

# A Phylogenetic Perspective on Distributed Decision-Making Mechanisms

**Linus Ta-Lun Huang (linushuang@ucsd.edu)**

Department of Philosophy, University of California, San Diego  
La Jolla, CA 92093-0119, USA  
Institute of European and American Studies, Academia Sinica  
Taipei 11529, Taiwan

**William Bechtel (wbechtel@ucsd.edu)**

Department of Philosophy, University of California, San Diego  
La Jolla, CA 92093-0119, USA

## Abstract

This paper challenges a common assumption about decision-making mechanisms in humans: decision-making is a distinctively high-level cognitive activity implemented by mechanisms concentrated in the higher-level areas of the cortex. We argue instead that human behavior is controlled by a multiplicity of highly distributed, heterarchically organized decision-making mechanisms. We frame it in terms of control mechanisms that procure and evaluate information to select activities of controlled mechanisms and adopt a phylogenetic perspective, showing how decision-making is realized in control mechanisms in a variety of species. We end by discussing this picture's implication for high-level cognitive decision-making.

**Keywords:** decision-making; phylogenetic refinement; heterarchical networks; hypothalamus; basal ganglia

## Introduction

We advance a heterarchical alternative to the hierarchical conception of decision-making common in cognitive science and neuroscience. Decision-making is classically construed, following our folk psychological understanding of *explicit* reasoning and decision-making, as distinctively human. According to this conception, roughly: (1) decision-making is a higher-level, cognitive activity, implemented by a unified neural mechanism in the prefrontal cortex (Gold & Shadlen, 2007); (2) this mechanism is situated between the perception and motor mechanisms, taking inputs from the former and sending output to the latter (Hurley, 2001); (3) decision-making is conscious in that we are aware of the alternative options, evaluative criteria, and the process of selection; and finally, (4) it is a deliberate, rather than automatic, activity (Gonzalez, 2017).

This classical conception has proven contentious and been subject to criticisms by theorists adopting a variety of theoretical frameworks in recent literature. For example: massive modularists argue that there are multiple reasoning modules, rather than a unified mechanism (Carruthers, 2008). Also, decision scientists have fruitfully applied the decision-theoretical framework to study lower-level sensorimotor and affective mechanisms (Glimcher & Fehr, 2014). Likewise, neuroscientists have recognized the important role of

subcortical components, such as the basal ganglia and thalamus, in decision-making (Delgado & Tricomi, 2011). Finally, the dual-process theories have argued for the existence of unconscious and automatic decisions, while their critics question the dichotomy between the conscious and deliberate vs. the unconscious and automatic decisions (Evans & Frankish, 2009).

Nevertheless, these debates still operate under a hierarchical framework that views the multiplicity of decision-making mechanisms as arranged on various levels with the most "cognitive" decision-making situated at the top-level and the sensory and motor ones at the lower-levels. More importantly, the lower-level decision-making mechanisms are, adopting Daniel Dennett's term, bureaucratic (Dennett, 1991) They function to provide information for the cognitive decision-making mechanisms and work out the detailed implementation of their decisions. As a result, there are no real conflicts between lower-level and higher-level decisions, since the lower-level mechanisms do not have their own agenda and function solely to serve those of the higher-level ones.

In defending a heterarchical alternative, we argue that cognitive scientists should adopt a much broader perspective on decision-making, one that recognizes it as a ubiquitous and widely distributed activity in all living organisms, even those that do not have neurons. We apply a similar distributed perspective to humans, arguing that human behaviors are the product of decision-making mechanisms that are (1) radically distributed in cortical, subcortical, and peripheral regions of the nervous system; (2) opportunistically structured in heterarchical networks and autonomous, instead of bureaucratic. (The notion of heterarchy was introduced by McCulloch, 1945.) Neglecting these leads to an over-intellectualized account of human decision-making. The heterarchical framework draws on the insights from distributed and embodied cognition (Clark, 1997) and is compatible with their stronger versions that view cognition as constituted by processes in the body or in the environment; however, we remain neutral on these stronger positions in this paper.

