see in animal populations spontaneously emerged (technically as a condition of stability or ESS), with a majority favoring one side and a minority — maintained by frequency-dependent selection — favoring the other side (as in the case of human left-handedness).

Do you have a scientific hero? Many. Some of them I have already mentioned here. But the most important is the man who first described filial imprinting, Douglas Spalding. His name is not very well known (certainly not as that of Konrad Lorenz). The reason is that he died very young. He initially studied in Aberdeen with the philosopher Alexander Bain. Then he did very original experiments in Ravenscroft, in the manor of Lord and Lady Amberley, while being the tutor of one of the couple's sons (their other son was Bertrand Russell). He dubbed filial imprinting as 'instinct imperfect'. His work was re-discovered when the biologist J.B.S. Haldane attracted attention to Spalding's studies and re-published them. Spalding can indeed be considered one of the fathers of ethology and for sure the father of the idea of making use of behavioral biology to investigate one of the oldest and most gangrenous problems of the philosophical tradition: the origin of our knowledge of the world.

If you had not made it as a scientist, what would you have become? Maybe a novelist. I do not know whether I have any talent for this actually, but I dream of writing a novel inspired by Douglas Spalding's life sooner or later. There is plenty of material on it. Spalding was sort of a romantic hero: suffering from tuberculosis, he traveled from England to the continent looking for a better climate, and he had a love affair with Lady Amberley. Before she and the Viscount Amberley died, the couple had asked Spalding to continue on in his role as tutor of both their children. However, once the grandparents discovered what had gone on in the home, they took the children away from him. Well, maybe after retirement… There are still lots of things to explore and a lot of fun to look forward to in science.

Center for Mind/Brain Sciences, University of Trento, Piazza della Manifattura 1, I-38068 Rovereto, Italy.
E-mail: giorgio.vallortigara@unitn.it

My Word

What is cognition?

Tim Bayne[1], David Brainard[2], Richard W. Byrne[3], Lars Chittka[4], Nicky Clayton[5], Cecilia Heyes[6], Jennifer Mather[7], Bence Ölveczky[8], Michael Shadlen[9], Thomas Suddendorf[10], and Barbara Webb[11]

cognition (n.)
mid-15c., *cognicioun*, "ability to comprehend, mental act or process of knowing", from Latin *cognoscere* "to get to know, recognize," from assimilated form of *com* "together" + *gnoscere* "to know" …

The etymology above (adapted from https://www.etymonline.com/word/cognition) shows that the word "cognition" has its origins in classical terms relating to the concept of knowing. A number of related contemporary English words have a similar etymology, for example recognise, cognizant, agnostic, and indeed knowledge itself, the "g" having morphed into a "k" in Germanic languages. The word seems straightforward, yet it is often a cause of debate in the psychological and neuroscience fields, particularly about whether a behaviour of an animal that happens not to be human is truly "cognitive", in a similar sense to human cognition. One example concerns the use by rooks of stones to raise the water level in a container so that they can reach a floating worm (see https://www.cell.com/current-biology/fulltext/S0960-9822(09)01455-9): to what extent does this ability mean the birds "know" about the displacement of water by sinking objects? Does it mean they are capable of complex, human-like cognition? Even more controversially, to what extent does it make sense to talk about "cognition" in the context of organisms that don't even have a nervous system, such as plants? And if one considers the flow of information between peripheral senses and motor output, does "cognition" apply only to certain abstract operations in between? And when it comes to psychiatric disorders like schizophrenia, how easy is it to define specifically cognitive impairments? The continuing arguments about these issues suggest a need for greater clarity and agreement on precisely what cognition means, and what is required to establish that a particular phenomenon is "cognitive". With this in mind we have invited a number of people from relevant fields of biology to write a short account of their understanding of the term "cognition", and their contributions are collected below.
Geoffrey North

Tim Bayne

School of Philosophical, Historical and International Studies, Monash University, Melbourne, VIC 3800, Australia

Definitions are tricky. Many of the most important and useful terms in science — 'gene', 'species', 'representation' — don't really have clear definitions, for the simple reason that they don't have single, stable, well-behaved meanings. Does 'cognition' have a single, stable, well-behaved meaning? That seems doubtful. Some definitions of 'cognition' may be better than others, but no single definition seems likely to cover all legitimate uses of the term. Arguably, any definition of 'cognition' must involve a certain amount of stipulation.

