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Cambridge University Press & Assessment
978-1-108-98705-9 — Biological Cognition
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1 Introduction

Cognitive scientists often note that neural networks *can be* organized to implement logical operations and execute logical functions. Some hypothesize that cognition is implemented directly by parallel processing algorithms that modify the connection weights within neural networks. Others claim that cognition is a matter of implicit symbol manipulation that exploits inferential operations that are implemented by neural logic gates. Each of these approaches has advanced our collective understanding of cognition and experience. But there is an approach to biological cognition that is less familiar and that highlights the diverse range of processes that are employed as animals navigate *biological and social challenges* to *preserve viability.*

Preserving viability often requires locating nutritional resources and remembering where they can be found, while avoiding predation and pursuing social support. These forms of cognition always unfold against the backdrop of metabolic demands that must be managed for an animal to survive and flourish. In complex and dangerous environments, this will often require tracking the likelihood of various risks and threats; an animal's sensitivity to these risks and threats will often be shaped by everything from the consequences of managing recent challenges to their histories of past trauma. Just as importantly, the demands that arise in contexts like breeding, pregnancy, and lactation, as well as the management of hunger and thirst, can shift the features of the world that are most salient to an animal. So, a plausible story about cognition must explain how animals are able to respond to sustained patterns of resource availability, adjust their behavior in light of current and anticipated needs, and manage fluctuations in bodily, ecological, and social variables.

There is no doubt that such capacities are organized by nervous systems in all mobile animals. But a precise and general account of the biological processes that sustain adaptive behavior has proven elusive. There are observable regularities in neural processes that are modulated by various chemical systems. But adjustments to one process often evoke changes in other processes as animals respond to biological challenges, prioritize physiological and social needs, weigh opportunities, and establish efficient trade-offs between diverse behavioral and cognitive strategies. Consequently, a biological approach to cognition must move beyond simplified forms of functionalism that attempt to establish the neurally based causal relations that instantiate familiar categories like beliefs, desires, and thoughts in two ways: (1) it must provide a characterization of the ecological and physiological constraints that organize *strategies for managing specific challenges and opportunities*; and (2) it must highlight the embodied strategies that animals internalize as they learn to manage predictable and unpredictable changes in access to things like food, water, minerals, and social support. Critically, this preserves a commitment to an empirically grounded form of functionalism, according to which the neural, chemical, and ecological phenomena that constitute animal minds are to be understood in terms of the causal roles that they play in guiding thought and behavior, as well as producing experiences of various challenges and opportunities.

Given these considerations, we will not defend an approach to cognition that is grounded in commonsense- or folk-psychology in this Element. Nor will we develop a priori claims about the nature of the mind. Instead, we will pursue a naturalistic approach to biological cognition that preserves a tight connection to data and methods from the cognitive and biological sciences. In this respect, our approach diverges from recent defenses of philosophical empiricism that have garnered support from results in machine learning (Buckner 2018). Such approaches suggest that domain-general forms of learning and abstraction suffice to explain all of the diverse capacities that are observed in cognitive systems. We disagree. But this is not because we accept a form of philosophical nativism that is anchored to traditional taxonomies of mental phenomena. We acknowledge that some cognitive capacities are resilient to differences in learning environments, and this is a point that we return to in the closing section of this element. Furthermore, as we argue in Section 3, there are cases where one-trial learning suggests that animals are biologically prepared to learn about specific domains of phenomena. But far more generally, we think that understanding *biological cognition* requires exploring the ways that ecological and physiological constraints shape the flow of information through embodied, situated, and complex biological systems. At many points, we will thus appeal directly to physiological considerations. We hope that this will clarify the roles that evolution and development can play in shaping cognition, while leaving room for diverse cognitive strategies to arise as animals manage ecologically and socially significant challenges. But to get a sense of what this means, it will help to consider the kinds of questions that arise when we focus on encouters with challenges and opportunities, in the context of preserving viability.

In the remainder of this introductory section, we thus provide a high-level overview of the kind of cognitive architecture that supports biological cognition. We then explore the implications of adopting this approach in the context of visual perception, a context where the importance of a biological perspective is likely to be clear to many philosophers and cognitive scientists (Section 2). We then turn to questions about learning and social cognition (Section 3 and Section 4), and we conclude with a brief discussion of how this approach might shape future inquiries in the cognitive sciences (Section 5). To ease into this approach, however, let’s begin by considering the behavior of free-roaming elephants (Figure 1).

Figure 1 A small family of elephants.
Public domain image, Elephant Family in Tanzania, Wikimedia Commons.

