the behaviour or mental states of individuals. As Barrett, Henzi and Rendall (2007) suggest, this kind of “just in time” learning—responding to circumstances *as* they occur—is much less demanding than “just in case” learning—which requires pre-conceived ideas about the world. Affordance-based approaches therefore also take issue with the individualistic assumptions of mindreading and behaviour-reading approaches: the idea that social cognition means predicting what another individual will do. Often, inference-based prediction is unnecessary: what is required is sensitivity to social context. Being responsive to what is happening in the environment (including what other animals are doing) and what oneself therefore can do, can “take over” the function usually ascribed to mindreading and behaviour-reading.

The sociomaterial nesting of affordances

The previous section described affordances as opportunities for action that constrain or organize the actions of animals. In addition, the importance of learning to attend to relevant aspects of situations that constrain action was highlighted. In this section, I argue for the importance of recognizing the environment as consisting of nested processes for understanding how affordances organize animals’ social interactions, rendering inference unnecessary (see van Dijk & Rietveld 2021; Van Dijk 2021a; Van Dijk & Withagen 2016; Gastelum 2020; Michaels & Palatinus 2014). Note that I talk here about *responsiveness* to affordances, not to the “ontology” of affordances.⁵

Affordances, though sometimes discussed as such, do not occur in isolation (Gibson 1979/2015). Affordances are always “nested” within other processes on larger and smaller spatiotemporal scales. As Heft (2018) puts it: “From an ecological point of view, the environment has a nested structure, and any action-environment transaction needs to be assessed in relation to the environmental structures that are relevant to the action. Actions in human habitats are coupled to structure not only at the level of affordances but also at the level of structures within which affordances are nested.” (p.119). This nested structure is not fixed but consists of processes occurring over multiple timescales. For instance, whether a peanut will be available to eat for a bird depends on its nesting (e.g. safe place to eat, the activities of fungi, chemical processes going on inside the peanut itself). The bird’s own activity, too, can be viewed as a process that makes the affordance available or unavailable. This implies

5. For discussions on this topic, see Van Dijk (2021a), Kiverstein (2020), Sanders (1997), Turvey (1992), Chemero (2009) and Reed (1996).

that affordances (such as the “edibility” of the peanut) can in fact also be understood as a (temporarily stable) process, nested within, and becoming available in relation to, these other processes.

Another helpful example that shows how affordances are nested is switching lanes with your car. The affordance of switching lanes is available (or unavailable) in relation to the position, movement and speed of cars surrounding you as well as your own position and speed over some period of time. This affordance persists—remains available—by either slowing down or speeding up depending on how fast the other cars are going. As long as certain relations hold between processes, the affordance of lane-switching is available for the driver (cf. Barrett, Henzi & Rendall’s observation about “just-in-time” learning). Or consider a third example (one that will be taken up later): a football affords passing, depending on where one’s teammates and the opponents are running to, and hence is also a temporarily stable opportunity for action within other ongoing processes. Despite the fact that sometimes affordances can be described apart from their nesting, then, in real-life situation there is no clear separation of being responsive to affordances of the material environment and the wider situation in which the affordance is nested (Van Dijk & Rietveld 2017) because the availability of affordances always depends on this wider context. Moreover, situations consist not just of single affordances but a multitude of affordances that animals can simultaneously respond to (see Van Dijk & Rietveld 2017; Rietveld & Kiverstein 2014; Rietveld, Denys & Van Westen 2018), as these examples show (e.g. in the car: giving gas, steering, watching behind you through the mirror and switching lanes).

What the football and car driving example also illustrate, is that in most situations nesting of affordances is not just “material” but *sociomaterial*. In Heft’s (2018) discussion of “places” he does not refer just to the “material” or “physical” space but equally to the regular social practices that inseparably belong to those places, something that Gallagher and Vincent (2019) and Barrett, Henzi and Rendall (2007) do too.⁶ In fact, if we return to the edibility of the peanut, the activities of other animals can be understood as processes alongside other processes that influence whether the bird will perceive the peanut as edible. That is to say, some processes *are* other animals responding to affordances in the same situation. In species with hierarchical social structures, for instance, a dominant’s actions—his response to affordances in the place—constrains a subordinate’s taking advantage of the “edibility” affordance. In this way, affordances are “nested and hang together” (Van Dijk & Rietveld 2018, p.4).

6. See also Heft (2001), chapter 7 and 8, on Roger Barker’s notion of “behavior setting” and the usefulness of this notion for Gibsonian ecological psychology.

The fact that affordances are nested within *socio-material* processes makes sense from an evolutionary perspective. Animals adapt to environments that have always already been tainted by the activities of other animals—both what they are actually doing and how they modify the landscape. As Costall (1995) puts it, “the nature we confront is nature already transformed [...] Any ecological psychology worth the name has to include living beings within the natural order of things, and recognize the difference they make. Otherwise, the social, the cultural, and perhaps life itself, are destined to become the secondary qualities of ecological realism” (Costall 1995, 478; see also Van Dijk & Rietveld 2017; Costall & Leudar 1996; Costall 2001; Ingold 1996; Kiverstein & Rietveld 2021; Heft 2018). There is only *one* environment, and that environment is sociomaterial.

Therefore, on an affordance-based approach, social situations in which one animal interacts with other animals requires, in a basic sense, the same skills as those required for responsiveness to a peanut’s edibility. In this vein, Gibson (1979/2015) wrote that “animals and other persons can only give off information about themselves insofar as they are tangible, audible, odorous, testable and visible” (p.135), making the point that the means by which animals can understand other animals are the same means by which they navigate the “material” environment (see also Reed 1996, p.98; Leudar & Costall 2009). Far from reducing animate beings to inanimate matter, however, or denying the major differences that exist between living and non-living entities, an ecological perspective points to the intertwinement of material and social aspects of the environment as sociomaterial for understanding social interaction. As Van Dijk and Rietveld (2017) write, social interaction “includes both being responsive to the opportunities for action, the affordances, offered by the material environment and to the opportunities for social engagement offered by other people. [...] there is no clear separation of the two because in acting skilfully one is attuned to the situation as a whole.” (Van Dijk & Rietveld 2017, p.2). So, while “The richest and most elaborate affordances of the environment are provided by other animals and, for us, other people” (Gibson 1979/2015, 127), the availability of these affordances too cannot be separated from their wider context, and interacting with other animals includes both what others affords (such as grasping them, say) and how their actions make other affordances of the situation available or unavailable. Again, from an evolutionary perspective, this sociomaterial intertwinement seems plausible: what has evolved are more refined and elaborate systems for perceiving and acting that allow animals to respond flexibly in complex and changing sociomaterial situations, instead of a cognitive capacity specifically and narrowly as a “cognitive solution” for specific “problems” such as the complexity of social life (cf. Cisek 2019).

Concretely, this sociomaterial intertwinement implies that to understand social interactions, the structure of the environment—as consisting of nested, sociomaterial processes—must be taken into account. Understanding social interaction should thus start with an understanding of how affordances are nested within sociomaterial processes, that is, how those processes constrain or control individuals’ responsiveness to affordances.⁷

Football players and ravens’ responsiveness to affordances

Having sketched the theoretical background, I will now describe and compare two examples of individuals’ responsiveness to sociomaterially nested affordances: the human activity of football and the corvid activity of caching. The former is described to make the latter more intuitive, because the pre-reflective kind of engagement that characterizes football and other sports is, I believe, a helpful analogy for thinking about nonhuman animals.

Consider this example: from an individual perspective—that of the right winger, say—affordances continuously become available and unavailable based on ongoing processes, and constrain or organize his activities. Some affordances are more persistent than others. The field affords walking on for him, clearly, and it does as long as the ground will be there and the opponent won’t break his legs. Similarly, the ball affords kicking for him as long as he is in ball possession. The goal affords scoring if he manages to come near. The defender on the winger’s team coming in ball possession on the far right, affords positioning oneself to the right. This affordance shows up as a possibility for action in relation to the momentary position of the defender, the winger himself and the opponent, but could become unavailable just as quickly. While running towards the corner flag, the space in the penalty box affords passing to while the goal stops to afford scoring. Throughout this activity, affordances come and go as the situation unfolds and the “place”—as the intertwining of the “material” field and the “social” activities of players—continues to change.⁸

7. Again, the distinction between the actual unavailability of affordances and normative constraints that result in organisms not *responding to* or *taking advantage of* an affordance whereas in principle they could, must be kept in mind (see section 2 and footnote 5). Normative constraints are indispensable in understanding social interaction (see Heras-Escribano 2019; Van Dijk & Rietveld 2017; Andrews 2016a). However, this section’s primary concern is how not-yet-available affordances can be prospectively perceived and made available through action. Both kinds of “unavailability” show that the processes that make up the environment may obviate the need for inference, which is the main point of this chapter.
8. In structuring this example, I’ve taken my inspiration from Van Dijk and Rietveld’s (2017) example of two persons interacting in a coffee bar (p.6).

As anyone who has ever played football—or any other sport, for that matter—will know, players are not deliberately aware of the effects of their actions on the game at large. As Heft (2018) writes, “places are ‘backgrounds of tacit understanding’, so we’re mostly unaware of them” (p.100). Nor are individuals deliberately planning their actions or aware of future possibilities; they let their actions be organized by the ongoing situation, by what is happening around them, based on extensive prior experience. This is not only true for immediately available affordances, such as kicking the ball, but also for positioning oneself at the best possible spot—an action that requires responsiveness to multiple affordances and to how affordances are nested. As players become more experienced, they learn to take a wider portion of the situation into account, thereby tuning in on the best possibilities for action given that situation.

Before explaining the matter of taking more of the ongoing situation into account (see sections 4 and 5), we can draw a comparison here with re-caching ravens. Being a re-caching raven, I believe, is not quite unlike being a football player—or at the very least, the analogy helps to make sense of raven’s pilfering strategies. First of all, it is well-known that members of the corvid family use several anti-theft strategies. Grodzinski & Clayton (2010):

When observed, western scrub-jays preferentially cache in trays placed in the shade compared with those placed in well-lit areas (Dally et al. 2004), and in trays placed far from the observer compared with those placed closer to it (Dally et al. 2005b). Ravens tend to be further away from other individuals during caching than at other times (Bugnyar & Kotrschal 2002a). Thus, storers act to decrease the quality of the information available to the observer (Dally et al. 2005b). When it is possible to altogether deny others of visual information by caching out of view, ravens preferentially cache behind objects that prevent observers from seeing (Bugnyar & Kotrschal 2002a; see also Bugnyar & Heinrich 2005) and scrub-jays prefer a tray that is out of view compared with an equidistant tray in view of the observer (Dally et al. 2005b). Scrub-jays do not make these distinctions when the observer’s view is blocked completely and caching is performed ‘in-private’ (Dally et al. 2004, 2005a), or when caching in far or close trays is observed by the jays’ partner (Dally et al. 2006b). Thus, jays do not simply prefer to cache in those locations that happen to deprive observers from information. Rather, they incorporate the pilfering risk (and aversity) specific to each caching event and act only when it is relevant (p.981).

In addition, throughout development, corvids clearly do learn to take the wider situation into account in some way, just like football players who improve their skills. Whereas the simple act of caching is already performed by very young corvids (such as the simple act of kicking a ball is performed by complete amateur players⁹) it does improve with experience. As Grodzinski & Clayton (2010) write,

[I]mprovements of caching efficiency in corvids, including cache-protection strategies, require experience (Emery & Clayton 2001; Bugnyar et al. 2007a). Young storers need to learn what makes a good cache site, how to cache different food items (e.g. killing or paralyzing prey before caching) and how to deal with the risk of pilfering. After they have mastered their techniques, adult corvids incorporate many factors into their caching decision-making. (p. 977)

It is precisely the incorporation of many factors—which include the activities of other ravens (see Grodzinski & Clayton 2010; Dally, Emery & Clayton 2010)—during caching and especially re-caching that leads to the idea that ravens, as well as other corvids such as jays, are mindreaders or behaviour-readers. Surely, in taking such factors into account, these animals must *infer* what the other will do, as they cannot *perceive*, at this moment, what the other is up to—which is something they clearly seem to know, given their non-random habits of re-caching? Considering the analogy between wingers and ravens, we can also describe this behaviour in terms of their responsiveness to nested affordances.