That said, the quest for a definition might still be illuminating. The key is to view it not as an attempt to say what 'cognition' means, but as an attempt to isolate the central and theoretically-interesting features that lie at the heart of cognitive phenomena. In my view, one of those features concerns concepts. Thinking, reasoning, perceiving, imagining, and remembering are cognitive processes to the extent that they involve the use of concepts.

Of course, invoking concepts doesn't get us very far unless we know what concepts are, and concepts are almost as tricky as definitions. I take concepts to have two crucial features [1,2]. First, they can be systematically recombined with each other. If Juliette has the concepts EAT, ME, WANT and LION, then she must be able to think both <The lion wants to eat me> and <I want to eat the lion>. Put it another way: if Juliette can represent a lion as wanting to eat her but cannot represent herself as wanting to eat the lion, then she doesn't really have the relevant concepts (and her mental states are not really cognitive).

Second, concepts are stimulus-independent. If Juliette's representation of a lion is triggered only when she is *en rapport* with lions, then it isn't a genuine concept. To have a fully-fledged concept of a lion, Juliette needs to be able to represent lions in their absence. This isn't to deny that concepts can be applied to perceptual objects. The point, rather, is that a creature must be able to 'decouple' the concepts that it deploys from its perceptual environment.

So, here's the proposal. The question of whether a particular state or process is cognitive can be understood in terms of whether it involves concepts; and that question can in turn be understood in terms of whether it involves representations that are systematically recombinable and stimulus-independent.

David H. Brainard

RRL Professor of Psychology, University of Pennsylvania, Philadelphia, PA 19104, USA

I approach the question of "what is cognition" from the perspective of someone who studies perception, where we try to disentangle "purely" perceptual from cognitive processes. Thus we seek to define and delineate the interface between perception and cognition, so that our measurements characterize the former without intrusion by the latter. Although this approach can be criticized — perhaps there is no such thing as pure perception — it nonetheless seems useful to consider how perceptual science has attempted to proceed along these lines. For current purposes, the premise is that understanding these attempts, and where they have been most promising, will inform a more general discussion of what constitutes cognition.

To elaborate, note that a central goal of perceptual science is to understand how things appear. We seek measurements and theory that quantify human perceptual experience, and to relate this experience to precise descriptions of the stimulus. In the case of vision, we start with the physics of light and how it reflects from objects to the eye, and seek accurate predictions of the perceived size, shape, color, material, and motion of the objects.

The challenge is that appearance is a subjective internal experience, private and potentially unique to each of us. Although most sighted subjects have an intuitive understanding of what it means to open our eyes and see, interposed between appearance and experimental data are cognitive processes, including memory and decision-making. If we are to study perception *per se*, we must find experimental methods that allow us to assess it independently of the effects of cognition.

One approach is to turn to objective psychophysical experiments that measure subjects' ability to (for example) distinguish between two stimuli. We call the methods objective because there is an objectively correct response on each experimental trial — the experimenter knows which stimulus was presented. By titrating the magnitude of the stimulus difference, these methods may be used to establish discrimination thresholds. The advantage of measuring thresholds is that there is mature and well-validated theory — the theory of signal detection [3] — that enables inferences about the perceptual representation of the stimuli in a manner insulated from effects of the subject's cognitive decision criteria. This line of inquiry also has the attractive features that the experiments may be designed so that subjects have little incentive to bring remembered knowledge to bear on their choices, that performance is often regular across subjects, and that performance can be linked to and understood in terms of the information processing performed by independently measurable visual mechanisms (for example, blur by the eye's optics, spatial and spectral sampling of the retinal image by the photoreceptors [4]). Moreover, the ideas may be generalized to supra-threshold stimulus differences [5]. In summary, objective psychophysical methods combined with theory that accounts for decisional processes provide a principled approach to separating perception from cognition.

The downside of objective approaches, at least for building theories of appearance, is that they are limited in what they can tell us: subjects are not asked about how things look. Thus, we also pursue subjective measurements, in which subjects scale, match, or null aspects of what they see (for example [6]). In cases where inferences obtained from objective methods account for reports of appearance obtained from subjective methods (for example [7,8]), our confidence that we are constructing well-constrained theories of perception, distinct from cognition, increases.

At the same time, there are limits to the success of the approach outlined above. As we move towards experiments with complex naturalistic stimuli, neither objective nor subjective techniques have yet proven entirely satisfactory. As stimulus complexity increases, the increase in dimensionality causes difficulties for using objective methods to make inferences about the underlying perceptual representations [9], results from subjective methods become more subject to individual variation as well as to differences in instructions provided to subjects [10], and the quality of the link between perceptual representations obtained using objective and subjective methods can break down [11]. Further work is needed to determine how to resolve these difficulties. Should they be taken as evidence that we cannot meaningfully separate perception from cognition? Or, can we improve our experiments and analysis in ways that allow us to generalize and sharpen our understanding of a reasonably defined interface between the two (for example [12])?

