Animal Cognition (2023) 26:1743–1750
https://doi.org/10.1007/s10071-023-01832-8

EDITORIAL

Basal cognition: shifting the center of gravity (again)

Pamela Lyon[1] · Ken Cheng[2]

Published online: 6 November 2023

Cognition: optional extra or biological necessity?

Readers of this journal are used to seeing diverse feats of cognition in animals. Growing evidence now suggests that cognition extends far beyond animals, arguably to all life (Lyon 2006, 2015, 2020; Scoles 2023). Learning about cognition outside of Animalia benefits those studying animal cognition. That is the chief reason for this collection of articles on basal cognition, although they take us well beyond the usual (and even unusual) suspects typically seen in these pages. The idea for the special issue was proposed in the meeting of this journal's editors in May 2022, and the idea was approved.

What do we mean by cognition? We endorse both Shettleworth's (2013) definition—that "*cognition* embraces all processes involved in acquiring, storing, and using information from the environment" (p. 1, italics in the original)—and the following expansion that adds functional and ecological dimensions:

> Cognition is comprised of sensory and other information-processing mechanisms an organism has for becoming familiar with, valuing, and interacting productively with features of its environment in order to meet existential needs, the most basic of which are survival/persistence, growth/thriving, and reproduction (Lyon 2020; p.416).

By both these definitions, all life engages in cognition. In fact, in considering how we might recognize extraterrestrial forms as being alive, Scoles (2023) names as one defining characteristic "Uses information about its environment to survive" (in a figure, p. 31)—cognition to us. (The other key characteristics can be called metabolism, homeostasis, and reproduction.) Life depends on processing information; cognition is part and parcel of life. Information cannot be processed unless there is an entity for which that stimulus or state of affairs makes a difference (Bateson 1979). It is hard to imagine how the internal conditions necessary for life can be kept without processing some information about the environment, including the internal environment of the body. Good illustrations of the diversity of cognition are provided by navigation (Cheng 2022) and the complex social behavior of bacteria (Liu et al. 2015b; Dinet et al. 2021).

Organisms from the bacterium *Escherichia coli* to single-celled eukaryotes such as *Paramecium* to small nematode worms such as *Caenorhabditis elegans* guide themselves to what are to them better places (Cheng 2022). They sense and process information from the environment, something that probably would not surprise any reader. Again, it is hard to imagine how an organism can choose to go to a better place without processing any information. These organisms all sense their chemical milieu, compare the current state with the state a moment before—hence requiring (at least) a short-term memory—and direct their actions based on the comparison.

Myxococcus xanthus is a predatory bacterium with a social lifestyle that often requires collective decisions (Dinet et al. 2021). The bacteria are motile and hunt together, and at other times aggregate to form fruiting bodies. Once more, it would be hard to imagine how such social coordination can come about without processing any information from the environment, which, of course, includes the social environment. In fact, Dinet and colleagues maintain that "signal integration, multi-modal sensing and memory are at the root of decision making leading to multicellular behaviour" (from the abstract, p. 1). All these ingredients are key components of cognition.

Whether the scientific community eventually adopts such a broad conception of cognition remains to be seen.

✉ Pamela Lyon
pamela.lyon64@gmail.com

✉ Ken Cheng
ken.cheng@mq.edu.au

1 Faculty of Arts, Business, Law and Economics, University of Adelaide, Adelaide, SA 5000, Australia

2 School of Natural Sciences, Macquarie University, Sydney, NSW 2109, Australia

Consensus remains elusive about what forms of life are cognitive and which are not. Such a state of affairs, concerning the identification criteria for a central concept in a science with a millennia-old pedigree, should be a matter of some embarrassment in the twenty-first century. As the readers of *Animal Cognition* would know too well, for most of recorded history, human beings have been the benchmark—indeed, the paradigm—of cognition, not just another species exhibiting a unique instantiation of a biological function (Lyon and Keijzer 2007). Nowadays, the field is much less parochial and much more ecumenical. It is, however, still dominated by a criterion bequeathed to us from Lamarck in the early nineteenth century: 'no mental function shall be ascribed to an organism for which the complexity of the nervous system of the organism is insufficient' (Bateson 1979; pp. 93–94).

We believe a rethink of this dogma is in order.

Rapidly accumulating evidence suggests that behavior mediated by what is readily regarded as cognition in humans and other mammals (to say nothing of bees, flies and nematodes) is found in more evolutionarily basal, aneural phyla as well. Moreover, a wide variety of mechanisms known to implement cognitive capacities in animals are also found to implement cognitive capacities in these earlier-appearing phyla (Lyon et al. 2021). These mechanisms include—in bacteria alone—network activity in chemical signal transduction pathways (Sourjik and Vorholt 2015), oscillations (Berleman et al. 2008; Baranwal et al. 2019), ion channel-mediated bioelectricity (Martinac et al. 2008; Prindle et al. 2015), oscillations coupled to servomechanisms (Cheng 2022), and hormone- or neurotransmitter-like molecular action-at-a-distance (Ham 2013). This basal cognition special collection, we hope, will be part of that 'rethinking' process.