Consider, by analogy with both the football example and Grodzinski and Clayton's (2010) description above, a raven (the cacher) who notices being watched by another raven (the pilferer) while caching a piece of meat. From the perspective of the cacher, affordances continuously become available and unavailable for some time based on ongoing processes, and constrain or organize his activities. Some affordances, again, are more persistent than others. The ground affords walking on, most of the time. The branches of trees afford landing on. But also, the pilferer's behaviour affords taking a few steps in the opposite direction. The pilferer's watchful eyes afford as-if caching. This latter possibility for action shows up in relation to the momentary position of the pilferer in relation to the cacher herself, but could disappear just as quickly as the pilferer moves forward. The shades of a large tree a few meters further away affords actual caching, just as the place behind a tiny rock, given that the

9. Some might object that the caching behaviour is “innate” whereas the kicking behaviour is learnt. However, instead of thinking in terms of a nature-nurture (or a similar) dichotomy, we could try to explain both activities in terms of responsiveness to affordances. This is always a combination of “nature” and “learning”. Compared to basic behaviours, more complex behaviour require us to take a wider portion of the environment into account.

pilferer's view is obstructed. Throughout this activity, affordances come and go as the situation unfolds, as the place—again, the intertwining of the “material” situation and the “social” activities of the pilferer—change.

Similar to the right winger, we can understand the raven's activity in terms of responsiveness to affordances nested in ongoing situations; activity without deliberate planning and unaware of their “tacit understanding” of the situation, but nonetheless keenly attuned to the situation based on prior experience. This holds up not merely for actions like walking, but also for finding a good spot to cache to minimize the chances of pilfering. The cacher understands the pilferer not by *abstracting* from the situation—becoming better at inferring concealed intentions or behavioural rules based on the other's behaviour—but by being more attuned or attentive to the ongoing situation as a whole, including the actions of the other. As mentioned, in such social interactions, being responsive to “material” and “social” affordances can't be pulled apart in real-life situations. In other words, the animal learns to attend to those processes in which affordances are nested. As Leudar and Costall (1996) have put it, “the situations alternative would be to regard development not as the individualization and increased isolation of the subject, but as the increasing ability to partake of what the social world can afford an individual” (p.104). Animals do not merely look at, but also participate in and influence social situations. The next section will discuss, in more detail, how this responsiveness develops in animals.

Making affordances available through activity

How does one know *how* to act in order to make certain affordances *available*? For instance, how does the winger know how getting past the defender on the right will get him into scoring position? And how does the raven know how walking a few meters along into the shadows will decrease the chances of pilfering? The answer to all of these questions is that animals, through practice, have become attuned to ongoing processes in which affordances are nested, including, essentially, their *own* activities. Or rather, one is continuously moving in coordination with other ongoing processes to make affordances available.

The key difference with mindreading and behaviour-reading then is that animals become increasingly better at attending to relevant aspects of ongoing sociomaterial processes, rather than abstracting from the behaviours of animals. Mindreading accounts are inclined to postulate an inferential process precisely because they start

from a “frozen perspective”. In analysing social interaction, they bring to a stop, theoretically speaking, what is in fact an ongoing process and try to explain the interaction by considering the kind of processes going on in the head of the animal. But frozen perspectives, as Gibson (1979/2015) observed, are uncommon. He noted that *not* moving at all is a special case—a pause in action—rather than the other way around, even if action is minimal: “[I]f an animal has eyes at all it swivels its head around and it goes from place to place”, and the reason for this is that “The single, frozen field of view provides only impoverished information about the world.” (p.xiv). To gain more information about the world and to perceive affordances, animals move. Uncertainty about how to act in situations, including social situations, can be reduced by actually moving, provoking a reaction, changing one’s perspective—that is, by activity in the world, rather than thinking, activity in the head (see also Dewey 1958/2000). This seemingly trivial observation has important implications.

Given that individuals join a world where affordances have become nested within sociomaterial practices in certain ways, they can, put colloquially, learn to “play the role” of that process. Not only do they learn to be sensitive to unfolding processes; they learn to regulate those processes themselves through their own activities (see Reed 1996, p.138). Put differently, since one’s own activities are also processes in which affordances are nested, responding to affordances is never just an *end* but also a *means* to make other affordances available. Each response to an affordance is a means to make other affordances available or unavailable. Importantly, even responding to an immediately available affordance is a process that takes time: a raven can be responsive to the edibility of a piece of meat, but the actual response takes time. With experience, this process can become extended spatiotemporally. While compared to immediately available affordances (e.g., a raven eating a piece of meat right in front of her), one has less “control” over such distal affordances since they become (un)available depending on more ongoing processes, the basic structure of making affordances available is preserved across longer timescales.

The difference between responding to immediate as compared to distal affordances is a question of the spatiotemporal scale that we take into account: some affordances require activity over longer timescales to become available (cf. Van Dijk & Withagen 2016; Van Dijk & Rietveld 2018; Gastelum 2020). As Gibson & Pick (2000) write, “Achievement of a primary affordance, the function of the task overall, is accomplished with greater complexity as subunits that involve use of varied means begin to be nested within the task as a whole. The means for accomplishing a task is learned as an affordance itself, but it can later develop into a subunit embedded in the larger and longer task structure.” (p.151, see also chapter 2). That is, the activity of responding to

an affordance becomes nested within—a subunit of—responding to another, distal affordance. If we understand activities as processes that make affordances available, then longer activities are processes that can make distal affordances available.

To illustrate, reconsider the affordance of scoring for the right winger. This affordance is nested within his own activity of getting past the defender and the actions of other defenders. Getting past the defender makes the affordance of scoring available. The winger, through practice, has learnt that acting on this affordance (itself a process) makes other affordances available, given other ongoing processes. Relations between affordances indeed form a complex meshwork, since each animal's activities changes the activities of others on the field.¹⁰ For instance, the winger's own movement are, for the defender, also processes that make some affordances available or unavailable—setting the defender up to respond in particular ways. Therefore, the winger must continuously stay in touch with those processes as they “change direction” and make the affordance unavailable again.

Now what is it that animals are learning, exactly, in becoming responsive to distal affordances? To illustrate this, it helps to make a contrast with mindreading and behaviour-reading accounts. Mindreading and behaviour-reading accounts would say that animals become better at inferring, from behaviour, mental states or behavioural rules. They learn to abstract from particularities: deducing mental states or behavioural rules, which are then applied to novel situations. An affordance-based approach would argue for precisely the opposite: animals become better at attending to those processes in which affordances are nested. What they learn are particular ways of attending which are coupled to ways of acting, which is what becoming responsive to distal affordances entails. Put differently, animals do not abstract from particular situations; instead, they become better at distinguishing situations in increasingly effective ways, through patterned and economic ways of attending (Gibson & Pick 2000).

Such situations are not distinguished like a game of “find the differences”, of course. Situations go on, and hence animals learn to perceive—given what is happening around them and what they are doing themselves—which affordances are available or can be made available. In being attentive to processes in which affordances are nested, one thus doesn't need to continuously track all ongoing processes. What is

10. Gibson (1979/2015) already mentioned the reciprocity of activity in social situations, writing “What the male affords the female is reciprocal to what the female affords the male; what the infant affords the mother is reciprocal to what the mother affords the infant; what the prey affords the predator goes along with what the predator affords the prey; what the buyer affords the seller cannot be separated from what the seller affords the buyer, and so on.” (p.127)

learnt is to look for sufficient information for one's ongoing activities. Much like knowing that something which disappears behind an object will reappear after a particular amount of time (see chapter 2; Heft 2020), temporarily attending to different aspects of the ongoing situation is often enough to know how those processes will unfold. One becomes better at where to and how long to attend to, responding increasingly to the minimal, optimal information available (Gibson & Pick 2000, p.157). As Gibson & Pick (2000) write, "Not all available information is *relevant* for differentiating affordances" (p.100).

A comparison between novice and expert behaviour may help to further illustrate the development of responsiveness to distal affordances. Someone who just starts playing football doesn't know where to look. The result is that if he receive the ball, he must pay full attention to the ball at his feet as well as to keeping the ball there while he is dribbling. Therefore, he won't be prepared for what's best to do next and he will need a lot of time for his subsequent action. To improve his game, he will need to focus less on his feet, learn to shift his attention, and learn to move skilfully across the field. That is, he has to reduce the information to specify dribbling with the ball—from visual (looking at the ball) and tactile (feeling with his feet), say—to only the minimum information required to know where the ball is given his ongoing actions—such that he can start to look around for ongoing processes in which distal affordances are nested.

With more practice, attentional patterns continue to improve, tuning in on those affordances that are most likely to lead to scoring chances. An expert looks at the defence, but before that he has already looked at the opponent's defence line and the striker and midfielder's position—ongoing processes—and does not need to look at his feet. Looking around, what he sees are implicitly recognized as temporary moments within larger-scale processes in which affordances are nested. As such, when the professional comes into possession, he barely needs any time to act—he has drastically reduced the opportunities for action by looking continuously at relevant aspects of the unfolding situation. Prior experience thus narrows down the number of relevant affordances by means of an increased attunement to how affordances are nested and hang together.

The case for the raven is not quite unlike that of the right winger. We might think of a newborn individual as being guided by immediately available affordances, such as picking up things, hopping a few meters along, drilling food in the soil, and so on. These are the first affordances that a raven young might learn about, unresponsive to how these are nested within other processes, including the activities of other

ravens. The “state” of a “novice” is *not* knowing what to attend to and thus having too *many* opportunities for action. She has the food in her beak, for instance, and caching requires all her attention—looking, feeling, perhaps smelling and hearing too. Through experience she reduces the information required to respond to this affordance, only needing to *feel* what is going on, such that she can attend to other ongoing processes that are going on around her at the time of caching, thus becoming better at perceiving how affordances are nested. The affordance of re-caching is nested within her own activity of moving a few meters away from the other. Walking a few meters away makes the opportunity for caching available. Through practice, she learns that acting on this affordance (itself a process) makes other affordances available. She has learnt to play this and other roles. Again, this availability is contingent on other ongoing processes, such as what the other raven does in response to her moving away—as moving away for the pilferer is a process that makes the affordance of pilfering unavailable. Like the right winger, the raven must stay in touch with those processes as they change direction and make the affordance unavailable.

It is worth mentioning again that being responsive to distal affordances based on the affordances one is currently responding to, is quite unlike watching a movie and thinking “I’ve seen this movie before, I know what will happen next”. It is not deductive, and one doesn’t reach a conclusion that subsequently evokes a response. Instead, someone’s activities are continuously organized not only by the affordances that one can immediately act on, but by means of the distal affordances that such actions make available. As such, attending to relevant aspects of ongoing processes already presupposes acting in a certain way to be able to attend in a certain way. One’s current position is always already informed by what has been and is currently going on. So, the ongoing process organize the animal’s activity as much as his activity organizes what he attends to. It’s a continuous coordination, informed by prior experience, rather than a linear process as in the case of mindreading and behaviour-reading. Moving to another spot is responding continuously to affordances as they come and go, as the processes in which those affordances are nested—the activities of the other(s) in the situation—unfold.