Richard W. Byrne

School of Psychology and Neuroscience, South Street, St Andrews, Fife KY16 9JP, UK

The term 'cognition' refers to all the activities and processes concerned with the acquisition, storage, retrieval and processing of information — regardless of whether these processes are explicit or conscious. This information-processing approach has dominated human experimental psychology for 50 years [13,14], following seminal advances in the 1950s [15–17]. More recently, cognition has arrived in behavioral biology, where it has sometimes been taken to be a hypothesis for how an animal solves a problem or organizes its behavior: to be tested against other hypotheses such as 'learning' or 'just lucky coincidence'. It is not. Anyone who asks "which animals are cognitive, and which are not?" or claims that their study species "solves the problem cognitively not by learning" is doomed to disappointment [18].

Taking the cognitive approach entails asking questions about what information is (in some way) *represented* by an individual: what it notices, remembers, and can perhaps compute with. So, a cognitive researcher might ask, successively, whether an animal can detect that among a group of conspecifics some are familiar; whether it distinguishes those familiar ones as individuals with differing implications for itself; whether its treatment of another is affected by remembering how it was received by them in the past; whether it can represent the possibility that the other is smart or completely misled. In contrast, a learning theory approach aims to treat these impostors just the same, relying more on rates of learning to account for differences in behavior and avoiding postulating any representations of knowledge in the brain of the animal. A clear example of the cognitive approach in biology, seldom labeled as such, comes from studies of navigation. Researchers have long investigated whether birds possess the mental equivalent of a compass, driven by observation of sun or stars, or a map, driven by geomagnetism: mental maps and compass bearings are representations of information that imply specific properties, the bread-and-butter of cognitive theorizing.

How representations are *coded* in the brain affects what can be done with the knowledge. For instance, if ‘cold’ is represented only as an aversive sensation, then learned avoidance of the circumstances linked to feeling cold can result; if it is represented as a point on a scale from very cold to very hot, then the possibility of moving up and down the scale (by exercise, huddling, fire, and so on) opens greater options. Error analysis is an important way of discovering the mental coding, used routinely in cognitive psychology but seldom in biology: again, bird navigation research is an exception.

The cognitive and learning-theory approaches are more like paradigms. Just as in physics it would be unhelpful to ask whether apples fall because of Newtonian or quantum mechanics and seek a critical experiment to tell us which, a test of whether behavior ‘is’ cognitive or learned will remain a mirage. Cognition is an approach to the scientific understanding of behavior which can and I believe should be adopted for all species, from invertebrates to humans [18]. But that is just my personal conviction, and I could be wrong. The cognitive approach may or may not be the best one for understanding the organization of behavior: only time will tell, not silver bullet tests.

Lars Chittka

Department of Psychology, School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK

Pioneers of the ‘cognitive revolution’ sought a contrast with the earlier trend of explaining behavioural flexibility largely in terms of associative learning processes; they made the study of mental processes — cognition — a focus of rigorous experimental psychology. More recently, the concept of cognition has been considerably broadened by some, to include, for example, “the mechanisms by which animals acquire, process, store, and act on information from the environment” [19]. Based on such all-inclusive definitions, some scholars discovered that by applying the term ‘cognition’ to any form of nifty biological problem solving, no matter if it is based on hardwired responses or mental processes, one can make fashionable claims about organisms’ intelligence, and pique the interest of prestigious journals’ editors. Claims of cognition in plants, or ‘distributed cognition’ in ant colonies, unfortunately extend beyond the metaphorical: they imply, in whispered tones, that some form of ‘thinking’ might occur in sessile organisms or distributed over groups of multiple individuals — when in fact the evidence simply shows some form of information processing.

Classical definitions of cognition typically revolve around concepts of knowing and thinking, and this implies some form of ‘offline processing’ — processing beyond neural activities that simply correlate with (or ‘represent’) sensory input. Cognition allows generating new information in a combinatorial manner from information acquired in separate events [20], or spontaneously through processes such as insight. To understand whether a particular case of problem solving qualifies as ‘cognitive’, it is essential to analyse animals’ behavioural strategies — for example, some visual spatial concept learning or counting tasks can be ‘hacked’ by animals structuring their sequential scanning strategies, and thus can be mastered without an ‘understanding’ of the concepts that experimenters see in such tasks [21,22]. However, cases where an animal is observed spontaneously to innovate new solutions to object manipulation tasks [23], or transfer shape information acquired in one sensory modality to another [24], do qualify as cognition. Likewise, attention-like processes show that animals know what they look for [25], and there is evidence that some animals ‘know what they know’ [26].