What basal cognition is

Basal cognition, as an emerging field with a label, is very young. It was born 5 years ago under this name, in this form, at a workshop entitled "The Ground-floor of cognition: from microbes to plants and animals, and everything in between" (June 2018) at the Konrad Lorenz Institute (Klosterneuburg, Austria).[1] The idea was to put a diverse collection of scientists and philosophers from a range of disciplines and research areas in one room to see if there was common ground for a plausible research enterprise. The workshop participants included leading experts in their fields. The result was a special double issue of *Philosophical Transactions of the Royal Society B*, printed in March 2021.[2] The project was organized around a phrase that appeared in a short slide presentation at the workshop's end by one of the organizers (PL) about possible steps forward.

Basal cognition thus became the organizing principle for the proposal to Royal Society Publishing for a special issue. While that was marinating, Michael Levin, one of the guest editors and a prolific theoretician in this space, used the phrase in a published work,[3] which kicked off interest in the developing endeavor (Manicka and Levin 2019). Since then, the concept ("basal cognition") has appeared in the form we employ it in (depending on database) 43 articles (PubMed), 55 (Scopus), or upwards of 100 (Google Scholar). The introductory essay of the first *PhilTransB* issue, "Reframing cognition: getting down to biological basics" (Lyon et al. 2021), was one of the fortnightly journal's five top-cited articles for 2021 according to journal administrators. Google Scholar lists 112 citations of the article as at 1 November 2023, which is surprising for an enterprise that is barely recognized as a field.

That said, scientists have been 'doing' basal cognition since Anton van Leeuwenhoek looked through a magnifying lens at plaque scraped from his own teeth and spied "very little animalcules, very prettily a-moving," as he wrote to the Royal Society of London on 17 September 1683 (Grogan 2015; p. 86). Two centuries later, post-Darwin, the behavioral study of microbes began in earnest, even if scientists did not always have a name for what they were doing, and even if not all of them thought they were explicitly studying cognition, although a substantial proportion did (Binet 1890; Verworn 1889; Jennings 1904). An early US devotee captivated by solitary amoeba began her influential textbook on comparative psychology with those voracious, aquatic, single-celled shape-shifters (Washburn 1936). Behaviorism and limited imaging technology put a halt to this work as a domain of interest to psychology.

When cognition was readmitted to prominence in the US research circles in the second half of the twentieth century, however, the Cognitive Revolution's obsession with computers shoved biology to the margins of the cognitive sciences for decades (Lyon 2020). So, when the systematic study of bacterial chemotaxis began in the late 1960s (Adler 1966, 1969) and exploded with one fundamental discovery after

[1] The workshop was organized by longtime colleagues Pamela Lyon and Fred Keijzer.

[2] Vol 376, issue 1820, "Basal cognition: conceptual tools and the view from the single cell"; Vol 376, issue 1821, "Basal cognition: multicellularity, neurons and the cognitive lens".

[3] A Google Scholar search of "basal cognition" (06-09-23) turned up an earlier usage in the same domain by William B. Miller (2016) "Cognition, Information Fields and Hologenomic Entanglement: Evolution in Light and Shadow," *Biology* **5**, of which we were not aware (sorry, Bill!) and an unrelated usage denoting a cognitive baseline used in medical diagnosis.

another in the 1970s (Berg and Brown 1972; Macnab and Koshland 1972; Tsang et al. 1973; Tso and Adler 1974; Berg 1974, 1975; Adler and Tso 1974; Larsen et al. 1974; Spudich and Koshland 1975; Taylor and Koshland 1975; Koshland 1977), no one in cognitive science, as the multidisciplinary enterprise was coming to be known, was particularly interested. When bacteria were suggested as models for the study of behavior (Koshland 1980b), and even for investigating the action of neurons (Koshland 1980a), the suggestions fell on deaf ears.[4]

Nevertheless, scientists continued (and continue) doing basal cognition, because they continue(d) to study sensing, movement, memory, valence, learning, decision-making, and communication in single-celled organisms, plants, aneural animals, and those with simple nervous systems. Basal cognition, in short, is a *method*, *not a kind of cognition*; it involves nothing more exceptional than (re)applying the approach that has proved most successful in biology, in general, to the biological function of cognition, specifically. Biologically speaking, the approach is as ordinary as dirt: find the *simplest possible instantiation* to investigate the target process or capacity, *extract principles* from the findings to the extent possible, and then *scale up* to more complex organisms to test the principles.

Inspired by Darwin, the guiding aim of basal cognition as a knowledge enterprise is to connect, in the sciences of cognition, such dots as exist across the vast domain of life, from prokaryotes to humans, identifying both continuities and discontinuities (Lyon et al. 2021). The notion that there are dots to connect is based on the hypothesis—stunningly borne out by comparative genomics—that evolution is a hoarder as well as an innovator. Components and processes that work tend to be conserved. 'Basal' thus refers to the reference species (model organisms) enlisted in the study of cognition and its myriad facets. These include microbes (prokaryote and eukaryote), plants, animals without nervous systems, and animals with very simple nervous systems. In short, those evolutionarily earlier, or more basal forms on the bush of life.