Proponents of mindreading and behaviour-reading might object that, by focusing not just on the prediction of individual behaviour, social interaction is no longer the main subject. However, from an ecological perspective, subjects are often not as isolated as they are on cognitivist views: one of my points throughout this chapter has been that social cognition is not about predicting individual behaviour, but about learning to act in situations that involve others—that is, becoming responsive to affordances

nested within sociomaterial processes. Animals do not learn what other individuals will do by means of behavioural rules or mental states. They learn how they are regulated by and, more importantly, can regulate ongoing sociomaterial situations through action. Indeed, it is action in “socially constrained situations” (Gallagher & Vincent 2019)—that is, an animal’s actions in situations that include the actions of others that make certain possibilities for action temporarily (un)available for each other—that is vital in order to understand the “social skills” of animals, not inference.

Conclusion

In Section 1 I mentioned, echoing Barrett & Henzi (2005) and Barrett (2011) that an affordance-based approach avoids a bias towards species that intuitively resemble us (and that will therefore be inevitably viewed as precursors or otherwise lesser versions of ourselves) and, relatedly, that it allows us to understand the social skills of nonhuman animals free from our current understanding of how human cognition works.

We can now see that it does so by providing the necessary constraints for thinking about the social skills or sociocognitive abilities of animals, in the sense that “perception-action mechanisms constrain (in the sense of canalize) the evolution of high-level processes” (Barrett, Henzi & Rendall 2007, p.569; see also Osvath, Kabadayi & Jacobs 2014). What we call “social cognition” emerges dynamically and over time, out of the practices of animals with their abilities for perceiving and acting in their particular niches. Once such practices have become relatively stable in a population, affordances can become nested in them.

An example is case was how the interaction between pilferer and cacher in corvids can be described as interconnected processes—alongside several other processes—in which the affordance of re-caching is nested, and newborn individuals become attuned to and learn to play the role of such processes, thus learning how to make caching affordances available. It is thus the nested structure of the (sociomaterial) environment, that animals can rely on to know what to do given their goals. In other words, if we understand the sociomaterial processes within a population—processes that itself have emerged out of the situated practices of those individuals—and understand how individuals become organized by these processes, there is no need to postulate inferential processes.

Hence, the social skills of animals remain firmly tied to their biological constitution and ecological niche—there is no need for mental processes that operate largely

independently of such biological and ecological constraints. Indeed, evolutionarily speaking, such a close interrelation between organism and environment—with the animals using perception and action flexibly to act in a complex, changing environment which includes other living beings—makes more sense than the evolution of a mindreading or behaviour-reading capacity that is specifically dedicated to the problems of social life only (alongside other dedicated capacities for solving other problems).

If one accepts this approach, action and perception—or, perceptually controlled action—are fundamentally and constitutively important for complex social interaction, because by moving, and the world moving around them, animals become attuned to affordances and the processes in which affordances are nested. Action and exploration is often extremely limited in mindreading experiments, however, likely due to the implicit assumption that sociocognitive processes, in some sense, reside in the heads of individuals. This means that we fail to learn a great deal about the flexibility of their behaviour, the different things they would do given ongoing processes in the situation. Improving our understanding on this point, means that we ought to look not merely at whether animals pass or fail a test, but also to questions such as: what are they attending to—moving and perceiving—during re-caching? (cf. Barret, Henzi & Rendall 2007). How do their attentional skills change throughout development? Do they have different patterns of movement and attention in different environments or in the presence of different individuals? When do they refrain from caching and decide on a different course of action? We can also start to ask similar questions about other animals, gathering knowledge about important sociomaterial processes in their niches, how their skills develop during development and how their actions vary with changing circumstances. By focusing on action and perception in sociomaterial practices, we have a method to understand nonhuman animals free from our ideas about how we navigate social situations.

As a final note, the view I have defended here fits well within current research that aims to put mindreading or theory of mind back in context. Understanding others in terms of mental states, for instance, might only be possible if one inhabits an environment similar to humans (see Zawidski 2018; McGeer 2007; Andrews 2016a; Barrett 2011; Hutto & Myin 2017; Moyal-Sharrock 2019; Gallagher 2021). From this perspective, we can also start to understand why, where and when we use mindreading, as opposed to our more basic abilities to respond to nested affordances that we share with many nonhuman animals (Andrews 2011; 2016a). However, although these basic abilities may be shared in a general sense, they are also unique—specific to the sociomaterial processes that our niche consists of and our specific ways of perceiving and acting—just like they are for all other animals.



6

Ecologies of navigation

Abstract

Do animals require rich internal representations, such as cognitive maps, to navigate complex environments? Some researchers believe so, as they argue that sensory information is “too poor” to account for animals’ wayfinding abilities. However, this assumption is debatable, as James J. Gibson showed. Gibson proposed that wayfinding involves detecting information about environmental structure over time and used the concepts of “vistas” and “transitions” to explain terrestrial navigation. While these concepts may not apply universally to animal navigation, they highlight the importance of exploiting stable environmental structures for wayfinding. By searching for species-relative environmental structures, we gain insight into the navigational abilities of different nonhuman animals, while recognizing the unique evolutionary histories and ecological contexts that have shaped these abilities—and once again, refrain from gauging the abilities of nonhuman animals based on a spectrum of sophistication compared to humans.

Introduction

When an albatross lands on a nearby island, she exhibits a simple form of navigation known as beaconing. However, albatrosses also voyage great distances and return to their home island, demonstrating a more complex navigational ability. What constitutes the difference between these two behaviours and what factors contribute to the perceived complexity of the latter feat? A renowned group of animal cognition researchers have proposed an answer to this question: the perceived difference is due to *representational* complexity (Wiener et al. 2011). To compare the navigational abilities of various species, Wiener et al. (2011) present a “navigation toolkit”, which has four levels, ranging from low to high: the sensorimotor toolbox, spatial primitives, spatial constructs, and spatial symbols (unique to humans) (see fig. 9). Each higher level builds on tools of the lower level, and higher-level tools encode the world in increasingly *configurational* ways (Heft 2013).

The term “configurational” captures a core tenet of the representationalist perspective, as it views cognition as a process of isolating and internally representing aspects of the environment, and then linking and combining these to construct more complex representations.¹ Researchers who think of animals as configurational knowers believe that animals—or their brains—run internal manipulations over representations of the environment. Their brains may calculate distance based on visible landmarks, for instance. As configurational knowers, animals are “detached from the landscape and disembodied rather than being immersed in it” (Heft, 2013, p. 268). Moreover, when animals voyage beyond what they can currently see, hear, smell, or feel, representationalists seem to think of them as even more configurational, disembodied knowers.

Gibson & Gibson (1955; see also Gibson & Pick 2000) used the term “enrichment” to describe theories, such as Wiener et al.’s (2011) toolkit, that advocate increasing abstraction from the environment. Enrichment thinkers assume that the information provided by perceptual stimuli to the perceptual systems is too poor to explain complex feats of navigation or wayfinding.² Because the information is too poor, it needs to be internally enriched—supplemented by memories, expectations, concepts, and other representations—to make navigational feats higher on the ladder possible. Gibson (1979/2015) disagreed that the information is too poor, and introduced alternative

1. I’m paraphrasing E. J. Gibson & Pick (2000, p. 150) here, who strongly oppose this type of view.
2. Gibson used the term “wayfinding” for his theory, as do for instance Heft (2013) and Ingold (2000) who build on Gibson’s work. I use the terms “wayfinding” and “navigation” here interchangeably to make clear that this debate is about animal navigation, not something (slightly) different.

concepts for explaining navigation: most notably, “vistas” and “transitions”. He employed these concepts to show that, at least for earth-dwelling humans, perceived navigational complexity doesn’t necessarily entail enrichment and abstraction from the environment (see also Gibson & Pick 2000, p.10).

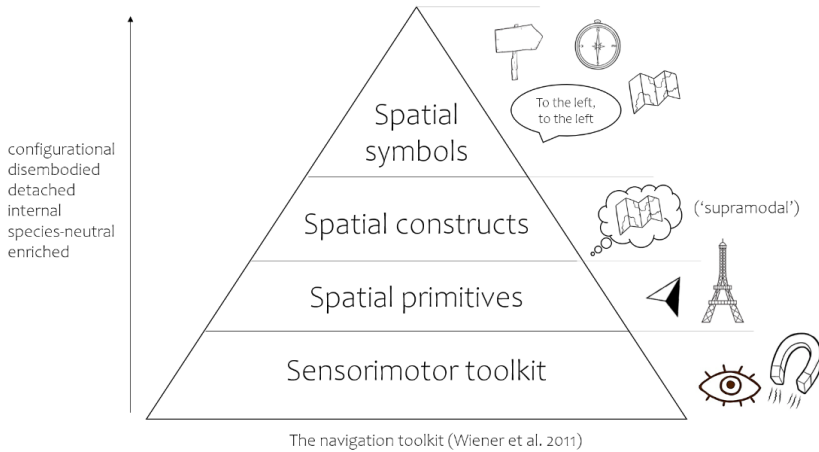


Figure 9. The navigation toolkit. The sensorimotor toolkit contains basic skills of sensing and acting, like visual perception and magnetoreception. The spatial primitives include tools like compass heading and landmarks. The spatial construct level lists, most prominently, cognitive maps. Spatial symbols are defined as uniquely human. This level includes wayfinding signage, actual maps, verbal directions and compasses. As perceived complexity increases, the tools that animals employ seem to become more and more detached from the specific action-perception systems of that animal.

Inspired by Gibson’s concepts, I will argue that we can better understand how nonhuman animals navigate by examining how they learn to perceive the environment’s nested structure over time. This alternative view ties navigational ability to the perceptual systems and environments of animals, even in cases of perceived complexity. As such, it fits better within an evolutionary perspective, or more specifically, the view that brains, and the cognition they support, evolved in tandem with a specific body to enable the control of action in dynamic ecological niches, rather than to harbour specific cognitive mechanisms or tools to solve the “problems” of navigation (see Barrett, Henzi & Barton 2022; Barrett, Henzi & Rendall 2007; see also Keijzer 2015).

I will first discuss, in more detail, the enrichment view: the view that animals utilize landmarks and relations between landmarks as a form of configurational knowledge (sect. 2). After offering some reasons to consider an alternative (sect. 3),

the remainder of the chapter will explore the view that animals learn to perceive their environment's nested structure over time. I start by introducing Gibson's concepts for terrestrial wayfinding (sect. 4). Then, I will discuss navigation over the oceans, to show that more dynamic features, such as winds and waves, provide stability and structure to a trained perceiver, and extract some general features of wayfinding—that is, not limited to terrestrial, vision-based navigation (sect. 5). After that, I discuss how albatrosses find their way around by relying on the oceanic scentscape (sect 6.) and how they are able to reach their destination without representing these destinations (sect. 7). I end with some general implications for research.

Navigation and enrichment

Animals, humans among them, employ various skills to navigate their environments. This includes beaconing, route following and path integration (Rescorla, 2018; Wiener et al. 2011). An animal that approaches a feature—say a tree—within the field of view by fixating on it, is beaconing. An organism that retraces a series of remembered turns is route-following—for instance, turning left when you meet the big oak tree and continuing straight ahead until you encounter the face-shaped rock. There's no need to know *that* you're on a particular route. Human beings can navigate familiar terrain while thinking about what to make for dinner. Path integration requires an organism to keep track of a starting position by monitoring distance and direction travelled. The organism could rely on a step-counting mechanism (e.g. desert ants, see Wittlinger et al., 2007), optic flow patterns, or something else. In the navigational toolkit, level-two elements, such as landmarks, compass heading and speed and acceleration monitors, enable these skills (Wiener et al. 2011).