There is, however, no clear demarcation between sub-cognitive processes — for example, non-associative learning such as habituation, or classical conditioning — and cognitive operations. Nor is it clear that the former evolved first and the latter were added sequentially over evolutionary time according to complexity. The same neural circuits that mediate ‘simple’ associative learning can also underpin basic rule learning and non-trivial logical operations such as the XOR problem [27]. Understanding even the earliest animals as simple input–output devices is misguided: invariably, animals *actively* probe their environment. Even in the humble fruit fly, this may involve a variety of processes that in their sum can certainly be regarded as cognitive, such as prediction, attention, and intentionality, all processes that originate in the brain rather than solely with environmental stimuli [28]. For the concept of cognition to retain its exclusive meaning as ‘something more complex than associative learning’ it will be essential to quantify complexity in neural processing terms: for example, to demonstrate that cognitive operations require more sequential processing stages than problem-solving capacities that are regarded as simple.

Nicky Clayton

Department of Psychology, University of Cambridge, Downing Street, Cambridge, CB2 3EB, UK

To address the question of what we mean by the term ‘cognition’, we need not just to consider the etymology of the definition: ‘thinking’, ‘knowing’, ‘understanding’ and so on, but also to appreciate the history of the scientific fields within which these words have been used and interpreted. I shall consider two of these fields: comparative cognition and developmental cognition.

Comparative cognition typically focuses on two questions. The first is whether animals possess cognitive processes, such as flexible problem solving that can be transferred to new contexts, or whether their behaviour is better explained by non-cognitive processes, such as heuristic rules (core knowledge) and associative learning mechanisms. The second concerns how cognition evolves, in other words what are the selection pressures that might drive and shape these processes? And might these selection pressures result in the convergent evolution of cognition in distantly related species, such as corvids and apes [29], and/or independent evolution of cognition in distantly related species that may have undergone very different selection pressures, such as cephalopods [30]?

It is often argued that behaviours that appear to reflect complex cognition might actually be controlled by non-cognitive processes, but these need not necessarily be mutually exclusive. Consider the water displacement task, which corvids solve by dropping stones and other sinkable objects into a tube to raise the water level to obtain a food reward. A series of interventionist experiments suggest that a combination of cognitive and associative processes best accounts for the data [31]. Core knowledge may also play a part, as when subjects, be they naïve corvids or human infants, show surprise when a stone fits inside a tube smaller than itself in a violation of expectancy paradigm. Recent experiments show that corvids can infer the weight/density of objects by observing their movements in a breeze [32]. These are sorts of issues that researchers in comparative cognition consider in their evaluation of an understanding of 'cognition'.

Developmental psychologists assume the eventual presence of cognition in young children and therefore ask: "when does a particular aspect of cognition develop?", for example, mental time travel and theory of mind; and "how do the reasoning processes of young children differ from those of adults?", for example, young children fail to understand that their thought processes might differ in other times and other minds.

An integration of comparative and developmental cognition may advance our understanding of what we mean by cognition by questioning what it is that evolves and whether we find similar roadblocks in the way thinking develops in children and corvids. Young children show a surprisingly late developmental trajectory in solving the water displacement task, and this may be explained by the fact that, on critical test trials, it is an understanding of tool functionality and not prior reinforcement history of tool efficacy that guides their choices [33].

Cecilia Heyes

All Souls College, University of Oxford, Oxford, OX1 4AL, UK

Many philosophers and some scientists are cognition conservatives. When they say a psychological process is cognitive, they mean it's got something fundamental in common with cherished varieties of human thought. For conservatives a cognitive process involves reasoning. It operates on propositions (sentence-like mental representations), involves beliefs, desires and other intentional mental states, and is typically available to conscious awareness. Like most scientists, I'm now a cognition liberal [34]. When we say a process is cognitive, we mean that it handles information in an adaptive way and can be modelled usefully as a form of computation [35].

Both positions are legitimate and valuable in some contexts, but they also have key weaknesses. The conservative view has a venerable history in Western thought but it's out of kilter with contemporary scientific practice. It implies that much of the research done by those who identify as cognitive scientists — for example, work on the behaviour of plants, shoals of fish and swarms of bees — has nothing to do with cognition. The liberal view matches the labelling of people, departments and journals, but it is famously vague. What exactly is information, computation, representation?