In making our case, we are, in significant part, inspired by the phylogenetic approach to cognition advanced by Cisek

(2019). Cisek argues for understanding cognitive capacities as the product of *phylogenetic refinement*. On this view, cognitive traits exhibited in organisms earlier in our phylogeny are still operative in us. Our cognitive abilities build upon these capacities but are also constrained by them. He contends that by examining cognition from this perspective, we are more likely to identify the processes underlying our abilities: "Ideally, that new taxonomy will progressively differentiate functions and subfunctions in a way that mirrors their progressive differentiation over evolutionary time, and the hope is that the resulting set of explananda will more naturally correspond to real biological circuits." There is no space in a short paper to fully develop a phylogeny of decision-making mechanisms. Instead, we focus selectively on examples from that phylogeny that motivate developing a more distributed perspective on decision-making.

In the next section, we advance a theoretical perspective on decision-making that provides a basis for understanding how evaluations enter the diverse mechanisms that organisms use to make decisions. We then turn to decision-making in organisms without neurons, which provides a perspective on how decision-making mechanisms arose in phylogeny. Next, we consider decision-making in organisms with nervous systems but without a central brain to illustrate how decision-making can be distributed throughout a nervous system before taking up decision-making in bilateral invertebrate nervous systems. Finally, we turn to vertebrates and show that even as a great deal of neural processing is concentrated in a brain, decision-making remains highly distributed.

## A Framework for Decision-Making

In approaching the phylogeny of decision-making, we need to be clear what is required to identify a process as making decisions. It is not enough that a mechanism randomly selects between alternatives. Decision-making involves evaluating alternatives and selecting one of them based on the evaluation. In explicit decision-making, the grounds for evaluations can be explicitly represented (e.g., as utility assessments) and reported. Our contention is that explicit decisions account for only a small percentage of the decisions that humans make. For example, humans do not consciously evaluate the options when deciding whether and what to eat, to adjust their posture, or to engage in social pleasantries.

To see how evaluations figure in decisions that are not the product of conscious deliberation, it is helpful to view decision-making as an activity of control mechanisms—mechanisms that operate on other mechanisms as to affect when and how they operate. The various activities of living systems—metabolism, growth, locomotion, reproduction, etc.—are performed by production mechanisms. The new mechanisms in philosophy of science have described how scientists in a host of life sciences develop explanations by identifying the production mechanism responsible for a given phenomenon and decomposing it into its parts, operations, and organization (Machamer, Darden, & Craver, 2000; Bechtel & Abrahamsen, 2005). They have, however, largely

neglected the fact that biological mechanisms, far more than human-made machines, are subject to being altered by control mechanisms. Since organisms are far-from-equilibrium and subject to processes that lead to their decomposition, it is critical that they deploy production mechanisms as needed to build and maintain themselves or reproduce (Moreno & Mossio, 2014). Not surprisingly, then, biological organisms include a vast number of control mechanisms, far outnumbering production mechanisms.

For one mechanism to control another, it must both be able to act on the other to change its operation and to procure and evaluate information about whether conditions are appropriate for its operation. Information is procured either by the control mechanism making measurements or taking advantage of the outputs of other mechanisms that carry information about the measured quantity. The design of the control mechanism determines how it will behave in light of this information—altering conditions in production mechanisms or not. A simple example of a feedback control mechanism makes this clear. A thermostat measures the temperature and sends a command to the furnace that makes changes in the furnace that alters its functioning.

In its activity, a control mechanism makes an evaluation: in sending a command to the furnace, the thermostat is evaluating the current temperature as too low. In the case of the thermostat, the evaluation it makes is determined by its design and the human user who sets the desired temperature. This, however, does not take away the fact that the thermostat, once set, itself makes the evaluation and selects an action accordingly. A significant difference in living organisms is that there is no external agent fixing the evaluation procedure in control mechanisms. A given control mechanism in an organism is either already equipped with its settings as a result of evolution and development, or is acted upon by yet another control mechanism that imposes settings on it.

Control mechanisms are introduced opportunistically into biological organisms over the course of evolution—if a control mechanism arises through variation in existing organisms and the organism is overall successful in reproducing, it is retained. There are typically many different control mechanisms operating on any given production mechanism, registering different conditions relevant to the deployment of the production mechanism and making decisions about when and how the production mechanism will be deployed. These are not organized hierarchically but heterarchically, with multiple control mechanisms exercising control both on production mechanisms and each other.