Higher on in the toolkit we find cognitive maps. Rescorla (2019) calls the cognitive map the “most controversial one” of navigational strategies in the field of animal navigation (p.34) and obscurity about the representational nature of cognitive maps surely contributes to the controversy. The term “cognitive map” was originally introduced by Tolman (1948) and is generally described as a mental representation that encodes information about landmarks and geometric relations among landmarks, as well as one's own position, in an allocentric way. Rescorla (2019) distinguishes maps in the loose sense from maps in the strict sense (see also Rescorla 2009). Loosely understood, a cognitive map is a “mental representation that represents geometric aspects of the environment” in a metric (distances, angles), topological (connectedness and adjacency) or other way. In the strict sense, a cognitive map is a “mental representation that has the same basic representational properties and

mechanisms as ordinary concrete maps” (Rescorla 2019, p.35). Put differently, a strict cognitive map is isomorphic with a real map; it is spatially organized in one way or another. A loose cognitive map only encodes the same information. I will refer to the less demanding loose sense from now on. Wiener et al. (2011) place cognitive maps on the third level (spatial constructs).

The step from lower-level skills such as beaconing, route following and path integration, to higher ones such as cognitive maps, is significant. The lower feats rely on an *egocentric* perspective. Animals can beacon with their eyes, ears and noses. They can follow routes by sniffing, feeling, or calling out and listening. Path integration, say by means of step-counting or optic flow, is constrained by the types of bodies and senses animals have. In contrast, complex tools such as cognitive maps imply an *allocentric* perspective. An allocentric view is a view from above or rather from nowhere specifically, on which the organism represents its *own* location in relation to visible and out-of-sight landmarks. Animals (or their brains) need to perform a “coordinate transformation” to attain this perspective (Rescorla 2019). Some researchers believe that taking novel shortcuts requires coordinate transformation (Bingman 2011, p.41; see also O’Keefe & Nadel 1978).³ Relatedly, the ability to “move toward a destination without using familiar landmarks” after displacement (Putman 2021)—sometimes called “true navigation”—also requires extrapolation from sensory input and hence allocentric perspective-taking.⁴

With respect to cognitive maps, neuroscientists have also discovered several cells in the mammalian hippocampus that are correlated with navigation. Place cells respond to specific spatial locations (O’Keefe & Dostrovsky 1971); head direction cells fire when the mammal’s head is at certain angle with respect to an external reference direction (Taube 2007); grid cells respond to the local environment, forming a local grid covering that local environment (Hafting et al. 2005) and “Metric information ... can be extracted from the firing patterns” (Rescorla, p.37); and finally, regarding border cells, different cells fire when the organism is near different borders (Solstad et al. 2008). Some researchers hypothesize that these cells form the neural underpinnings

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3. Interestingly, Rescorla (2019) herself mentions that there’s also evidence that animals often do not use the shortest routes to return. This seems in line with the ecological approach, that predicts animals to normally follow meaningful routes (i.e. routes that pass through important resources) rather than the shortest routes (Heft 2013, see also section 3 and 4).
 4. A predominant theory for “true navigation” is the gradient hypothesis. Since animals are displaced outside their familiar range, they must extrapolate from what they know about environmental gradients, such as geomagnetic field gradients (Kishkinev et al. 2021) or odour gradients (Bingman 2011). Whether gradient sensing is sufficient as a mechanism for cognitive maps remains a topic of debate (see Lohmann, Lohmann & Putman 2007), but not one I will delve into here.

of a cognitive map, at least in what Rescorla (2019) calls the “loose” sense in that they encode configurational information.⁵

Further support for configurational knowledge seems to come from so-called displacement studies. In displacement studies, animals are relocated from familiar to unfamiliar territory. The big question is, can they return, and if so, how? Animals can't use familiar cues and so must put their cognitive machinery to work. Rescorla (2019) cites a study by Tsoar et al. (2011) done with Egyptian fruit bats. These bats were moved in a cloth bag 44 kilometres outside their normal flight range, and freed in a large crater (Tsoar et al. 2011). This procedure disabled path integration, beaconing and route-following. Despite initial disorientation, the bats could fly back to their home cave or a familiar feeding site.⁶ Rescorla (2019) concludes that the bats initially needed to orient, given the sensory input available, and then “computed a route to the goal. An explanation along these lines presupposes that bats have a large-scale representation of landmark locations” (p.36). Researchers have carried out displacement studies with many animals, including migratory birds (Thorup et al. 2007; Kashetsky, Avgar & Dukas 2021), pigeons (Wiltschko & Wiltschko 2017; Wallraff 2005), salmon (DeBose & Nevitt 2008; Hasler & Scholz 1983) and crocodiles (Read et al. 2007) with similar results.

The philosophical and empirical research discussed here, is conducted with the premise that organisms will “internalize” their knowledge of the environment. With experience, the structure of the inner world becomes more important and the structure of the outer world less so. Wiener et al. (2011) make no secret of this view. They believe comparative navigation research is most interesting on the levels of spatial primitives and spatial constructs—that's where functional similarities despite sensory differences can be discovered. They urge that “The challenge for the field [of animal navigation] as a whole is to understand the semantic structure of spatial representations in general, which ultimately entails understanding the behavioral and neural mechanisms by which semantic content is synthesized from sensory inputs, stored, and used to generate behavior” (Wiener et al. 2011, p.51) and that “the hallmark of navigational complexity is the synthesis of internal representations” (p.54). Rescorla (2019) even claims that “Numerous navigational phenomena are difficult or impossible to explain unless we

5. These discoveries are not sufficient to support the cognitive map hypothesis: an ecological approach turns the tables on this claim and says that the structure of the environment, through the animal's explorations, organizes the firing patterns of these neurons, rather than the other way around. However, an investigation of these findings is beyond the scope of this chapter (but see Bruineberg & Rietveld 2019; see also Hutto & Myin 2017).

6. Where they would fly to, depended on whether they were hungry or not.

posit cognitive maps in the loose sense. Animal navigation therefore provides strong evidence for a broadly representationalist approach to psychology” (p.42).

Against enrichment

Enrichment thinkers will be inclined to say that some of the extraordinary navigational achievements of animals simply can't be explained without positing cognitive maps or other configurational tools. In other words, complex navigation is “representation-hungry” (Clark & Toribio 1994). There are, however, at least three related reasons to consider an alternative. All have to do with neglecting the tight coupling between organisms and their environments.

Firstly, the attribution of cognitive maps to nonhuman animals might be anthropomorphic. Wiener et al. (2011) list “external maps, wayfinding signage and human language” on top, whereas on the subordinate level they list, amongst others, cognitive maps (p.53). They tacitly assume that possessing a cognitive map *underlies* map-making. Heft (2013) defends precisely the opposite view: the cultural invention and practice of map-making in humans have made it possible to think in a map-like fashion (see also Ingold 2000). That is, configurational knowledge—such as map-like thinking—develops within and is sustained by sociocultural practices. Collectively and over generations, humans have invented abstract concepts such as objective space, geometric relations and cardinal directions alongside cultural artefacts such as compasses, maps and satellite imagery. Such inventions make it possible—literally, with the aid of GPS⁷—to look at and reflect on landscapes allocentrically or “from above”.

These inventions, now routinely relied upon by humans, shape individual thinking about the environment during development and throughout life (Heft 2013, p.277, see also Henrich 2016, Ch.14). Since children naturally come to participate in social practices pervaded by these inventions, it becomes all too easy to think that map-like, allocentric thought is “natural”, a product of our evolutionary history. These practices have in a sense become “invisible” to us, and we fail to see how they have shaped and continue to shape map-like thought and allocentric perspective-taking. If Heft (2013) is right about the development of allocentric, map-like understanding, anthropomorphism⁸ looms: we apply a mode of thinking that emerges within a sociocultural niche, and

7. At the same time, using GPS can decrease sensitivity to environmental patterns (see Heft, Schwimmer & Edmunds 2021), decreasing the ability to learn specific routes.

8. Or what could better be called WEIRDocentrism: applying concepts employed by people in Western, educated, industrial, rich and democratic societies (Henrich 2020) to non-WEIRD beings.

which relies on skilful use of a range of technologies, to other animals who live in vastly different niches and don't use any of these technologies. In other words, endowing nonhuman animals with map-like thought would result from undue consideration of what our human environment contributes to our abilities.

Secondly, representational or enrichment-based frameworks of navigation devalue the unique bodies and varying niches of nonhuman animals. When perceived navigational complexity increases, on this type of account, the type of tools researcher credit animals with become *less species-specific* and *less environment-dependent*. Wiener et al. (2011) embrace these features rather explicitly, writing that we can think of cognitive maps and other spatial constructs as “being *supramodal* (i.e., independent of or “lying above” specific sensory modality” because they provide semantically [i.e. geometrically] equivalent information about space” (Wiener et al 2011, p.56). Even more, the authors suggest that supramodality makes meaningful comparisons among species possible. The notion of “supramodality”, however, overlooks the ecological and biological constraints that have shaped the perceptual systems of various animal species. From an evolutionary perspective, it is reasonable to assume that constraints on navigational abilities should continue to hold for “higher” cognitive processes, as they do for “lower” processes.

Thirdly, one of the key premises of enrichment thinking is that low-level sensory information is too impoverished to fully explain complex navigation and cognitive processes (Gibson & Gibson 1955; Gibson & Pick 2000). However, this assumption has been challenged by ecological psychologists (Gibson 1979/2015; Gibson & Pick 2000) and others who draw on their ideas (Kiverstein & Rietveld 2018; Van Dijk & Withagen 2016). These scholars argue that environmental information is typically rich and abundant, and animals must learn to detect, differentiate, and utilize the relevant patterns. In fact, the two earlier critiques of enrichment thinking follow logically from this fundamental assumption: when researchers underestimate environmental richness, they overlook the important contributions of the body and the environment to perception and cognition.

On land: vistas and transitions

Gibson (1979/2015) introduced alternative concepts for navigation with the aim of overcoming simple-complex dichotomies and enrichment-based arguments. He writes that “Neither is adequate. Wayfinding is surely not a sequence of turning responses conditioned to stimuli. But neither is it the consulting of an internal map of

the maze, for who is the internal perceiver to look at the map?” (p.189). As alternatives to these behaviourist and cognitivist concepts, he coined the complementary ecological terms *vista* and *transition*.

“A vista is what is seen from here, with the proviso that ‘here’ is not a point but an extended region”, writes Gibson (1979/2015, p.189). Vistas are not things we *look at*, but extended regions that we inhabit or that surround us and in which we look and move around and do things. He adds that “in a terrestrial environment of semienclosed places each vista is unique, unlike the featureless passageways of a maze. Each vista is thus its own “landmark” inasmuch as the habitat never duplicates itself” (Gibson 1979/2015, p.189). As an organism travels *through* a vista, a pattern of optic flow is generated that uniquely specifies a route.

As Gibson writes, vistas are almost always surrounded by environmental features that occlude extended views: a tall and wide building, a hill, a dense pack of trees—anything that (partially) occludes another vista. As an organism walks up to and then moves around, over or beneath an occluding feature, a new vista gradually reveals itself at the edge of the current vista that is gradually concealed. This optical boundary between the occluding surface and the occluded area is called the *occluding edge* (Gibson 1979/2015; Heft 1983; 2019, see also chapter 2). Gibson (1979/2015) referred to these between-vista changes, specified by occluding edges, as *transitions* (see also Heft 2013). Transitions “afford looking ahead”, as Heft puts it (Heft 1983, p.183; Heft 1996, p.112). They invite an animal to survey the upcoming area.

Crucially, transitions are reversible. The reversibility of transitions plays a critical role in providing navigational information to the organism. By being able to bring into view what has been left behind, and vice versa, the organism is able to accomplish wayfinding in terrestrial environments as a continuous sequence of vistas marked by transitions that uniquely specify a route to a specific destination. Heft (1983) demonstrated that transitions are particularly salient: participants who were shown a video of the transitions along a route were better at finding their way on the actual route afterward and were more confident about their decisions compared to those who were only exposed to a video of the vistas. What’s more, the achievements of the transition-only group were comparable—just slightly worse—to a third set of people who were shown a video of both the vistas and transitions. In addition, his experiments showed that participants became responsive to the order or sequence of the transitions.