Philosophers offer a variety of answers to these questions, and most cognitive scientists get along just fine without knowing them. That's probably because the concept of cognition isn't doing, and doesn't need to do, much scientific work. It's just a generic term for a bunch of phenomena that are more precisely defined — like learning, memory, perception, attention, categorisation and motor control. And each of *those* terms is a generic for a set of yet more precisely defined processes. It's important to tighten up as you drill down, but — like 'life', 'force' and 'species' — the job of 'cognition' is merely to gesture towards a domain of investigation [36].

To a first approximation, cognition is what is studied by cognitive scientists, just as life is what is studied by life scientists [37]. The legitimacy and value of extending cognition-talk to new domains depends on the productivity of the research programmes built around the extension [36].

In my experience, trouble arises only when liberals and conservatives get their wires crossed — when L-cognition gets confused with C-cognition. For example, rooks that drop stones in water to reach a floating worm [38] are undoubtedly using L-cognition — handling information in an adaptive way — but they're no more likely than rats that press levers for food pellets to be engaged in C-cognition. Either all reinforcement learning involves reasoning, an eccentric view [39], or the rook paper made it into a prestige journal because reinforcement learning, a variety of L-cognition, got confused with reasoning, C-cognition.

A familiar sort of moral looms: When we talk about cognition, we should be clear about whether we are being liberal or conservative. In the conservative case we should also say exactly what the agent is supposed to 'know' or 'understand', and why reasoning is a more likely explanation for their behaviour than another (cognitive) process.

Jennifer Mather

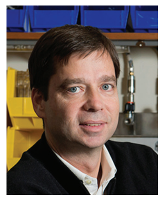
Department of Psychology, University of Lethbridge, Lethbridge, AB Canada T1K 3M4

Cognition in humans is defined as "all the processes by which the sensory input is transformed, reduced, elaborated, stored, recovered and used" [40], a very general definition that focuses on a series of operations. Such generality is necessary to encompass evaluation of many thoroughly different animals, but the study of cognition must also be filtered through our understanding of an animal's *umwelt* [41] or its sensory and action world. For octopuses, that means lateralized monocular vision of lens eyes and 60% of all neurons residing in the arms rather than the central brain. Does that mean cognition is differently 'embedded' in each nervous system? I take it for granted that these operations occur in a brain, and the octopus brain qualifies, being significantly larger than that of a mouse, with about 40 lobes and a vertical lobe similar in function to the mammalian frontal lobe [42].

What kinds of cognitive operations can octopuses perform? Such operations can be divided into categories: for example, *flexibility*, as in predation routines; *causal reasoning*, as in predator avoidance sequences; and *imagination*, as in play [43]. Most interesting for cognition is *prospection*, generating actions that would acquire information or items for a previously desired end. Octopuses, for example, perform a head bob to gain motion parallax information for their monocular view, send a passing cloud skin display to startle immobile prey, and even carry a split coconut shell out onto the sand to use later on as a shelter [44]. Yet there is a caveat to this ability: it has been suggested that octopuses do not monitor the performance of their many arms and their place in space within the brain. Perhaps they really have 'two brains' and the brachial plexus collectively carries on 'the autonomous performance of behavior' [45]. Would that mean cognitive operations were carried out differently than in vertebrates?

Why are there so many neurons and chains of ganglia in the arms? The octopus arm is controlled by a muscular hydrostat system [46], which theoretically gives an unlimited number of degrees of freedom of action. To achieve this, some muscles stiffen as temporary skeletons and others articulate against them, demanding a huge amount of local control and modulation. Walking is an excellent example of this flexibility — no central pattern generator produces an organized sequence of arm movements [47]. Yet the modal heading is 45 degrees left or right, controlled by the focus of one of the lateral eyes. Arm choice in a reaching task is also directed by monocular eye gaze [48], and arms can be visually directed in a similar reaching task [49]. Arms can be visually monitored, and information processed at a low level in all those local ganglia does not unite across the arms. What happens in the arm may usually stay in the arm.

This suggests that we do not have to make a radical difference in our definition of cognition to accommodate its production by different nervous systems. Acting within the bounds of their nervous systems structures and *umwelt*, different animals still converge on parallel cognitive operations.