About this issue

For this collection, we have invited leading authors in the field to produce reviews and perspectives on selected topics in the wider domain of comparative cognition. Authors were given a topic area with a mandate to make the piece comprehensible to those studying cognition in animals. They were not given free rein to write about any topic in their repertoire. What follows is a brief synopsis of what these valued colleagues agreed to.

First up is an edited version of a book chapter that should be a classic, from which (we believe) all who study animal cognition can learn: Chapter 2 of Peter Sterling and Simon Laughlin's *Principles of Neural Design* (2015, MIT Press). Also inspired by Darwin, Sterling and Laughlin undertook the unfashionable task of distilling principles from facts in the technique-driven, data-saturated domain of neuroscience, focusing on the metabolic (energetic) cost of information processing, calculations pioneered by Laughlin and colleagues (1998) and exemplified in Sterling's equally influential concept of allostasis, which refers to the physiological wear and tear sustained in response to and recovery from repeated stressors (Sterling 2004).

Sterling and Laughlin's starting point for deriving the organizing principles of brains are two brainless single-celled organisms, *Escherichia coli* and *Paramecium*, and the 302-neuron, highly distributed 'brain' of the nematode *Caenorhabditis elegans*. The book is an exemplar in how to connect the dots between simpler and (much) more complex organisms in a particular area. Here, they have generously agreed to republish an abridged version of their chapter—"Why an Animal Needs a Brain"—in which many of their principles are first described. It is instructive to compare how these 'simple' organisms, which in fact all show a great deal of complexity (hence the scare quotes), accomplish such life-enhancing tasks.

Reviews of cognition in two groups of unicellular organisms were invited, because one group, choanoflagellates, sheds light on the origins of animal cognition and the other, the plasmodial slime mold *Physarum polycephalum*, displays so much cognition. Choanoflagellates are a group of single-celled, occasionally facultatively multicellular organisms that are recognized as the sister group to animals (Brunet and King 2017). In the absence of anything currently akin to a unicellular Urmetazoan from which all animals arose, choanoflagellates provide a window into the cognitive evolution of animals. Núria Ros-Rocher and Thibaut Brunet (this issue) describe the *Umwelt*, the subjective perceptual world, of choanoflagellates, including chemosensation, photosensation, and mechanosensation—all building blocks of animal cognition.

The slime mold *Physarum polycephalum* (featured on the cover) is single-celled but multinucleated. It spreads over the forest floor and grows big enough to be visible. Chris Reid (this issue) provides a review of cognition in this organism, including its biology, sensation, communication, navigation, decision-making, memory, and learning. Much of its behavior and cognition is accomplished by shuttling cytoplasm back and forth. Reid reports on how such oscillations are used to generate *Physarum*'s suite of cognitive capacities.

[4] Exceptions included Karl Popper, the influential philosopher of science, and psychologist Donald Campbell, who each were working toward a version of evolutionary epistemology.

Hydra, an animal without a brain but with a very simple nerve net, is featured here, because (perhaps uniquely) it can shed direct light on what a nervous system contributes to the life of one organism in which it has evolved. *Hydra* is a small, tentacled freshwater cnidarian polyp (Holland 2011). Cnidaria, one of the five clades that constitute Animalia, also comprises sea anemones and corals, box jellyfish, and true jellyfish. These organisms do not possess centralized clumps of neural matter that can be called a brain but do possess a diffuse nerve net as a nervous system. Alison Hanson (this issue) reviews what is known about behavior in nerveless *Hydra* and compares these experimentally altered specimens to polyps with intact nervous systems.

Many animals rely on vision for behavior, and visual cognition has formed the theme of many articles in this journal. As already mentioned, the sister group to animals, choanoflagellates, displays photosensation (Ros-Rocher and Brunet, this issue). Photoreception and behavior generated by it are, however, found in a wider range of organisms than in animals and choanoflagellates. Emelie Brodrick and Gáspár Jékely (this issue) provide a review of photoreception across life. Brodrick and Jékely make a careful distinction between vision and nonvisual photoreception. They describe how even the nonvisual variety can be used to orchestrate a suite of useful behaviors.

All the sensing in the world comes to naught unless organisms can do something with the sensory information. For small beings, an important and challenging task—because the constraints of physics pose large obstacles for microbes moving in what to us would be heavy slush—is to move in a coordinated manner, sometimes for vital reasons such as escaping deadly environments. For coordinated movement, it would not surprise the reader that the effectors that do the moving, from flagella and archaella to cilia to limbs, must move in a coordinated manner and not flail about quasi-randomly. Kirsty Wan (this issue) reviews the use of locomotor apparatuses in microbes and argues that oscillations at multiple scales form a crucial theme in such tasks.