1.1 Preserving Viability

Elephants are large animals who cover long distances in search of nutritional resources (Bates et al. 2008; Bradshaw 2009). They must eat huge quantities of plants and fruit to survive, and they spend most of the day foraging. But they don't do so randomly; they display a pronounced sensitivity to the demands of competition with other herbivores and other groups of elephants. They must also access substantial volumes of water, and elephants sometimes dig wells and cover them over so other animals will not find them. Finally, elephants must seek out minerals such as salt that are necessary for survival but difficult to obtain in sufficient quantities; in one striking example, elephants who found a high-quality salt mine followed remembered routes to this mine for many years, adjusting their timing and strategies when challenges to their survival and well-being emerged (Schulkin 1991).

Elephants are also highly social animals, and their lives are organized by lasting friendships, robust family bonds, and patterns of alloparenting (Archie et al. 2011). They also communicate in diverse ways to manage challenges and opportunities collectively. Over short distances, they use approximately thirty different calls and eighty visual and tactile displays; over long distances, they use low-frequency vocalizations, which can be detected as sounds and

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vibrations. These long-range vocalizations can be used to alert distant elephants to the presence of various challenges and opportunities, including the presence of predators. Few predators (other than humans) will attack elephants. But, in recent years, the ability of elephants to call out to others has had disastrous effects. Poachers will sometimes kill off the mature elephants in a herd and wait for other elephants to arrive in response to these long-range calls. The result is that huge numbers of mature elephants are killed, and many young elephants end up witnessing their entire herds being killed off.

Human activity has brought about robust changes in resource availability, alongside these extreme disruptions of elephant social relationships, so many elephants have developed novel cognitive and affective strategies for managing human-generated challenges. For example, the salt-mining elephants that we mentioned above must cope with a pervasive fear of poachers, who sometimes wait for them to arrive at the salt mine; and animals who have witnessed the violent deaths of their herds experience anxiety and distress, as well as heightened patterns of anticipatory aggression. Some of these traumatized elephants engage in uncharacteristically aggressive behavior within their communities; others direct hostility toward humans and other animals. But just as strikingly, many of these elephants have developed capacities to track the subtle cues that indicate human group membership, such as clothing and scent, and they are more vigilant after experiencing cues associated with the groups who tend to attack them. Finally, there is suggestive evidence that social regulation, driven by interactions between adolescent males and less-traumatized bulls, can sometimes mitigate the effects of past trauma (Bradshaw 2009).

To explain these patterns of experience and behavior, it is necessary to ask how elephants learn about their world while managing metabolic and social needs, as well as dealing with various form of stress and trauma. This requires looking beyond the kinds of information that can be collected in a laboratory environment, and it requires looking beyond simple appeals to beliefs, desires, or other categories that are commonly discussed by philosophers. Specifically, it requires examining: (1) the physiological processes that are employed as elephants anticipate changes in internal and external states; (2) the strategies they employ to accommodate anticipated changes using chemical signaling systems; and (3) the changes in physiological and hormonal regulation that arise and persist in the wake of trauma, yielding pronounced changes in the elephant's willingness to seek social support (Bradshaw & Schore 2007).

By highlighting processes that organize responses to *biological challenges and opportunities*, an approach to cognition that highlights *allostatic* regulation comes into view. An 'allostatic system' attempts to preserve viability through change, and 'allostatic regulation' is the process by which animals adjust and

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adapt to changing circumstances, often using diverse forms of anticipatory regulation to coordinate diverse bodily systems. A biological approach to cognition that centers allostatic regulation reveals a wide range of information-processing strategies that are involved in producing and regulating behavior, as well as managing physiological and social challenges (compare Allen 2017; Heyes 2019). These information-processing strategies are sustained by forms of analog and digital signal manipulation, which are implemented by neural and chemical signaling systems, and they are supported by diverse forms of affect, which organize perception and learning. But just as importantly, a biological approach to cognition must accept a kind of *embodied pluralism* that is sensitive to the way that various challenges and opportunities affect embodiment, experience, cognition, and behavior. The implications of this approach are wide ranging, or so we argue over the course of this Element. This approach entails that appeals to computational or representational considerations should be integrated within a broader account of how animals preserve viability through change, and it entails that claims about processes like remembering, planning, and linguistic processing must be situated within an account of how animals navigate the physiological and social challenges that they face.