Bence Ölveczky

Department of Organismic and Evolutionary Biology and the Center for Brain Science, Harvard University, Cambridge, MA 02138, USA

Whisking away a pesky fly doesn't require much introspection or deliberation; a simple sensorimotor reflex will do. A pivotal chess move, on the other hand, calls for complex information processing and access to memories and learned models of the world. These processes clearly lie at different ends of a spectrum, the principal axis of which we can call cognition.

So far so good. But 'cognition' also implies something categorical and well delineated, and here things get murkier. Over the past month I have been asking colleagues favoring the term to define it for me. Cognition, I have learned: "requires learning"; "isn't a reflex"; "depends on internally generated brain dynamics"; "needs access to stored models and relationships"; "relies on spatial maps", and so on. The lack of a clear consensus isn't very surprising. Mental activities, after all, make up a sprawling continuum that isn't easily parcellated and labeled. Yet, we keep using terms like cognition. Why?

Part of the reason may be historical inertia and human chauvinism. For a long time, we used 'cognition', 'intelligence' and 'consciousness' to contrast the human experience with those of other animals, justifying our superiority in the process. We humans, Descartes argued, are cognitive beings with thoughts and feelings. Animals, in contrast, are mere machines. Then Darwin comes and challenges this neat anthropocentric order, and suddenly we are all one big family with shared ancestry. Differences between the human and animal mind are, in his words, "one of degree and not of kind". Today, proposals to study 'cognition' and 'intelligence' in honeybees and octopuses receive serious consideration — a clear victory for Darwin. Describing animal behavior as 'cognitive' certainly rights a wrong, but it also further muddles the meaning of the term.

Archaic as this terminology may be, we neuroscientists have a really hard time letting go of it. It's imperfect, but it's what we have to manage, categorize, and compartmentalize the immense diversity of mental processes we deal with. It's part of the language we use to frame our research and generalize our findings. Our problem is that neural circuits do not implement 'cognition' or other vague concepts inherited from philosophy and psychology; they implement algorithms that need to be rigorously characterized and defined. After all, our understanding of the brain can only be as clear as the language we use to describe its underlying processes. Doing away with slippery and outdated terms like 'cognition' would force us to come up with a new vocabulary suited to delineate and specify what we are studying. It's not going to be easy, but it's a challenge we should seriously consider.

Michael N. Shadlen

Department of Neuroscience, Zuckerman Mind Brain Behavior Institute, Kavli Institute of Brain Science, Howard Hughes Medical Institute, Columbia University, New York, NY 10032, US

For neuroscience, a precise definition of *cognitive* is less essential than the recognition of its elemental features: flexibility, contingency and freedom from immediacy. We recognize these elements in behaviors that escape characterization as a reflexive, scripted program — even a complicated behavioral program. From an evolutionary perspective, these elements were essential for adapting to environments that were unanticipated by dedicated circuits for basic survival such as feeding, fleeing, courtship, and parenting. Neural processes that support cognitive functions are not beholden to moment-by-moment changes in the environment and they do not control the motor system in real time. This freedom from immediacy coupled with an elaborate association cortex is probably what gave rise to inchoate cognitive capacities, which when developed more fully, manifest in higher cognitive processes in humans.

The *inchoate* designation carries an important implication. We can study the neural mechanisms of the elemental cognitive features in simpler organisms by using contrived tasks that need not qualify as cognitive in their own right, but which permit the study of mechanisms that underly cognitive processes in humans. The neural mechanisms of decision-making, foraging, executive control and attention furnish examples. Depending on one's ultimate goal, one might desire biological insight about neural structures similar to those in humans. This would seem to require a mammal with a neocortex, at least, and an association cortex, but the study of homologous (and analogous) structures in model organisms confers other advantages. The choice of model system does not rest on whether the behavior is cognitive but on whether mechanistic insight into an elemental feature can be obtained and whether such insight might apply to the analogous element in human cognition.

Neuroscience is not the only path to understanding cognition. Cognitive psychology still dominates because it studies the real thing — not just elemental features. However, neuroscience is the discipline of choice if one wishes to gain insights about the biology. And if it is with the goal of ameliorating cognitive impairment in human patients, then an animal model with relevance to human biology — structure and function — is desirable. I suspect that the breakdown of cognition in a wide array of human disorders involves the elemental features and that we will target the neural mechanisms of these elements in our efforts to remedy dysfunction, even if the fundamental culprit is a gene or toxin of some sort. Such efforts will require reductionist investigations of the mammalian neocortex and its connections.