An enrichment thinker may suggest that vistas and transitions could provide a *developmental basis* for cognitive maps or other complex representational tools. Tolman (1948), a self-proclaimed “purposive behaviourist” who introduced the concept of cognitive map (being unconvinced by stimulus-response theories of other behaviourists) held a position like this. He believed that cognitive maps are latent effects of extensive exploration, an idea that has taken hold in representationalist thought. This, however, would be a misreading of the ecological concepts. The *information* for animals are not *stimuli* for the sensory receptors, but *patterns* generated by an active and moving organism over time. Environmental patterns provide a wealth of information for wayfinding, but they often escape scrutiny because of a tendency towards enrichment.

At sea: wind, water and weather

Gibson (1979/2015) and followers were mostly concerned with vision-based navigation on land, but structure over time is also available, for instance, on the open oceans—and not only through vision but also by means of touch, for instance (e.g. brushing of the wind against the skin). In this section, I will discuss the well-known example of the Micronesian and Polynesian navigators of Oceania and their reliance on so-called *etak* segments. Through this example, I will develop some generic concepts for understanding animal navigation without invoking configurational knowledge. These concepts are intended to be broadly applicable while acknowledging the species-specific and niche-dependent aspects of navigation.

About the Polynesian and Micronesian navigators, Hutchins (1995) writes,

The world of the navigator, however, contains more than a set of tiny islands on an undifferentiated expanse of ocean. Deep below, the presence of submerged reefs changes the apparent color of the water. The surface of the sea undulates with swells born in distant weather systems, and the interaction of the swells with islands produces distinctive swell patterns in the vicinity of lands. Above the sea surface are the winds and weather patterns which govern the fate of sailors. Seabirds abound, especially in the vicinity of land. Finally, at night, there are the stars. (p.76)

Swell patterns, apparent colours, wind, weather and the whistling of birds; the environment provides much more support than apparent to an untrained eye, ear, nose, or what sense organ have you. Though Gibson (1979/2015) seems to restrict his analysis to land-bound navigation (which is cluttered with objects), wind, water,

weather, and so on, are also *features* of environments that mark the uniqueness of certain locations, and can be used to navigate. The navigational skills of Polynesian and Micronesian navigators, I admit, are tied up with culture and social learning. But the point here is that these navigators don't transcend their egocentric perspective. They aren't contemplating how the wind touches their cheeks. They don't need to "internalize" the information (i.e., stimuli) they gather over time to "construct" routes or maps. Instead, they learn to differentiate among formerly undifferentiated patterns or flows, to selectively attune to relevant patterns given their goals and the circumstances, and where, when and what to do and to attend to (Gibson 1979/2015; Gibson & Pick 2000; Szokolszky et al. 2019). That is, they know *how* to get around by generating or amplifying environmental patterns as they sail. Tim Ingold (2000) offers a precise and lively description of how we should imagine their voyages:

Throughout the voyage he [the seafarer] remains, apparently stationary, at the centre of a world that stretches around as far as the horizon, with the great dome of the heavens above. But as the journey proceeds the island of embarkation slips ever farther astern while the destination island draws ever closer. At the same time an island off to one side, selected as a point of reference for the voyage, is supposed to swing past the boat, falling as it does so under the rising or setting positions of a series of stars.

The voyager remains *apparently* stationary as the world—the stars, wave patterns, distant islands—flow by. The way the world flows by is, of course, partially generated by the voyager. Moving ahead, the world flows by not just any one way, but in a way that uniquely specifies the direction and path of travel. Again, the voyagers aren't pondering, measuring and calculating. They are coordinating their movements with environmental patterns. This perspective, as Ingold (2000) points out, makes sense of an otherwise puzzling fact: these voyagers rely on a reference point, called an *etak*, but the *etak* is usually invisible, if it exists at all:

The fact that the reference island (etak) is normally invisible below the horizon, and may not even exist at all, has been a source of puzzlement to many interpreters who—assuming that the mariner's task is to navigate from one spatial location to another—have proposed that the etak is used to obtain a locational fix. [...] Rather, pointing to the etak is the mariner's way of indicating where he is in terms of the temporal unfolding of the voyage as a whole [...] the Micronesian mariner remembers an inter-island voyage as a sequence of etak segments, each of which begins as the reference island falls under one particular star and ends as it falls under the next in line. (Ingold 2000, p.240)

As Ingold makes clear, the *etak* is not a landmark. An *etak* is part of a conglomeration, which may include “The flow of waves, wind, current and stars” (Ingold 2000, p.239). The voyagers keep specific patterns stable during specific legs of the voyage. An *etak* is a mnemonic device, factually summarizing “an immensely variegated terrain of comings and goings, which is continually taking shape around the traveller even as the latter’s movements contribute to its formation” (p.223). These patterns are inconspicuous to an untrained eye, but “For the experienced inhabitant of this region, the environment is sufficiently differentiated in stable ways to provide some structure” (Heft 2013 p.281). A seafarer may be prodded by a significant change in the patterning of waves and wind, anchor his gaze to another patch of the night sky and adjust course, sail in some direction for a while, until nudged by the next change.

This example of navigation at sea, I think, illustrates well that “stability” and “structure” don’t always entail concrete objects and surfaces (cf. Ingold 2011, p.117). As dominantly terrestrial navigators, humans are used to concrete objects (“landmarks”) as features for navigation. But winds come and go, and stars appear on the move throughout the night. Nonetheless, within movement, stability or invariance can be found. Waves, if you know where and how to look, flow by regularly even if not constantly and despite occasional perturbations, small and large. Currents, upwellings and downwellings, for instance, are continuously regenerated and sustained, but they are predictable and regular and hence provide stability and structure.

While specific conglomerations of wind and water flows follow each other reliably and provide structure, waves do not occlude other waves, nor do winds occlude other winds. Unlike in terrestrial navigation there are no occluding edges at sea and hence no transitions in the strict sense. Still, these navigators carve up their journeys in clear and distinguishable *etak* segments, and as one *etak* moves beneath the horizon the navigators gradually enter into the next *etak* segment. Obviously, learning to perceive these patterns and discover these structures asks for hands-on experience—but they are out there to be exploited, so to speak. I will adopt Ingold’s more general, less vision-based term “segment” to signal similarity, though not identity, with vistas, and for the same reason, use “shift” instead of “transition”. The *etak*-based navigational technique is just one example of wayfinding rooted in segments, shifts and sequences. It is a localized interpretation that is developed in response to distinct environmental patterns within a specific niche. These terms are equally valuable for comprehending nonhuman animal navigation from an organism-environment relational perspective.

Accordingly, I suggest the following way forward: if we wish to explain animal navigation without invoking configurational knowledge, we could focus on identifying (i) segments, which are specified by environmental patterns; (ii) shifts, which are the relatively larger changes *between* segments; and (iii) sequences, which are higher-order sequential patterns of segments and shifts. All of these environmental structures are detectable over time, and only over time. And while there may be substantial variation in segments and shifts depending on the coupling between the kind of animal (given its particular perceptual systems) and the structure of the environment, these concepts offer a general approach to address questions about complex feats of navigation without invoking configurational knowledge.

The segments, shifts and sequences of the scentscape

In this section, I will delve into the topic of olfactory navigation by albatrosses over the vast open oceans.⁹ Despite the seemingly unpredictable nature of this environment, we can observe unique segments, inter-segment shifts, and discernible structural information over time.¹⁰ I will use the case of the albatross to exemplify a broader point: that despite the apparent lack of structure, the environment offers a remarkable degree of stability and structure. Accordingly, discovering patterns and structure in unexpected places can help us develop a less human-centred understanding of how animals navigate their environments.

Albatrosses cover hundreds of kilometres over the oceans and *smell* the oceans to stay oriented. Initially, odour may seem to lack the structure that is required for navigation. Due to the dynamics of odour dispersal, the concentration of scents can be patchy and irregular, rather than forming smooth gradients (Nevitt, Losekoot & Weimerskirch, 2008, p.4576). The process of scent-based navigation for albatrosses is far more intricate than simply homing in on a loud sound, following a trail, or sensing a gradient. One of the odours that albatrosses rely on is referred to chemically

9. For good measure, wayfinding is likely to be a multisensory, situated endeavour, constrained by what information is available to specify environmental structure rather than by any specific sensory mechanism (see Cheng & Newcombe 2005; Heft 2013, p.287). Albatrosses may additionally exploit patterns of wind and water, other types of smells, and perhaps geomagnetism (Wynn et al. 2020) and infrasound (Patrick et al. 2021), but I will focus on smell here. See Stoffregen, Mantel & Bardy (2017) who are against individuating perceptual systems, and argue that we should consider the senses as *one perceptual system*.

10. Gibson (1966) wrote about smell, but mostly about odours directly emanating from a source, such as food, predators or mates—though he also mentions Hasler's work, if only in passing, on how salmon are able to find their way back to their natal stream by relying on their sense of smell (see e.g. Hasler & Scholz 1983).

as dimethyl sulphide (DMS) and smells fishy or sea-like to us. DMS is produced when zooplankton (such as krill, which albatrosses eat) graze on phytoplankton; phytoplankton excrete a chemical precursor of DMS which rapidly converts into DMS. As a consequence, areas with higher concentrations of phytoplankton have higher concentrations of DMS (see fig. 10).

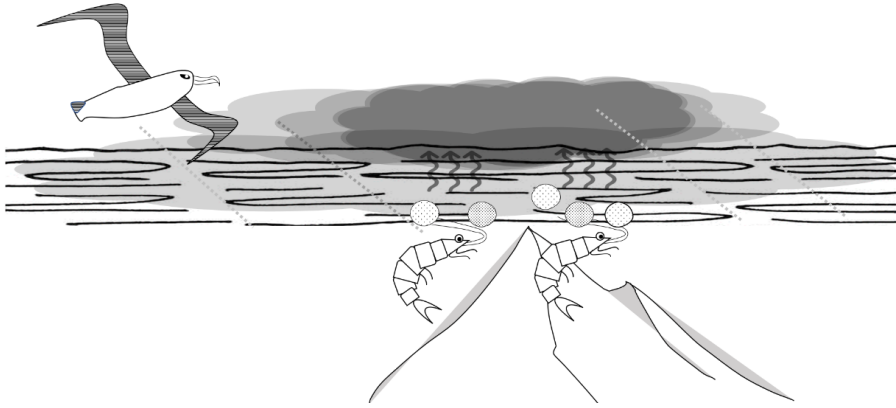


Figure 10. Segments and shifts in albatross navigation. On large spatial scales, concentrations of dimethyl sulfide (DMS) reflect seabed topography, providing structure and stability for navigation over the open oceans. The cloud signifies high concentrations of DMS: concentrations are higher at the location of the submerged mountain. The dotted lines signify a shift between a segment of relatively stable (low) scent levels, a segment of increase, a segment of relatively stable (high) scent levels, a segment of decrease, and another segment of relatively stable (low) scent levels.

Interestingly, researchers have found that DMS concentrations over large spatial scales—stretching thousands of square kilometres—vary with the topography of the seabed, and that concentrations are particularly high around seamounts, because seamounts create upwellings and currents that bring nutrients to the surface, which allow phytoplankton to grow. Hence, the ocean provides an odour structure that albatross can use to navigate (Nevitt 2008; Nevitt 2000; Nevitt & Bonadonna 2005).