1.2 Embodiment as a Core Principle of Biological Cognition

An influential understanding of this form of *embodied pluralism* was articulated by Claude Bernard. Building on his knowledge of digestive enzymes, glucose synthesis, and the response of blood vessels to changes in temperature, he hypothesized that regulating the internal milieu was essential to life, and he argued that biological systems always have the purpose "of maintaining the integrity of the conditions for life in the internal environment" (Bernard 1974, 89). Bernard was not primarily concerned with mentality or cognition, but Ivan Pavlov (1927) extended the claim that biological systems preserve viability by regulating their internal milieu to questions about learning and decision-making, exploring the ways that animals adapt to contextual changes. He showed, for example, that interactions between the brain and digestive glands support a form of adaptive learning, where *anticipating* food passing through the oral cavity triggers insulin secretion, preparing the animal to absorb vital nutrients. This was a significant advance because it showed that a cognitive state could use a chemical signal to organize system-level behavior, while the digestive glands could use that signal to shape experiences of hunger and satiation. Pavlov hypothesized that extensions of this approach could provide a basis for a scientifically grounded theory of 'psychic activity,' including a wide range of psychiatric phenomena.

Drawing upon Pavlov’s research, Ernest Starling (1905) examined a diverse range of chemical signals that could carry information through the bloodstream to organize nervous activity and regulate various organs. He called these chemical messengers ‘hormones’ (‘ὁρμάω,’ ‘setting in motion’), to highlight their role in exciting and arousing behavior. When his critical insights were taken up by Walter Cannon (1917, 1932), it became clear that there is a tight connection between the adrenal glands and the sympathetic nervous system. Cannon spent much of his career showing that the secretion of adrenaline played an important role in adaptive responses to deviations away from biological set-points, or desired states of critical biological variables. For example, he proposed that the ‘flight-or-fight’ response is regulated by neuroendocrine systems that motivate actions that would restore homeostasis through the management of biological or social challenges.

In the context of biological cognition, the management of biological and social challenges will always be complex. Recall the elephants who must track and respond to numerous variables, ranging from the availability of nutritional resources to the stability of their social communities and the likelihood that specific humans pose a threat to their continued survival. These elephants must manage access to water and minerals, and they must determine when it makes sense to seek social support. In doing so they employ diverse anticipatory control systems, which are responsive to: (1) variations in internal variables; (2) variations in the social, ecological, and physiological factors that constrain behavior; and (3) variations in the interactions between these diverse constraints (Bechtel 2009; Schulkin 2011). A wide range of brain-based systems *actively* monitor physiologically significant events; and they trigger anticipatory activity within diverse chemical signaling systems (including endocrine, neuroendocrine, and neurotransmitter systems), which play multiple roles in the organization of behavior, the management of uncertainty, and the preservation of viability.

Over the past several decades, it has become increasingly clear that numerous interacting processes are coordinated as animals confront various challenges and opportunities. These processes depend upon chemical signals, which operate over multiple timescales to organize behavior in response to changing needs for things like salt, glucose, water, and social acceptance; and they depend upon interactions between chemical and neural systems, which support the anticipation of challenges and opportunities, as well as the compensatory strategies that must be employed to preserve viability (McEwen 2004, 2007; Richter 1953; Sapolsky 1996; Schulkin 2004; Schulkin & Sterling 2019).

Research on these forms of physiological regulation have often focused on the forms of cognition that are employed in specific contexts, where specific

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chemical and neural processes are employed to cope with specific regulatory demands. But it is difficult to generalize from these precise and detailed explanations to the range of strategies that animals must employ as they accommodate shifting needs and priorities in naturalistic environments. This is a problem that commonly arises in biological contexts (Levins 1966; Odenbaugh 2003), but it will be crucial to keep this claim in mind over the course of this Element: the internal complexity and inherent variability of biological systems make it difficult to model behavior and physiological structure in ways that are precise, general, and biologically realistic, and these difficulties are exacerbated where a diverse array of biological and social constraints shape cognition in an ongoing way.

1.3 Pluralism about Processes

Animals must track potential dangers while monitoring fluctuations in metabolically significant resources and maintaining an awareness of where shelter and social relief are likely to be found. Likewise, many animals need to regulate social contact and social withdrawal in ways that allow them to manage social relationships. Finally, each of these processes must unfold as animals pursue some degree of ‘predictive coherence’ among the diverse processes that are dedicated to monitoring everything from the status of specific bodily tissues to the availability of resources and the structure of the social hierarchies that shape perception and learning (Schulkin 2015). Our claim about the difficulties inherent in modeling behavior and physiological structure in ways that are precise, general, and biologically realistic might therefore seem to make the study of cognition impossible.