Thomas Suddendorf

School of Psychology, University of Queensland, Brisbane, Queensland 4072, Australia

In what is often regarded the founding book of cognitive psychology, Ulric Neisser [14] proclaimed: "*the term "cognition" refers to all the processes by which the sensory input is transformed, reduced, elaborated, stored, recovered, and used. It is concerned with these processes even when they operate in the absence of relevant stimulation*…" (p.6).

This is what I was taught. Cognition so broadly defined clearly did not evolve *de novo* in humans. Other organisms perceive, attend, evaluate, remember and expect. Natural selection favoured animals that can use incoming sensory information to predict dangers and opportunities; to escape threats and find resources. There is even evidence that some can think about matters in the absence of direct stimulation. We found that chimpanzees, for instance, can reason about hidden trajectories of a target [50] and make inferences by exclusion [51,52]. In this light, the question "*whether a behaviour of an animal that happens not to be human is truly "cognitive"*", is an odd one. Cognition is not uniquely human.

What a particular behaviour signifies, however, can be difficult to establish. Functionally similar behaviour, from communication to way finding, can be produced by different mechanisms in different animals. Indeed, even the very same behavior may be driven by distinct cognitive processes (e.g. I may pass a task because I understand, because I guessed correctly, or because I cheated). So careful studies are required to identify what capacities are involved.

Associative learning mechanisms are often considered "lean" alternatives that need to be ruled out to establish "richer" interpretations. But note that by the above definition associationism is cognitive too. Though there is debate about the role of associative processes in animal cognition [53], modern associative learning models encompass concepts such as *prediction errors* and phenomena that involve processing in the absence of relevant stimuli, such as *retrospective revaluation*.

The follow-up question *"Does it mean they are capable of complex, human-like cognition?"* requires specification of which aspect of multifaceted human cognition one is asking about. Evidence that certain animals engage in certain human-like cognitive processes need not mean they do engage in others. Cognitive psychology distinguishes intentional and unintentional, conscious and unconscious, effortful and automatic, slow and fast processes (for example [54]), and humans deploy these in diverse domains from foresight to communication, and from theory-of-mind to morality. To establish a particular cognitive capacity in another species we need careful observations and replications, as well as systematic experiments aimed at ruling out other cognitive processes (as well as chance) (for example [55]).

The ongoing to and fro between researchers advocating 'lean' and 'rich' interpretations of animal behaviors may look at times like a series of futile attempts at either securing human superiority or of dispelling human arrogance, but such exchanges can help us narrow down the facts of the matter. I suspect research in comparative cognition will establish more complex and diverse animal capacities than is widely assumed [56]. Nonetheless, given our peculiar position on the planet (e.g. our species comprises several times the biomass of all other wild terrestrial vertebrates combined), it should not surprise if it turns out humans are exploiting the *cognitive niche* [57] in unique ways. Though there may be very few underlying characteristics — perhaps only two — that transformed the cognitive capacities we share with other animals [58].

Barbara Webb

Institute for Perception, Action and Behaviour, School of Informatics, University of Edinburgh, 10 Crichton Street, Edinburgh EH8 9AB, UK

I know that I am cognizing, but I can only surmise that cognition has occurred in other animals by observing their actions. Yet almost any behaviour, however simple, can be viewed through a 'cognitive lens'; for example, when a bacterium is triggered to switch from swimming to tumbling by a change in a chemical gradient, it is sometimes described as 'decision making' [59]. Both intuitively and functionally, however, I believe it is better to reserve 'cognition' and associated terms for a smaller set of cases, for example, to behaviours in which an animal performs an action directed towards a goal it cannot currently perceive. This would exclude any behaviour to a goal stimulus that is actually present to the animal's senses, such as reflexes, taxis, or simple tracking (or evasion). By extension, it would exclude behaviour when the available stimulus is one that (innately) signals or substitutes for the goal, such as a cricket tracking a sound source to find a mate, or simple learned associations, such as avoiding an odour previously paired with shock.

It is worth noting that direct stimulus–action relationships can potentially produce quite complex behaviour. This point is beautifully illustrated by Braitenberg's 'Vehicles' [60], which imagines an agent with bilateral sensors connected to bilateral actuators, steering it towards or away from stimuli. If the input–output relationship is non-linear, multiple such control loops are interacting, and new sensors can become associated to existing responses, the agent's behaviour might appear to be considered and intelligent. So is there some amount of complexity in stimulus processing, integration or association that crosses the boundary into cognition?