To specify, albatross navigation (i) consist of segments, which are specified by environmental patterns. That is, each segment (“what can be smelled from here”) smells unique and moving through a segment generates a unique pattern of olfactory flow. The scent-based segments are similar to vistas in that they have different properties, such as varying levels of scent, whether these levels increase or decrease or are relatively constant, and how much they do. These segments—increase, decrease, constancy—are invariant structures within the constant flux of scent. Secondly, there are (ii) shifts, which are the relatively larger changes *between* segments. For instance,

a shift from “relatively constancy” to “major increase”, or from “major decrease” to “minor decrease”. These are not aptly called *transitions* for lack of occluding edges, but the environmental, olfactory structure is such that the scentscape is heterogenous and variegated, rather than homogenous and evenly distributed—hence, there will be relatively large, more drastic, olfactory changes, as compared to the smaller shifts one may find within a segment. These shifts too are higher-order invariant structures, as they are, effectively, larger changes in patterning within smaller changes in patterning, and so these too are only detectable over time. Thirdly, there are (iii) sequences, which are higher-order sequential patterns of segments and shifts. As in the case of terrestrial navigation by vision, albatrosses are able to find their way around through sequences of segments and shifts that uniquely specify the route to multiple destinations. Instead of unique paths specified by a series of vistas and transitions, however, knowing as an albatross where you are and where you are going, is a series of increments, decrements and relative constancy—for instance, minor increase – increase - constant(high) - slight decrease - constant(low) - increase—towards a distal resource.

My albatross example is meant to illustrate a general point: wayfinding is bound up with the perceptual systems and environmental niches of animals. To the extent that we can speak of “similarities”, we won’t find them in similar “internal” capacities, but rather in ways that animals exploit persistent environmental features. For instance, other species such as certain fish, harbour seals and whale sharks also exploit underwater structures by means of DMS (Nevitt 2008, p.1707)—even if segments and shifts for these animals may not map *exactly* onto each other, given differences in their perceptual systems. Compared to olfactory navigation over the oceans or visual navigation on land, navigating *in* water, *through* the air or *beneath* the surface—be it by touch, vision, hearing or any other perceptual system—will be different again; segments and shifts will be specified differently and uniquely depending on the organism-environment system under investigation.

Goal directedness without goal representation

Can the ecological view, which emphasizes the gradual uncovering of environmental structure over time, truly make cognitive maps and other configurational tools in nonhuman animals obsolete? One remaining question seems to be: wouldn’t animals need to know where they are going in advance, and does that not imply that they represent their destination? The possibility of goal-directedness without goal-representation is difficult to fathom within an enrichment paradigm. This

difficulty explains why even Nevitt (2008) speculates that albatrosses “build up a map of these [oceanic] features over time” (p.1707), despite the richness of information in oceanic structures that she has discovered.¹¹ The ecological approach renders configurational knowledge redundant by appealing to the *hierarchically nested structure* of the environment.

Gibson (1979/2015) wrote that, “for the terrestrial environment, there is no special proper unit in terms of which it can be analyzed once and for all. There are no atomic units of the world considered as an environment. Instead, there are subordinate and superordinate units.” (p.5) For instance, an apple is nested within a branch, which is nested within the tree, which is nested within the wider landscape, and so forth. We find this nested organization in navigation too, where “a particular series of vistas would be nested within some higher-order unit” (Heft 1996, p.118), as in figure 11: segment 1, 2 and 3 are nested within the superordinate “Path from Nest to Nearby Food Source”, segment 4, 5 and 6 are nested within the superordinate “Path from Nearby Food Source to Distal Food Source”, and these two superordinate units are nested again within the superordinate “Path from Nest to Distal Food Source”.

Path from Nest to Distal Food Source					
Path from Nest to Nearby Food Source			Path from Nearby Food Source to Distal Food Source		
Segment 1	Segment 2	Segment 3	Segment 4	Segment 5	Segment 6

Figure 11. Higher-order patterns in navigational activity. This table is an adaptation of one provided by Heft (1996).

The environment’s nested structure is reflected in the activity of organisms; activity can also be described as a “temporally-structured, hierarchically-nested event” (Heft 1996). For instance, a tree affords climbing, which affords reaching higher branches, which affords gathering apples, and hence when we stand in front of the tree we perceive the apples as “gatherable”—even if the apples are occluded by the surrounding leaves and you can’t directly see them. The activity of gathering the apple from the tree is temporally extended and hierarchically nested. The activities of walking to the tree, climbing it and picking the apple are activities for a particular organism that, with experience, have become nested within, and subordinate to,

11. As Heft (1996) writes, representational explanations may also be, in large measure, logically unnecessary after one has articulated a sufficiently rich description of the environmental information available to be perceived.

the superordinate activity of “gathering the apple”. In this example, activity is goal *directed* without goal *representation*. The activity is fully situated and embodied, and can be explained by referring to the nested structure of the environment.

Similarly, in the case of navigation, an animal may initially limit its search to a nearby food source. On subsequent journeys, the animal will venture farther. The environmental patterns, specifically the shifts, will come to offer opportunities for *further exploration* for that organism, in addition to the resources found within that segment. With experience, then, subordinate activities (e.g., locating the nearby food source) will have become nested within superordinate activities (e.g., finding the way to the distal food source). Similar to how a terrestrial animal can learn to perceive the occluded apple as gatherable, an albatross, for instance, can learn to perceive that plenty of fish are edible even if the albatross can't currently smell them (see also Van Dijk & Withagen 2016; Kiverstein & Rietveld 2018). What's more, since there's no proper unit of analysis, there's no principled limit to these abilities, as each superordinate activity (e.g., to the distal food source) can itself become subordinate (e.g., to the activity of finding an even more distal food source).

Here, again, activity is goal directed without goal representation. Animals are able to find their way by exploiting environmental structure. At no point do they need to combine isolated aspect of the environment and calculate their direction and distance to their destination *before they go* (i.e., configurational knowledge). Instead, nonhuman animals can gradually determine their destination *as they go along* (see Van Dijk & Rietveld 2018). They learn to perceive environmental structure over time and become attuned to segments and shifts *as they occur*. So, while animals can engage with affordances beyond what can be perceived through sight, smell, or touch in their immediate surroundings, this must not be thought of as representational, or as implying configurational knowledge.

Conclusion

Enrichment thinkers, such as Wiener et al. (2011), argue that as perceived navigational complexity increases, the organism becomes more and more detached from the environment. As far as their theories are concerned, the details of concrete situations that animals navigate *through* are barely relevant—what matters is whether there is *something* to see, hear, smell, or in more complex cases, calculate, visualize, think. In this chapter, I have offered an alternative for the hypothesis that navigational complexity should be accompanied by internal (representational) complexity. The

alternative, that animals become responsive to segments, shifts and sequences (i.e., information about environmental structure detectable over time) through processes of perceptual learning, avoids anthropomorphism (such as ascribing configurational knowledge) and respects biological and ecological constraints (by taking all navigational skills and tools to depend on transactions between an animal's perceptual systems and concrete ecological circumstances).

An ecological approach also yields implications for empirical research. The discovery of structures that animals rely on (i.e., segments, shifts and sequences), the emergence and persistence of environmental structure, and the streamlining of navigation with experience due to perceptual learning, are ecological phenomena that are foregrounded by an ecological approach. Such ecological circumstances are at least equally important as sensory mechanisms, since two animals of the same species in different environments may well use different perception-action strategies precisely because they have to rely on different environmental structures. An ecological approach also demands a sensitivity to scale (what could be a segment and shift for a desert ant?) and embodiment (how can the animal gauge the structure with its specific body and perceptual systems?). Moreover, investigating similarity (such as reliance on particular environmental structures, such as DMS in several marine creatures) and diversity (how these marine creatures may, because of their different bodies and ways of living, nonetheless be immersed in different segments and shifts) are equally important and valuable. These focus points follow naturally when wayfinding or navigation abilities are tied to, or constrained by, the perceptual systems of animals and the particular niches they occupy.

Finally, an ecological approach heightens awareness of the ecological relations that enable animal wayfinding (see also Van Dijk 2021b). As we saw, the ability of albatrosses to find their way around depends on what other creatures in that same environment are up to. Consequently, changes in the presence and activity of zooplankton related oceanic acidification due to increased CO₂ concentrations in the atmosphere, may eventually impact the structures that albatrosses depend on to navigate (Hammill et al. 2018). Not least because of its pragmatist roots, any ecological psychology that lives up to its name—being truly *ecological*—tries not only to understand isolated phenomena—such as how a particular animal finds its way around—but also how living and acting organisms, including us, are tangled up with each other in particular environments so as to enable and maintain, or disable and distort, these navigational abilities.



7

Toward an ecological comparative psychology

Summary

How can we understand and study the abilities of animals in *species-specific* ways, that is, without contrasting their abilities against preconceived notions of human abilities? Through the concept of anthropofabrication and three debates in comparative cognition, I have defended a less anthropocentric, more species-specific perspective by steering away from representation-hungry capacities allegedly “underlying” complex behaviour. Instead, I argued that we should see behaviours as organized processes involving active organisms within an intricate landscape of nested affordances. Saying that affordances are *nested*, means that what the immediate environment affords can't be separated from the “larger-scale” affordances the animal is enacting. Any activity that seems like a completed action is often part of a larger, ongoing sequence of actions.

In the prevailing anthropocentric framework in comparative cognition, researchers often apply cognitive concepts derived from human contexts to other species, without considering the validity of this move. This framework assumes a universal understanding of cognition, in terms of dedicated, representation-based capacities, placing human capacities at the apex. As a consequence, access to certain immediate affordances is typically restricted, while their ability to engage with nested affordances in species-specific ways is largely overlooked. This approach stems from a lack of historical perspective: overlooking how our abilities are shaped by our unique environments and bodies. As a result, we have ignored how the bodies and ecological niches of other animals have shaped and shape their abilities, too, resulting in *anthropofabrication*: we have made other animals *appear similar to us*, by selectively emphasizing similarities and disregarding differences, based on our current understanding of human abilities. The underlying assumption, then, is that animals *can have* the same abilities as we do—which isn't necessarily true, given that many of our human abilities are inseparable from our human-specific bodies and niches.

An ecological framework which acknowledges this inseparability, better fits the evolutionary concept that brains evolved alongside bodies within specific niches, collectively shaping cognitive abilities. Three case studies, examining episodic memory, social interaction, and navigation, shed light on behaviours often attributed to complex internal representations, by highlighting how these behaviours can be understood by considering how animals, given their abilities, can make use of nested affordances. The chapters, in their own ways, challenged the process of anthropofabrication and expanded the notion of nested affordances, advocating a

deeper appreciation for the complexity within environmental structures and the diverse ways animals adapt and develop skill for exploiting these structures over time. In short, the acts of remembering, social interaction, and navigation can be understood as the exploitation of higher-order affordances of animals' niches. What's more, these abilities are not something that animals possess or don't, but achievements they enact in concrete circumstances. This approach keeps animals' abilities constrained by biological factors (bodies and perceptual systems) and ecological ones (the environment they live in), significantly reducing the role and impact of our ideas about human cognition within comparative cognition.

Rather than presenting a one-size-fits-all model rooted in our questionable model of the human mind, an ecological approach is tailored to the particularities of each species while maintaining broad applicability across different contexts. In other words, this approach to psychology is not confined to a single species or environment but rather serves as a flexible lens through which researchers can explore and understand the diverse abilities exhibited across different species.

Key findings

Practically speaking, I have suggested an approach to study animals (including humans) in a comparative context: systematic variation of available affordances (and relations among affordances, i.e., how they are nested). This method directly follows from an ecological approach, as this approach doesn't allow for cognitive abilities to be "decoupled" from the environment. This method is exemplified, as mentioned, by Darwin's work on earthworms, who investigated the adept ways in which these worms would drag leaves down to plug their burrows. Even for the humble earthworm, he found, what leaves afford depends on the larger-scale activity of burrow-plugging behaviour, expressed in the ways they select particular leaves and grasp them in particular circumstances. That is, they select leaves of particular shapes and thickness depending on the shape and size of their burrows, and tend to drag them down at the pointed end to do so most effectively (Darwin 1881; Reed 1982).