Finally, in a perspective written specifically for the *Animal Cognition* readership that brings together many strands of his multi-faceted work, Michael Levin (this issue) reviews the topic of bioelectricity. Bioelectricity is much used by animals. Introductory textbooks in biology and psychology tell us that our (animals') nervous-system functioning depends on electricity generated by the flow of ions. However, electric signaling is required for organisms that are much smaller in scale than multicellular animals. Calculations show that in single-celled eukaryotes such as well-studied *Paramecium*, a signal from one end of the organism traveling by chemical diffusion would take ~ 40 s to reach the other end (Sterling and Laughlin 2015, and this issue). This is far too slow for coordinating action. Diffusible molecules are also too slow, it turns out, for coordinating action-at-a-distance in a structured bacterial colony called a biofilm. At least in *Bacillus subtilis,* the prokaryotic reference species in which its functional deployment was discovered and continues to be studied, bioelectricity is necessary to carry out complex, existentially critical behaviors (Liu et al. 2015a; Süel et al. 2006; Dong-yeon et al. 2019; Martinez-Corral et al. 2018; Kikuchi et al. 2022). Levin makes a case for bioelectricity as the "cognitive glue" that turns physiology to mind, citing a "deep symmetry" between developmental processes and behavior-generating processes, for example, the navigation of morphospace in development and of physical space in behavior.

The basal cognition collection will continue in a later issue with a trio of related articles.

We thank the authors heartily for their efforts in the continuing campaign to shift the center of gravity in the sciences of cognition toward a more stable point of balance, which better accommodates the contribution to cognitive evolution of organisms that have been evolving longer—in some cases much, much longer—than the usual animal suspects. We hope that readers will relish the products of these researchers' exertions as much as we have, and, ideally, make use of them. Some readers may wish to dive in to the special collection at this point, but in the final section, we present a highlight package of what we mean by shifting the center of gravity in the cognitive sciences.

From computers (back) to animals: shifting the center of cognitive gravity in the 20th century

A shift in the center of gravity—a substantial change in direction of where research energies are focused, what constitutes useful sources of information and why—has happened in the cognitive sciences in living memory. We are all beneficiaries of the readmission of biology to cognitive science that took off in the last decade of the last century. *Animal Cognition* came into being 25 years ago this year due to this long overdue repositioning, critically necessary for making any kind of progress not only in understanding cognition but also in artificial intelligence (AI), then suffering through an intellectual winter of dashed hopes. This shift did not begin in 1991, but it arguably got its greatest boost in that year, judging from the outpouring of research that rapidly followed the article we will now discuss.

The article was "Intelligence without representation" (Brooks 1991).[5] The author, Rodney Brooks, was a leading light of the robotics subfield of AI—the driver of cognitive

[5] Google Scholar reports 8,199 citations as at 02 October 2023.

and computer science (whose fruits we are just beginning to grapple with now), and the article was published in the journal that then served as the industry bible. In it Brooks argues that progress in the cognitivist project had "foundered" on one of its central pillars: representation. Representations were (and are) conceived to be cognitive entities, somehow instantiated in the brain, that represent —'stand in for' (Bickhard 2001)—elements of the world. The idea is ancient and derives from the human introspective experience of memory and language. Computation was (and largely remains) king in the sciences of cognition; at the time representations were what computations were alleged to be carried out over. Brooks worked at the Massachusetts Institute of Technology (MIT), the heartland of cognitive science, AI and robotics, whose associated MIT Press was the leading publisher in the area, particularly via the Bradford Book series. A take-down of representation from someone of Brooks' stature not only was surprising and provocative but also seriously non-trivial.

Brooks' seminal paper had—typically with such cases—earlier precursors. The non-technical part of Brooks' argument relied, unusually, on evolution and biology. Although results from the study of human and other animal behavior often informed computer design that fed AI, the putative engine of cognitive scientific theory, philosophy, had little to do with organisms, biology (evolutionary and otherwise), animal ethology, ecology, comparative psychology, or the body for that matter.[6] Not surprisingly, all alternative approaches to cognitivism arose in what came to be known as 'embodied' perspectives. First, from the hotbed of early AI, came "Biology of cognition," Chilean neurobiologist Humberto R. Maturana's (1970) research report for Heinz von Foerster's Biological Computer Laboratory at the University of Illinois Urbana-Champaign. This report formed the basis of Maturana's ultimately paradigm-shifting construct of *autopoiesis*, a complex framework that simultaneously described the self-constructing (not merely self-maintaining) nature of biological organization and the critical role of cognition in that process. Developed in more detail in the coming years with his graduate student, Francisco Varela (Maturana and Varela 1973), today, the central tenet of autopoiesis (self-production) is unremarkably mainstream, even if the cognitive implications are not, much as Alan Turing's proposed test for machine intelligence was fundamental to cognitive science but not his concept of the mind being imitated (Turing 1950).[7]