I find it useful at this point to approach the issue from the mechanistic side, by drawing on a distinction often used in AI approaches to reinforcement, between 'model-free' and 'model-based' learning [61]. If behaviour is considered as a sequence of state-action-state transitions, an agent can learn through reinforcement an estimate of the long-term pay-off (with respect to its goals) for each possible action in a particular state. It can subsequently choose actions based purely on their stored value given the current state — it is then operating in a 'model-free' mode. Alternatively, it can explicitly learn about the state–action–state transitions it experiences, and hence choose actions by 'looking ahead' through alternative series of states and actions to find which sequence will ultimately lead to its goal — this is 'model-based' control (planning). Model-based control can provide more flexibility for an agent — for example, it can rapidly adjust to changes in the world that alter the state transitions, or to a change in its goals, rather than continue executing (by habit) actions in a particular state that are no longer effective — with an accompanying representational cost. In my view, this is the point at which we can really start to say the animal knows what it is doing. Cognition is the ability to use a model.

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E-mail: [1]timothy.bayne@monash.edu (T.B.), [2]brainard@psych.upenn.edu (D.B.), [3]rwb@st-andrews.ac.uk (R.W.B.), [4]l.chittka@qmul.ac.uk (L.C.), [5]nsc22@cam.ac.uk (N.C.), [6]cecilia.heyes@all-souls.ox.ac.uk (C.H.), [7]mather@uleth.ca (j.M.), [8]olveczky@fas.harvard.edu (B.Ö.), [9]shadlen@columbia.edu (M.S.), [10]t.suddendorf@psy.uq.edu.au (T.S.), [11]B.Webb@ed.ac.uk (B.W.)

Quick guide

Supergenes

Daniella Black and David M. Shuker*

What are supergenes? Supergenes are clusters of physically linked genes inherited as a single unit. Supergenes are often involved in the control of common complex phenotypes, such as body coloration or reproductive strategy (Figure 1). For alleles to stay together and co-segregate, recombination must be suppressed or absent within the supergene cluster.

How do supergenes come about? If alleles at two or more genes work together to produce an advantageous phenotype, whilst different allelic combinations at these loci are less advantageous, selection is expected to reduce recombination between these loci, keeping beneficial allelic combinations together. When this occurs, a supergene may be created. Some supergenes span large stretches of the chromosome and can include many hundreds of genes. The expansion of a supergene can occur when a further favourable allele arises near the original locus and is recruited to the supergene (under the increasing umbrella of reduced recombination).

How is recombination suppressed? Recombination among linked genes can be reduced in a number of ways: chromosomal inversions, the distance from the centromere and structural differences between homologous chromosomes can all influence recombination rates. In general, the closer a gene is located to the centromere, the lower is the recombination rate it will experience. The best studied recombination suppressors are chromosomal inversions. In these cases, suppression typically occurs via mechanical complications arising during crossover, followed by selection against recombinant inversion heterozygotes, which tend to have low fitness. For instance, inversion loops may form during recombination in an attempt to maximize base pairing, creating abnormal chromatids.

Aren't supergenes a bit old fashioned? The supergene concept does indeed have a long history, and in some cases hypotheses proposed almost a century ago have only recently been tested. Ronald Fisher first described a recognizable supergene concept (which he termed co-adapted gene complexes) in 1930, as part of the debate in evolutionary biology between gradualism and mutationism. Fisher hypothesized that the polymorphic wing-pattern of the butterfly *Papilio polytes* was under the control of a supergene (as opposed to the monogenic control hypothesis proposed by mutationists). Fisher's long-suspected prediction has only recently been shown to be true (Figure 1). Of course, the idea of a single locus controlling traits harkens back to the birth of Mendelian genetics, in contrast to the contemporary view that many traits are polygenic in nature.

Which traits are associated with supergenes? Complex balanced polymorphisms are the classic kind of trait controlled by supergenes. The lack of recombination allows the maintenance of more than one morph in a population, as a lack of recombination keeps the different forms of the supergene intact, while also preventing the production of low-fitness recombinants with a mix of alleles from different co-adapted gene complexes. The control of numerous such balanced polymorphisms has now been attributed to supergenes. For example, alongside the famous case of the wing patterns of *Papilio polytes*, the wing patterns of some *Heliconius* butterflies that form the basis of classic Müllerian mimicry rings are also controlled by sugergenes. Communication signals such as these often experience antagonistic selection pressures because of their simultaneous roles as signals to predators and conspecifics. Despite involvement in Müllerian mimicry rings, for which convergence of signals is thought to be advantageous, seven distinct colour morphs controlled by supergenes are maintained in populations of *Heliconius numata*. Each morph closely resembles an unpalatable butterfly species from the genus *Melinaea.* The supergene