In chapter 3, I described how researchers could, for example, establish a higher-order pattern between a specific olfactory or auditory event and the decay rate of wax worms, observe if the jay succeeds in the task, and collect where and how they move around. Later, the olfactory or auditory affordance could be removed, to see whether the animal will now *fail* to achieve the task, or *change* strategy. Understanding these abilities ecologically still demands controlling certain ecological factors, as this

ensures that animals truly rely on the created higher-order pattern established by researchers. Yet, this method sets aside the presumption that animals *could* solve tasks by employing specific “decoupled” capacities. Once this ability is confirmed, researchers can expand upon it by introducing more intricate or diverse patterns. This method unveils the environment that bears cognitive significance for the animal, that is, what affordances are relevant and available for the particular task confronting that animal.

Systematic variation of higher-order perceptual invariants is not an all-encompassing strategy, though. For instance, some navigational behaviours, where environmental structures sometimes only become apparent over very large spatial scales (see chapter 6), couldn't have been discovered by systematically varying available affordances. This is why ethological methods such as tracking (group) movement patterns, prolonged observational studies, playback experiments, studying environmental structure and many more methods should go hand-in-hand to study animals' reliance on nested affordances. Still, systematic variation stands as a promising alternative to the widely adopted Morgan's canon, even if I only sketched an outline of this method. By preventing abilities that are decoupled from the body and environment to enter theorizing and experiments, systematic variation effectively guards against anthropofabulation and anthropofabrication (see chapter 3).

A related finding is that an ecological approach prompts the development of a more pragmatic and species-specific interpretation of cognitive concepts. I've framed my discussions of animals using “traditional” mentalistic terms like “episodic memory”, “social cognition” (including “mindreading” and “behaviour-reading”), and “cognitive maps”. Perhaps some of these terms should be reserved for humans only. Reliance on cognitive maps is a case in point, as this ability may be entangled with our actual map-making practices. However, some mentalistic terms may serve as descriptive umbrella concepts, leaving room for variation within and between species. Take episodic memory. Instead of asking “does that jay *really* have episodic memory?” we may ask “How is that jay episodically remembering?”. The *how*-question can be answered by referring to the nested affordances jays are relying on.

Relatedly, within an ecological approach, abilities are defined in *species-specific* ways and tied to specific observable behaviours or tasks. In other words, we first need to understand how animals perceive the world; what their environment affords them. This can, in theory, be done without referring to the capacities of other species—and humans in particular. For instance, I have suggested that instead of starting from episodic or episodic-like memory, a jay may have a “worm-caching-and-recovery” and

a “peanut-caching-and-recovery” capacity. Given that the events of a worm decaying and a peanut decaying take place over very different timescales, they may attune an animal to different affordances—affordances that are useful to achieve these tasks (recall chapter 3).

The ecological approach defended here also impacts our ideas about “similarity” and “difference” regarding the cognitive capacities of humans and other species. That is, from an ecological viewpoint, we should distinguish between two levels of comparison: one concrete and local, the other more abstract and more global. To start with the first: we should study and chart similar sensitivity to relatively stable environmental features or events. Think about the oceanic scentscape (see chapter 6), but also solar and lunar cycles, humidity and temperature fluctuations, behaviour of other animals, and so on (see chapters 3 and 4), or particular places or settings (see chapter 5). From an ecological perspective, we should expect relatively stable environmental events to be used by a wider range of species. Comparing animals locally—that is, those sharing an environment—then, is initially more meaningful than comparing animals in very different habitats, as animals that inhabit a similar environment will be able to exploit similar environmental structures.

On a more abstract level, animals with elaborate perceptual systems in different environments may have something else in common: the ability to engage with affordances far removed in space and time, precisely because they have more elaborate perceptual systems. This is an important point from an evolutionary perspective. More elaborate perceptual systems make it possible to engage with more affordances, and more importantly, to exploit increasingly higher-order patterns or affordances. That is, the ability to recognize and distinguish among affordances also makes it possible for animals to perceive more *relations* among affordances, which can be experienced as affordances themselves (see Gibson & Pick 2000). However, if we’re making such a comparison across environments and perceptual systems—perhaps to say something about the “evolution of cognition” in general terms—it’s critical to remember that this “similarity” is of a rather abstract kind, not rooted in particular biological or ecological processes.

I have barely scratched the surface of the future of cross-species comparison, having primarily focused on the development of species-specific explanations of various behaviours. The key point is that similarity and difference, on an ecological view, are rooted in observable anatomical, behavioural and ecological features—more specifically, in the *relation* between organism’s abilities and environmental features.

Animals are similar not because they have similar “capacities”, but because they *can* and *do* use the environment in (partially) similar ways.

Finally, throughout this dissertation I have, even if indirectly, tried to reshape our image of human beings. Our abilities are unique, but not because we are more sophisticated or evolutionarily advanced; evolution is not hierarchical. What makes our abilities unique, must be understood in terms of organism-environment relations, just as the abilities of every other animal. Several ecologically minded authors have been doing this over the years. They have made great strides in explaining human abilities as the products of our niches, rather than in terms of evolved capacities (e.g. Reed 1996; Ingold 2006; Barrett 2011; Van Dijk & Rietveld 2020; Van Dijk & Myin 2022). In this sense, they portray us as animals in our unique ecological niches, and explain our abilities—including grand and unique ones such as building art installations—in human-specific ways. From the outside in, I have tried to contribute to this perspective, by showing what abilities we should *not* expect to find in nonhuman animals—such as map-like thinking, constructing a personal past and ascribing mental states—because these abilities are the product of our typical sociomaterial environments.

Discussion and future directions

The ecological approach that I have portrayed and defended is just a start, and there are a lot of areas, both empirical and philosophical, that demand attention. A first critical line of future research must be concerned with studying the nested affordances that animals exploit in various tasks. Examining different animals in different environments using this approach could validate the practical value of the systematic variation method and establish a more robust foundation, that could be used to further develop this method. There’s already a wealth of data that could be interpreted within an ecological framework (similar to what I did in my chapters). What’s more, the method must be integrated with other methods and tools to contribute to bridging the gap between different research fields. At least, I hope to have offered some initial tools to move forward with.

Potentially, the strategy of systematic variation could enhance the integration between experimental studies and observations in natural settings. Many experiments exclude specific variables to unveil animals’ capabilities, indicating that animals can function without certain resources. However, these experiments fail to demonstrate whether animals regularly employ these resources in their natural routines. By systematically

mapping higher-order affordances under controlled experimental conditions, we gain clearer insights into the affordances animals rely on in the wild—instead of assuming that their alleged “cognitive capacities” are transferable, like taking a Swiss army knife with you. Empirical work is required to test how well this works, and accordingly, to improve theorizing and develop the method.

Interdisciplinary effort is imperative to do so. We need collective efforts from various fields to bring depth and detail to the initial method. Besides philosophers, we require scientists well-versed in experimental methodology, experts in the perceptual abilities of diverse animals, alongside experts specializing in ecological structures. This includes comparative psychologists, biologists, and (sensory) ecologists. Despite the fact that I disagree with the assumptions of their experiments, studies such as those by Clayton and colleagues are valuable for all the data they have generated—and we do need more of such rich data sets of specific animals (see also Penn 2011), so that they can be analysed from an ecological perspective. They have taught us a lot about all the affordances jays can potentially do *without*. But of course, from an ecological perspective we still need to find out what affordances they *do* rely on. It would be extremely valuable to know as much about environmental structure in fields such as social interaction, remembering or future planning for various animals. This knowledge would give a rich source of information to start studying animals’ reliance on nested affordances in systematic ways—granted that we, too, have sufficient knowledge on the perceptual abilities and sensitivities of animals. These abilities and sensitivities often diverge significantly from or surpass our human abilities. We can’t simply assume that, because no (higher-order) affordances seem available *to us* in certain settings, that no affordances are available for the animals that we study.

Relatedly, given that an ecological approach favours local comparisons, we could let animals solve *actually similar* tasks, rather than tasks we *deem* different across widely different species. Besides jays, we could study rooks, magpies and nutcrackers on their “worm-caching-and-recovery” ability, for instance. I think we should not expect any *identity* here—in the sense of “these animals both have this capacity”—and defining what is “similar” may to some extent remain arbitrary. Then again, our classifications are “conceptual and classificatory, not causal and explanatory” (Danziger 2008, 175). Still, we can look at whether these closely related animals make use of similar environmental structures. Within this framework, we can and should also look at individual and inter-individual variation in the future.

Moreover, the topic of “similarity”, and the words we use to signal it, remains an enduring theme for discussion. I have made some suggestions in this regard, but

the debate is intricate. For instance, Andrews (2020b) worries that, “if we invent new words for nonhuman animals and keep old words for human beings, then we are going to introduce unnecessary problems when trying to draw comparisons between animals” (p.7). This tension has especially been discernible in chapters 4 and 5, with terms such as episodic-like memory, what-where-when memory, and mindreading and behaviour-reading. Even when we employ terms pragmatically or as umbrella terms, issues remain. What words *should* we use as umbrella concepts and apply across the board, and what words do we reserve for humans—and why? These questions demand ongoing attention.

We can and should also start to describe other behaviours from an ecological viewpoint. My focus was on memory, social interaction and navigation, but the concept of nested affordances also allows us to see feats such as nest-building, migration, camouflage, making burrows, web-making and much more from a fresh perspective. Such behaviours, on an ecological framework—like every other behaviour—are forms of expertise that involve perceptual learning and the exploitation of nested affordances. Taking an ecological perspective will help us to further understand those abilities in species-specific ways and to transcend the dichotomy between largely automatic or unconscious behaviour and human-like learning and capacities (see Buckner 2018).

Another line of research must be the development of conceptual links between ecological psychology and certain evolutionary theories. My approach suggests a theoretical perspective on the evolution of cognition in terms of the ability to engage with ever higher-order affordances (due to enlarged perceptual systems, intricately linked to enlarged nervous systems). It's this ability that could facilitate what we intuitively label “complex” cognition. This perspective on the evolution of cognition also provides a way to integrate neuroscience with evolution and ecological psychology (see e.g. Cisek 2019). Combining these fields better will, I think, be a major area of research in the near future, and is critical to further establishing the scope and power of ecological psychology as a comprehensive alternative to representationalism.

Finally, animals reminds us that there's a wealth of information out there beyond our human senses. There's a magnitude of ways that animals can use structure in their environment. Notwithstanding the massive impact of our social practices, material practices and cultural practices, we remain animals. We should start asking questions about humans from a nonhuman perspective. This is especially pertinent given that we don't always hold humans to the same standards as other animals. Put differently, we routinely favour “simpler”, association-based explanations for nonhuman animals

if we can conceive of them, but rarely apply the same rigid guidelines to humans—even if we still don't know a lot about humans.

However, it's those very social, material and cultural practices that may have “numbed”, or downplayed the emphasis on, our perceptual sensitivities: clocks and calendars, the language of past, present and future, the language of mental states, as well as pavement, signage, maps, GPS and shoes (see Heft 2013, Ingold 2004). On the other hand, we know that humans' sensory potential is larger than we commonly assume: to some extent at least, humans are able to echolocate (Thaler & Goodale 2016) have a much keener sense of smell than expected (Porter et al. 2007) and are majorly impacted by the sense of smell in various social interactions, even though this goes largely unnoticed (Barwich 2020), to mention a few. Relatedly, a lot of research is focused on WEIRD societies, and non-WEIRD societies don't necessarily employ mental state talk, geometry-based maps, or neat distinctions between past, present and future (Heft 2013). I think, in this regard, there are major opportunities to further shape our understanding of ourselves as animals and of our place in the animal kingdom.