Next, in *What Computers Can't Do* (Dreyfus 1972), Berkeley philosopher Hubert Dreyfus produced a searing phenomenological critique of AI, just as the field was beginning to experience stiff methodological headwinds. There followed over the next 14 years three books addressing fundamental issues in cognitive science generally and AI specifically based on biological and ecological considerations. Two focused on the psychology of perception, emphasizing the perceiving animal with a biological organization to sustain: William T. Power's perceptual control theory (Powers 1973) and James J. Gibson's influential affordance-based 'ecological' approach to vision (Gibson 1979). The third, arriving in the mid-1980s from within the field of AI itself, proposed a "new foundation" for computer design inspired by Maturana and Varela's theory of autopoiesis (Winograd and Flores 1986). Terry Winograd, who migrated to Stanford from MIT, was then a leading designer of computer programs for understanding natural language. All three books emphasized the importance of direct interaction between animal sensory systems, the environment from which the animal gathers information, and action taken based on that information. This interdependency of sensorium, environs, and behavior depended rather less on a database of existing knowledge (representations) for processing 'inputs' to produce correct 'outputs'; it depended crucially on iterative feedback loops engaging with the ongoing dynamics of action, changing organism needs, and evolved error-detection and correction mechanisms. This on-the-fly intelligence is sorely needed to complement, not replace, information processing with representations.

Then, in 1990, came three works that prepared the ground for what was to come. First was an unexpected blast of fresh air: *Intelligence as Adaptive Behavior: An experiment in computational neuroethology* (Beer 1990). The revised doctoral thesis of Randall Beer, a freshly minted PhD in computer science inspired by Maturana, Varela, Winograd and Brooks, the book was full of novel ideas about how cognitive science and AI might proceed. Beer, the series editor declared, "abandons" the traditional goal of AI (Beer 1990; no page number).[8] He does this by introducing, first,

[6] Notable exceptions include Fred Dretske, Ruth Garrett Millikan, and Mark Johnson.

[7] Turing, one of the greatest mathematicians of the twentieth century, found experiments in extrasensory perception convincing, despite statistical arguments against their validity, which raised questions about nonlocality no one (including Turing, apparently) wanted to address.

[8] The three pages of the Editor's Note that precedes the main text of Beer's book are not numbered. A note of caution: There is an egregious mistake in the Google Scholar entry about *Intelligence as Adaptive Behavior*, whose authorship is credited to the editor of the book series (B. Chandrasekaran) instead of Beer. The mistake appears to have been made by Google Books, which then carried over to Google Scholar. Consequently, the book does not appear on Beer's personal profile on Google Scholar, nor do the citations from it accrue to him. We alerted Beer to this problem, who told us he attempted to address this (to our minds, awful) mistake several years ago, but could never get through to a human being to satisfactorily deal with it. One of us (PL) owns a first edition of the book, which is why we know that the series editor has been credited with authorship by Google. Wikipedia, on the other hand, has it right.

a radically (in the sense of being at root) biological notion of intelligence and, second, "a particular methodology for the construction of autonomous agents" based on knowledge about simple nervous systems which required no representations. Beer is worth quoting at length, because he so lucidly reimagines the interdependent package of cognitive science, AI, and robotics along lines which, 33 years later, are taken utterly for granted in research traditions relating to both animal cognition and autonomous agents, computational and philosophical.

> Rather than focusing on the apparently uniquely human skills of language and logical reasoning, I wish to emphasize instead the more universal ability of animals to cope continuously with the complex, dynamic, unpredictable world in which they live. To me, this penchant for *adaptive behavior* is the essence of intelligence: the ability of an autonomous agent to flexibly adjust its behavioral repertoire to the moment-to-moment contingencies which arise in its interaction with its environment. Our higher cognitive functions are our own particular human elaborations of this more fundamental capability, and are deeply inseparable from it. (Beer 1990, pp. xv–xvi)

The other two books were produced by two highly regarded psychologists, one an unreconstructed computational-representationalist, C. Randy Gallistel, and the other a defector from the cognitive revolution, Jerome S. Bruner. In *The Organization of Learning* (Gallistel 1990), Gallistel introduces the sophisticated computations involved in how animals from insects to humans keep track of (represent) space, time, number and rate, connects these to animal memory and learning, and teases out implications for the cellular basis of memory. No work before this in the twentieth century, and vanishingly few following it, made such wide and deep use of experimental findings in zoology, biology, psychology, and neuroscience to theorize about how animals represent aspects of their environment and the computations required to put them to use in behavior. *Acts of Meaning* (Bruner 1990), a slim volume of rare influence,[9] begins with a history of the cognitive revolution, to which the author's early experimental work was a significant contributor, and describes how the information-processing view diverted attention from a key goal of psychology: understanding mind as a creator of meaning. Meaning, Bruner argues, depends to an irreducible extent on cultural narratives that shape human interactions, the social institutions that constrain them and constructions of the self.

Thus, by 1991, Brooks' message had already been rehearsed in different ways by different authors, in considerable detail. None of these researchers, however, had as much clout in cognitive science writ broad as Brooks. Therefore, when he said AI needed to move beyond abstract notions of representation to more biologically realistic models of computation, his views could not be brushed aside or challenged with the confidence of backing by the rest of the field. The key non-technical message of Brooks' influential article was simple: "problem solving behavior" is "pretty simple once the essence of being and reacting are available…This part of intelligence is where evolution has concentrated its time—it is much harder." (Brooks 1991, p. 141).