However, it is important to note that many of the simple and low-cost forms of signal processing that manage the flow of bioelectric signals through neural networks are well understood. Some strategies for channeling the flow of activity are implemented directly by connections within neural networks, but more typically the activity of a neuron will be regulated by numerous chemical signals, which: (1) adjust the strength of connections between neurons; (2) affect the likelihood that neurons will fire; and (3) transform the ‘shape’ of a neuron’s spiking or bursting activity (Brezina 2010). Consider Eve Marder’s (2012) groundbreaking work on a bundle of approximately thirty neurons (the stomatogastric ganglion) that regulate the activity of crustacean stomach muscles. A diverse range of chemical signals are employed to adjust the frequency of spiking, the number of spikes per burst, and the phase relationships between different cells within this network to yield different patterns of activity. A single circuit can be modulated in different ways by serotonin, dopamine, and octopamine. Moreover, a single chemical signal like dopamine can modulate the currents through a single cell in multiple different ways by binding to different locations on a cell, and it can modulate activity differently in different neurons. By boosting or suppressing activity in specific circuits, and filtering specific kinds of information, chemical processes shape experience across changing contexts. Consequently, it will sometimes be useful to interpret neural processes as analog computations that rely upon medium-dependent representations. Where this is true, we will need to understand the physical properties of the neural system if we are to understand how it does what it does (Maley 2021, 14745); this means that it will often be more productive to focus on the ways that neural activity is constrained by chemical signals that orient animals directly toward ecologically and socially salient information.

From this perspective, we might therefore say that while neural activity is essential to the ongoing regulation of thought and behavior, it is often shaped by chemical signaling systems that convey physiological demands from distributed bodily systems. These demands must be satisfied for the body to cope with challenges and opportunities. Moreover, in many cases, widely distributed networks of neural and bodily processes will need to be integrated to sustain active engagement with ecologically and socially relevant phenomena. In this context, appeals to functional localization and decomposition, and to claims about the computational processes that are employed by a system, should not be taken for granted. On the one hand, although chemical signals are often produced locally, within a specific neural network, they can also be produced in distant parts of the brain or in distant bodily locations; but in every case, they will shape activity across a wide range of bodily and neural systems, ranging from various peripheral organs – including the gastrointestinal tract, heart, kidneys – to diverse cortical and subcortical neural networks.

This situation is further complicated by three significant features of the brain. First, the processes that must be integrated to preserve viability will often be distributed across the brain, body, and world, and a diverse range of strategies will need to be employed, often in parallel, to manage numerous social and ecological challenges. Second, neural activity often unfolds across multiple temporal scales. Some processes are regulated by local patterns of neural spiking and rapidly dissipating chemical signals; others depend upon more robust chemical signals that affect embodied activity over longer timescales (for example, serotonin and dopamine). Finally, and perhaps most importantly, brains are heterarchical systems (see Section 1.4) that employ networks of distributed, flexibly coupled, interacting processes that collectively create and manipulate the diverse sources of information that are necessary to preserve viability in changing environments.

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With regard to the first two claims, biological processes will often be specialized for processing certain kinds of information. But this does not entail that processing should be understood as modular, in the sense that localized components will correspond to meaningful psychological categories (such as attention, language, or social cognition). There are a couple of reasons for this. First, the chemical signals that are employed to regulate the flow of information throughout the brain and body can be used in different ways, by different systems, in different contexts. Second, neural processes are often reused and integrated into different networks, as animals cope with diverse challenges and opportunities. In both cases, the guiding hypothesis should be that "resource constraints and efficiency considerations dictate that whenever possible neural, behavioral, and environmental resources [will be] reused and redeployed in support of any newly emerging cognitive capacities" (Anderson 2014, 7). Against this backdrop, it is worth saying a bit more about the heterarchical organization of the brain, given that this suggestion is likely to be unfamiliar to many readers.

It is perhaps easiest to conceptualize heterarchical control in political domains, where it is clear what it would mean to say that there is no central controller and no 'top' to the system. This doesn't mean that the political domain lacks organization. But the interactions between different parts of a heterarchical society can change, in ways that are sensitive to the needs of the broader system of social organization, and the management of different kinds of challenges can lead a heterarchical society to exploit different kinds of control structures, in different contexts. For example, the management of long-range trade agreements might exploit higher-order control structures, while communal interactions and local manufacturing might be organized by neighborhood or shop. But things get interesting when trade-offs must be negotiated between these different social processes. In a heterarchical society, such trade-offs must be carried out flexibly and dynamically, without any top-level system to regulate them. Sometimes coordination will unfold at lower levels of aggregation, and sometimes higher-level patterns of cooperation will arise, with collective interactions serving to regulate the interactions that occur at the lower level. Finally, strategies that are accepted in the short run can become deeply entrenched if they are not challenged. But the key thing to note is that the observed patterns of organization should not be assumed to exist necessarily: they are structures of control that were established for specific purposes, and many of them can change in response to different demands, often by reorganizing the interactions between multiple control systems.

In the context of cognitive and neural architecture, many kinds of processes and constraints, operating across numerous different timescales and numerous patterns of interaction, must be organized to preserve viability in the face of