It is undeniable that embracing the complexity of environmental structure and of animal's activities, including those of our own, makes the science of comparative cognition more challenging—and one could argue this places significant limitations on an ecological comparative psychology. However, the world in which animals live is inherently complex. The concept of nested affordances provides a framework to address this complexity, emphasizing observable relations between organisms and their environments. In addition, it provides a way to think of ourselves *as animals*. In doing so, we move closer to uncovering the abilities of animals, including us—removing ourselves from the centre of comparison. While this path may be more challenging, it is one that ultimately brings us closer to a deeper understanding of the intricacies of comparative cognition.



Appendices

Samenvatting (NL)

Summary (EN)

Acknowledgements

References

About the author

Samenvatting (NL)

Charles Darwin heeft mensen lang geleden van hun bevoorrechte status in het dierenrijk onttroond. Toch blijft onze kennis over dierlijke cognitie verbonden aan onze ideeën over menselijke cognitie. Een belangrijke reden hiervoor is dat we veronderstellen dat de ideeën die wij hebben over *menselijke* cognitie een neutrale basis vormen voor een systematische, hiërarchische manier om cognitie te begrijpen—en daarbij plaatsen we onze eigen capaciteiten bovenaan die hiërarchie. Om dit probleem op te lossen, is een nieuw kader met nieuwe conceptuele gereedschappen en methoden nodig. Deze moeten breed toepasbaar zijn en tegelijkertijd afgestemd op elke soort, losgekoppeld van onze vooropgezette ideeën over mensen. Maar hoe? Hoe kunnen we dieren begrijpen zonder de mens centraal te stellen?

In het huidige kader van de vergelijkende psychologie worden cognitieve vermogens gezien als geëvolueerde capaciteiten geworteld in de hersenen, slechts losjes verbonden met het lichaam en de omgeving—een beetje zoals een Zwitsers zakmes. De opkomst van moderne computers versterkte dit perspectief, waarbij denkprocessen werden vergeleken met de informatieverwerkingsoperaties van computers. Deze computermetafoor, inmiddels ook bekritiseerd als model voor menselijke cognitie, bracht een nieuwe reeks termen met zich mee, waaronder “input”, “output” en “informatieverwerking”. Toegepast op cognitie vernauwde deze woordenschat onze focus verder op de processen in de hersenen, waarbij de unieke en gevarieerde manieren waarop de lichamen en zintuigen van dieren (inclusief mensen) hun vermogens vormen, werden genegeerd.

Hoewel dit beeld oorspronkelijk ontwikkeld werd om de menselijke geest te begrijpen, werd het verondersteld “soort-neutraal” te zijn—van toepassing in het hele dierenrijk. Hierdoor ontstond het geloof in een systematische, hiërarchische benadering van het begrijpen van cognitie, waarbij een twijfelachtig beeld van menselijke capaciteiten werd gepositioneerd als maatstaf binnen de vergelijkende psychologie. Deze ontwikkelingen versterkten een antropocentrisch beeld van dieren, waarbij zij óf werden verheven tot dit problematische beeld van onszelf, óf werden afgeschilderd als inferieur aan onze vermeende vermogens.

In mijn proefschrift ontwikkel ik een ecologisch kader voor vergelijkende psychologie om deze problemen te overwinnen, waarbij ik drie vaardigheden bespreek: het opnieuw beleven van wat, waar en wanneer iets is gebeurd (episodisch geheugen), het begrijpen en voorspellen van de acties van anderen (*theory of mind*) en het vormen van een mentale kaart om in je omgeving te navigeren (cognitieve kaart). Binnen

dit kader zijn cognitieve vermogens geen hersenprocessen, maar slimme manieren waarop dieren gebruikmaken van patronen en regelmatigheden in hun omgeving.

Neem bijvoorbeeld de gaai, een kraaiachtige. Gaaien verstoppert verschillende voedingsmiddelen voor later gebruik tijdens schaarste. Studies tonen hun opmerkelijke vermogen aan om niet alleen te onthouden wat en waar ze hun voedsel verstoppert, maar ook wanneer ze dat deden. In een bekend experiment werden gaaien in een opstelling geplaatst waarin ze zowel meelwormen, een zeer gewilde maar ook zeer bederfelijke voedselbron, als minder gewenste maar langer houdbare pinda's konden verstoppert. Toen ze na zeven dagen hun voorraad mochten terughalen, vlogen de vogels meteen naar de pinda's, ondanks dat deze minder gewild waren als voedsel, en vermeden ze de bedorven meelwormen.

Sommige onderzoekers geloven dat de prestaties van de gaaien wijzen op een capaciteit voor episodisch geheugen, vergelijkbaar met dat van mensen. De onderzoekers komen tot deze conclusie door deze capaciteit eerst te definiëren op basis van hoe we geloven dat het bij mensen werkt. Vervolgens passen ze deze definitie aan om deze geschikt te maken voor niet-menselijke dieren. Deze aanpak leidt echter tot eindeloze discussies over hoe we hoe “episodisch geheugen” moeten definiëren en of dieren dit bezitten.

Mijn alternatieve verklaring is dat deze gaaien op slimme wijze leren om gebeurtenissen te verbinden, zoals een rottende worm met veranderingen in vochtigheid of temperatuur, en om effectief te vertrouwen op patronen in hun omgeving met hun scherpe zintuigen. Met andere woorden, “herinneren” is geen proces dat plaatsvindt in de hersenen, maar een verworven manier van handelen in een specifieke situatie. Afhankelijk van de taak, leren dieren waar en hoe te ruiken, luisteren of kijken, zonder dat ze nadenken “in hun hoofd”. We moeten dieren dus als een soort experts zien. Hun vaardigheden zijn vergelijkbaar met die van voetbalspelers, die bijvoorbeeld door veel oefening hebben geleerd om op het juiste moment en tempo een steekpass te geven tussen de verdedigers van de tegenstander. Door systematisch te variëren in het type en de duur van bepaalde gebeurtenissen in het leven van dieren, kunnen we erachter komen van welke patronen zij gebruik maken om bepaalde taken te volbrengen.

Dit ecologische kader sluit beter aan bij evolutionair gedachtegoed, met name met het idee dat hersenen samen met lichamen evolueren in specifieke omgevingen. Bovendien verankert dit kader het onderzoek naar cognitie in waarneembaar gedrag. Hierdoor biedt het een perspectief waarin de unieke lichamen van dieren, uitgerust

met unieke zintuigen en levend in specifieke omgevingen, hun cognitieve vermogens vormen—en onze intuïties over menselijke cognitie op afstand worden gehouden. En, door onszelf uit het middelpunt van de vergelijking te halen, krijgen we ook duidelijker zicht op onszelf en onze plaats binnen het dierenrijk.

Summary (EN)

Charles Darwin dethroned humans from their privileged status in the animal kingdom a long time ago. Yet, our understanding of animals remains tethered to our current ideas about human cognition. An important reason for this is that we assume that our ideas about human cognition provide a neutral basis for a systematic, hierarchical way of understanding cognition, with our capacities at the top. To alleviate this issue, a novel framework with new tools and methods is needed. These tools must be broadly applicable yet tailored to each species, detached from our preconceived notions about humans. But how? How can we understand animals on their own terms?

In the prevailing framework of comparative psychology, cognitive abilities are understood as evolved capacities rooted in the brain, only loosely linked to the body and the environment—rather like a Swiss army knife. The advent of modern computing further bolstered this perspective, likening thought processes to the information-processing operations of computers. This computer metaphor, now under pressure even as a model of the human mind, came with a new set of terms, including “input”, “output” and “information-processing”. Applied to cognition, this vocabulary further narrowed our focus on the processes *in* the brain, neglecting the unique and variegated ways the bodies and senses of animals (including humans) shape their abilities.

Originally developed to understand the human mind, this view of cognition was unquestionably assumed to be “species-neutral”, applicable across the animal kingdom. Consequently, it led to the belief in a singular, systematic, hierarchical approach to understanding cognition, positioning a questionable image of human capacities at the pinnacle within comparative psychology. These developments entrenched an anthropocentric view, either *boosting* them to this problematic view of ourselves, or portraying them as inferior to our alleged abilities.

In this dissertation, I develop an ecological framework for comparative psychology to overcome these problems, discussing three abilities: re-experiencing what, where and when something happened (episodic memory), understanding and predicting the actions of others (theory of mind) and building a mental map to navigate your environment (cognitive map). Within this framework, cognitive abilities are understood as brain processes. Instead, they indicate clever ways in which animals use the environment’s resources.

Take jays, a species of crow. They stash various foods for later use during scarcity. Studies reveal their remarkable ability to remember not only for what and where they hide their food, but also for when they did so. In a famous experiment, the birds were placed in a setup where they could cache both mealworms, a highly desired but also highly perishable food source, and less preferred but longer-lasting peanuts. When they were allowed to retrieve their stash after seven days, the birds immediately went for the peanuts, even though these were less favoured as food, and avoided the now spoiled mealworms.

Some researchers believe this behaviour indicates a capacity for episodic memory akin to that found in humans. They come to this conclusion by first defining this ability according to how we believe it works in humans. Then, they adjust this definition to make it fit for nonhuman animals. This approach sparks ongoing debates about how to define “episodic memory” and whether animals possess it, resulting in endless discussions.

In my view, these jays cleverly connect events, like a decaying worm and changes in humidity or temperature, effectively learning to rely on *patterns* in their environment with their keen senses. In other words, “remembering” is not a process taking place in the brain, but an acquired way of acting in a specific situation. Given the task at hand, they learn where to smell or listen or look, without the need to think. In this sense, animals are more like experts than they are like computers. Their skills are similar to those of soccer players, who through extensive practice have learnt to pass through defenders at just the right moment and pace. By systematically varying the available events, as well as for instance the length of these events, we can uncover the patterns animals utilize to accomplish specific tasks.

This ecological framework aligns more naturally with evolutionary thinking, in particular with the idea that brains evolve together with bodies in specific environments. Additionally, it grounds the examination of cognition in observable behaviour. As such, it offers a perspective on which the unique bodies of animals, equipped with unique senses, and occupying unique niches, constitute their cognitive abilities—keeping our intuitions about human cognition at bay. By removing ourselves from the centre of comparison, we also gain a clearer understanding of ourselves and of our place within the animal kingdom.

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About the author

Bas van Woerkum-Rooker completed his Research Master's in philosophy of mind at Radboud University in 2019, graduating *cum laude*. Since 2019, he has worked as a PhD candidate at Radboud University, within the Center for Cognition, Culture, and Language. His research, supported by the Netherlands Organization for Scientific Research (NWO), focuses on developing a less anthropocentric perspective on nonhuman animals. He spent time as a visiting researcher at Lund University (Lund, Sweden), Egenis Research Centre (Exeter, UK) and the Barrett-Henzi Lab (Lethbridge, Canada). Additionally, he taught several courses focusing on the philosophy of animal minds and presented his work to diverse audiences.

IN THE REALM of comparative cognition, researchers often seek specific cognitive abilities in other species without questioning the validity of such pursuits. Many of the abilities we explore in nonhuman animals stem from a view on human cognition that neglects the influence of our unique environments and bodies on our cognitive capacities. This framework not only centres on humans but also disregards how the bodies and environments of other animals shape their abilities. This dual oversight leads to “anthropofabrication”, the inclination to make animals appear similar to us by selectively emphasizing (allegedly) human-like features while disregarding species-specific variations.

Considering provocative debates on episodic memory, theory of mind and cognitive maps, Van Woerkum-Rooker introduces an approach that avoids anthropofabrication, by viewing abilities as skilful behaviours within an environment consisting of nested affordances—opportunities for action interconnected across multiple levels and in various ways.



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