There followed in rapid succession a tsunami of influential publications supporting biologically based (embodied) cognitive science, beginning with *The Embodied Mind* (Varela et al. 1991; MIT Press), an audacious synthesis of Merleau-Ponty, autopoiesis theory, and Madyamaka Buddhist philosophy that gave its name to the embodied cognition movement, to which influential philosophical cognitive scientist Andy Clark (1997) provided a manifesto: *Being There: Putting brain, body and world together again*. In June 1992, MIT Press established the journal *Adaptive Behavior,* the first issue of which included an article by Beer. In 1993, York University in Toronto hosted a conference of leading experts to discuss *Reassessing the Cognitive Revolution*, the result of which was a generally downbeat collection of articles by major players (Johnson and Erneling 1997), which took in the dynamical-system challenge to cognitive science that unfolded in the intervening 4 years (Thelen and Smith 1994; Kelso 1995; Beer 1995; van Gelder 1995, 1998). In 1995, neuroscientist Antonio Damasio (1995) published *Descartes' Error,* which focused on the neglected topic of emotion which alluded to the importance of homeostasis to affect, for neither of which cognitive science then had much use.

Animal cognition finally, after making a solid beginning in the 1980s, emerged into the spotlight in a major way during the decade. Emory University primatologist Frans de Waal began his continuing series of books illuminating primate behavior in 1990 with *Peacemaking Among Primates* (de Waal 1990), followed by *Good Natured: The origins of right and wrong in humans and other animals* (de Waal 1996). A collection entitled *The Epigenesis of Mind: Essays on Biology and Cognition* (Carey and Gelman 1991) edited by psychologists Susan Carey and Rochel Gelman appeared in 1991. *Species of Mind* (Allen and Bekoff 1997) made the first direct appeal to cognitive scientists to consider animal ethology as a guide to understanding cognition. The following year, 1998, marked the debut of *Animal Cognition* and first edition of Sara Shettleworth's ground-breaking *Cognition, Evolution and Behavior* (Shettleworth 1998). The Comparative Cognition Society was officially founded in 1999, although the Comparative Cognition Conference (CO3) had been gathering

[9] 27,614 citations as at 01 November 2023 (Google Scholar).

since 1994. In short, within a decade the sciences of cognition and cognitive science had shifted dramatically to become what we now consider utterly normal.

The basal cognition approach is in its infancy. Randy Beer, who is still expanding the borders of the territory he pegged out 3 decades ago, has already incorporated basal cognition into his thinking (Beer 2023). There is no telling how the field will grow or which paths it will lead to. This collection will hopefully illuminate some of those paths. If history is anything to go by, we should be prepared for new insights and ways of thinking.

Acknowledgements The authors again thank heartily the authors who have contributed to the special collection on basal cognition to which this article is an introduction.

Author contributions PL and KC contributed to conceiving, writing, and revising this review.

Funding No funding supported the writing of this review.

Availability of data and materials This article contains no original data or materials.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval This review contains no original research, so that ethical approval does not apply.

References

Adler J (1966) Chemotaxis in bacteria. Science 153(3737):708–716

Adler J (1969) Chemoreceptors in bacteria. Science 166(3913):1588–1597

Adler J, Tso W-W (1974) ‘Decision’-making in bacteria: chemotactic response of *Escherichia coli* to conflicting stimuli. Science 184(4143):1292–1294

Allen C, Bekoff M (1997) Species of mind: the philosophy and biology of cognitive ethology. MIT Press/Bradford, Cambridge and London

Baranwal J, Lhospice S, Kanade M, Chakraborty S, Gade PR, Harne S, Herrou J, Mignot T, Gayathri P (2019) Allosteric regulation of a prokaryotic small ras-like GTPase contributes to cell polarity oscillations in bacterial motility. PLoS Biol 17(9):e3000459. https://doi.org/10.1371/journal.pbio.3000459

Bateson G (1979) Mind and nature: a necessary unity. E.P. Dutton, New York

Beer RD (1995) A dynamical systems perspective on agent-environment interaction. Artif Intell 72(1–2):173–215

Beer RD (2023) On the proper treatment of dynamics in cognitive science. Top Cogn Sci. https://doi.org/10.1111/tops.12686

Beer RD (1990) Intelligence as adaptive behavior: an experiment in computational neuroethology. Perspectives in artificial intelligence. Academic Press, San Diego

Berg HC (1974) Dynamic properties of bacterial flagellar motors. Nature 249(5452):77–79

Berg HC (1975) Chemotaxis in bacteria. Annu Rev Biophys Bioeng 4(1):119–136. https://doi.org/10.1146/annurev.bb.04.060175.001003

Berg HC, Brown DA (1972) Chemotaxis in *Escherichia coli* analysed by three-dimensional tracking. Nature 239:500–504

Berleman JE, Scott J, Chumley T, Kirby JR (2008) Predataxis behavior in *Myxococcus xanthus*. Proc Natl Acad Sci 105(44):17127–17132. https://doi.org/10.1073/pnas.0804387105

Bickhard MH (2001) Why children don’t have to solve the frame problems: cognitive representations are not encodings. Dev Rev 21:224–262

Binet A (1890) The psychic life of micro-organisms: a study in experimental psychology by Alfred Binet. Translated from the French by Thomas McCormack. Chicago, 1889. J Mental Sci 36(152):89–91. https://doi.org/10.1192/bjp.36.152.89

Brooks R (1991) Intelligence without representation. Artif Intell 47(1–3):139–159

Bruner JS (1990) Acts of meaning (Jerusalem-Harvard Lectures). Harvard University Press, Cambridge

Carey S, Gelman R (eds) (1991) The Epigenesis of Mind: Essays on biology and cognition. Erlbaum, Hillsdale

Cheng K (2022) Oscillators and servomechanisms in orientation and navigation, and sometimes in cognition. Proc Roy Soc B 289(1974):20220237

Clark A (1997) Being there: putting brain, body and World back together again. MIT Press/Bradford, Cambridge

Damasio AR (1995) Descartes’ error: emotion, reason and the human brain. Avon Books, New York

de Waal FBM (1990) Peacemaking among primates. Harvard University Press, Cambridge

de Waal FBM (1996) Good Natured: The origins of right and wrong in humans and other animals. Harvard University Press, Cambridge. https://doi.org/10.4159/9780674033177

Dinet C, Michelot A, Herrou J, Mignot T (2021) Linking single-cell decisions to collective behaviors in social bacteria. Philos Transact Royal Soc B Biol Sci. https://doi.org/10.1098/rstb.2019.0755

Dong-yeon DL, Galera-Laporta L, Bialecka-Fornal M, Moon EC, Shen Z, Briggs SP, Garcia-Ojalvo J, Süel GM (2019) Magnesium flux modulates ribosomes to increase bacterial survival. Cell 177(2):352-360.e313. https://doi.org/10.1016/j.cell.2019.01.042

Dreyfus HL (1972) What computers can’t do: a critique of artificial reason. Harper & Row, New York

Gallistel CR (1990) The Organization of Learning, vol 8. Learning, development and conceptual change. MIT Press/Bradford, Cambridge and London

Gibson JJ (1979) The ecological approach to visual perception. Houghton Mifflin, Dallas

Grogan D (2015) The microbes within. Sci Am 312(3):86–87. https://doi.org/10.1038/scientificamerican0315-S1

Ham JH (2013) Intercellular and intracellular signalling systems that globally control the expression of virulence genes in plant pathogenic bacteria. Mol Plant Pathol 14(3):308–322. https://doi.org/10.1111/mpp.12005

http://www.nature.com/nature/journal/v527/n7576/abs/nature15709.html#supplementary-information

Jennings HS (1904) Contributions to the study of the lower organisms, vol 16. Carnegie Institution of Washington, Washington

Johnson DM, Erneling CE (eds) (1997) The future of the cognitive revolution. Oxford University Press, New York and Oxford

Kelso JS (1995) Dynamic patterns: The self-organization of brain and behavior, hardback. MIT Press, Cambridge

Kikuchi K, Galera-Laporta L, Weatherwax C, Lam JY, Moon EC, Theodorakis EA, Garcia-Ojalvo J, Süel GM (2022) Electrochemical potential enables dormant spores to integrate environmental signals. Science 378(6615):43–49. https://doi.org/10.1126/science.abl7484

Koshland DE Jr (1977) A response regulator model in a simple sensory system. Science 196(4294):1055–1063
Koshland DE (1980a) Bacterial chemotaxis in relation to neurobiology. Annu Rev Neurosci 3(1):43–75. https://doi.org/10.1146/annurev.ne.03.030180.000355
Koshland DE, Jr (1980b) Bacterial chemotaxis as a model behavioral system. Distinguished lecture series of the society of general physiologists. Raven Press, New York
Larsen SH, Adler J, Gargus JJ, Hogg RW (1974) Chemomechanical coupling without ATP: the source of energy for motility and chemotaxis in bacteria. PNAS 71(4):1239–1243
Laughlin SB, de Ruyter van Steveninck RR, Anderson JC (1998) The metabolic cost of neural information. Nat Neurosci 1:36. https://doi.org/10.1038/236
Liu J, Prindle A, Humphries J, Gabalda-Sagarra M, Asally M, D-yD L, Ly S, Garcia-Ojalvo J, Süel GM (2015a) Metabolic co-dependence gives rise to collective oscillations within biofilms. Nature 523(7562):550–554. https://doi.org/10.1038/nature14660
Liu J, Prindle A, Humphries J, Gabalda-Sagarra M, Asally M, D-yD L, Ly S, Garcia-Ojalvo J, Süel GM (2015b) Metabolic codependence gives rise to collective oscillations within biofilms. Nature 523(7562):550–554. https://doi.org/10.1038/nature14660
Lyon P (2006) The biogenic approach to cognition. Cogn Process 7:11–29
Lyon P (2015) The cognitive cell: bacterial behavior reconsidered. Front Microbiol 6:264
Lyon P (2020) Of what is "minimal cognition" the half-baked version? Adapt Behav 28(6):407–424. https://doi.org/10.1177/1059712319871360
Lyon P, Keijzer F, Arendt D, Levin M (2021) Reframing cognition: getting down to biological basics. Philos Trans Royal Soc B Biol Sci. https://doi.org/10.1098/rstb.2019.0750
Lyon P, Keijzer FA (2007) The human stain: Why cognitivism can't tell us what cognition is and what it does. In: Wallace B, Ross A, Booth Davies J, Anderson T (Eds) The mind, the world, and the body: psychology after cognitivism. Imprint Academic, Throverton, UK, pp 132–185
Macnab RM, Koshland DE (1972) The gradient-sensing mechanism in bacterial chemotaxis. PNAS 69(9):2509–2512
Manicka S, Levin M (2019) The Cognitive Lens: a primer on conceptual tools for analysing information processing in developmental and regenerative morphogenesis. Philos Transact Royal Soc B Biol Sci 374:20180369
Martinac B, Saimi Y, Kung C (2008) Ion channels in microbes. Physiol Rev 88(4):1449–1490. https://doi.org/10.1152/physrev.00005.2008
Martinez-Corral R, Liu J, Süel GM, Garcia-Ojalvo J (2018) Bistable emergence of oscillations in growing *Bacillus subtilis* biofilms. Proc Natl Acad Sci 115(36):E8333–E8340. https://doi.org/10.1073/pnas.1805004115
Maturana HR, Varela FJ (1973) Autopoiesis: The Organization of the Living. In: Maturana HR, Varela FJ (Eds) Autopoiesis and Cognition: The Realization of the Living, vol 42. Boston Studies in the Philosophy of Science. D. Reidel Publishing Company, Dordrecht, pp 59–138
Maturana HR (1970) Biology of cognition. biological computer laboratory, department of electrical engineering, University of Illinois
Powers WT (1973) Behavior: The Control of Perception. Aldine de Gruyter, Chicago
Prindle A, Liu J, Asally M, Ly S, Garcia-Ojalvo J, Suel GM (2015) Ion channels enable electrical communication in bacterial communities. Nature 527(7576):59–63. https://doi.org/10.1038/nature15709
Scoles S (2023) Life AS WE DON'T KNOW IT: Scientists are abandoning conventional thinking to search for extraterrestrial creatures that bear little resemblance to Earthlings. Sci Am 328(2):32–39
Shettleworth SJ (1998) Cognition, evolution and behavior. Oxford University Press, New York and Oxford
Shettleworth SJ (2013) Fundamentals of comparative cognition. Oxford University Press, New York
Sourjik V, Vorholt JA (2015) Bacterial networks in cells and communities. J Mol Biol 427(23):3785–3792. https://doi.org/10.1016/j.jmb.2015.10.016
Spudich JL, Koshland DE (1975) Quantitation of the sensory response in bacterial chemotaxis. Proc Natl Acad Sci USA 72(2):710–713
Sterling P (2004) Principles of allostasis: optimal design, predictive regulation, pathophysiology and rational therapeutics. In: Schulkin J (Ed) Allostasis, Homeostasis, and the Costs of Adaptation. Cambridge University Press, New York
Süel GM, Garcia-Ojalvo J, Liberman LM, Elowitz MB (2006) An excitable gene regulatory circuit induces transient cellular differentiation. Nature 440:545–660. https://doi.org/10.1038/nature04588
Taylor BL, Koshland DE Jr (1975) Intrinsic and extrinsic light responses of *Salmonella typhimurium* and *Escherichia coli*. J Bacteriol 123(2):557–569
Thelen E, Smith LB (1994) A dynamic systems approach to the development of cognition and action. MIT Press, Cambridge MA
Tsang N, Macnab R, Koshland DE Jr (1973) Common mechanism for repellents and attractants in bacterial chemotaxis. Science 181(4094):60–63
Tso W-W, Adler J (1974) Negative chemotaxis in *Escherichia coli*. J Bacteriol 118(2):560–576
Turing AM (1950) Computing machinery and intelligence. Mind 59(236):433–460
van Gelder T (1995) What might cognition be, if not computation? J Philos XCI 7:345–381
van Gelder T (1998) The dynamical hypothesis in cognitive science. Behav Brain Sci 21:615–628
Varela FJ, Thompson E, Rosch E (1991) The embodied mind: cognitive science and human experience, 3rd edn. MIT Press, Cambridge
Verworn M (1889) Psycho-Physiologische Protisten-Studien: Experimentelle Untersuchungen. Verlag von Gustav Fischer, Jena
Washburn MF (1936) The animal mind: a text-book of comparative psychology. Animal behavior series. The MacMillan Company, New York
Winograd T, Flores F (1986) Understanding computers and cognition: a new foundation for design. Ablex Publishing Corporation, Norwood