Control mechanisms draw upon information and select between alternatives. They are, thus, making decisions in the sense we adopt in this paper. From this perspective, decision-making is a ubiquitous activity that is widely distributed in organisms. One might object that this perspective cheapens the notion of decision-making. We contend, however, that control mechanisms embody its central features—employing an evaluation procedure to select actions in response to information. In the last section, we will suggest how

recognizing this enables us to better understand explicit decision-making that is perhaps uniquely human.

### Decision-Making Without Neurons

Given this framework, we should expect to identify decision-making activities in all living organisms, not just those with a nervous system. Indeed, there are plentiful examples that have already been investigated. Here, we discuss just one. *E. coli* employs a relatively simple mechanism for locomotion—flagella that form into a bundle and drive the bacterium forward when they are rotated counter-clockwise but separate and allow the bacterium to tumble when rotated clockwise. The decision to move forward or to tumble is made by a chemical mechanism that integrates information from five transmembrane proteins that detect various chemicals in the external and internal environment. When this sensing mechanism registers that the concentration of nutrients is declining or that of toxins is increasing, it initiates a phosphorylation cascade. When the final component, CheY, is phosphorylated, it acts on the motor, causing it to rotate clockwise, thereby allowing the bacterium to move forward rather than tumble (Falke & Piasta, 2014). Individual bacteria exhibit variants in the numbers of different receptor types, resulting in different decisions. Further, bacteria also appear to adjust the percentage of different receptors depending on the presence of other bacteria (Sourjik & Wingreen, 2012).

Although this control mechanism is relatively simple, it suffices to enable bacteria to select actions based on information collected and evaluation procedures realized in the mechanism—that is, it is a decision-making mechanism. Moreover, this is just one of many decision-making mechanisms in bacteria. Others make decisions affecting the social interactions of bacteria in biofilms so as to distribute food between organisms at the periphery and those at the center of the biofilm (Prindle et al., 2015). Some decisions, such as whether to reduce one's body to a spore, have major consequences for the lineage of bacteria (Stephens, 1998).

What is important for our purposes is that each such decision is made by a separate control mechanism, illustrating the radically distributed nature of decision-making in single-cell organisms. This distribution of decision-making is maintained in multi-cell organisms.

### Decision-Making Without a Central Brain

A distinctive feature of animal life, at least since the Eumetazoa-Bilateria split, is the use of neurons in control mechanisms. There has been considerable speculation and theorizing about the origins of neurons. All organisms living today are the product of a long history of evolution, but many theorists regard modern *Cnidarians* (a phylum comprising jellyfish, corals, sea anemones, and other soft-bodied polyps) as most reflective of organisms with neurons before the evolution of bilateral organisms. A distinctive feature of *Cnidarians* is the occurrence of a network of sensory and ganglion neurons situated next to contractile epithelial cells constituting the bell. These have been characterized as

constituting a *skin brain* (Holland, 2003; Keijzer, van Duijn, & Lyon, 2013), which enables coordinated contractions required for swimming.

In the process of carrying out the activity of coordinating contractions, these neurons integrate inputs from a variety of further control mechanisms and alter behavior in response. This is illustrated in *Aequorea victoria*, a small transparent jellyfish with 60-80 tentacles containing muscles that extend from around the lower margin of the bell. Fourteen distinct neural control mechanisms, each making decisions leading to different behaviors, have been identified (Mackie, 2004).

To illustrate how these control mechanisms make decisions, we focus on the capacity of *Aequorea* to decide between two distinct modes of swimming, slow and escape (Mackie, 1980). In both cases, the contractions of the bell are directly controlled by neurons in the nerve net, but the activity of these neurons is modulated by those in the inner of two nerve rings that circumvent the margin of the bell. In slow swimming, these ring neurons serve as a pacemaker, which modulates the nerves in the nerve net to generate slow, regular contractions (Mackie, 2004; Satterlie, 2018). Escape swimming is initiated by the same ring neurons when they are induced by mechanical or electrical stimulation of the tentacles, resulting in much stronger muscle contractions (Arkett, Mackie, & Meech, 1988). Another control mechanism also operates on these ring neurons: default slow swimming is briefly inhibited with the initiation of feeding. Mackie, Meech, and Spencer (2012) investigated this circuitry in another Cnidarian species, *Polyorchis penicillatus*, from which it was easier to record. They established that when food is encountered, an electrical pulse is transmitted along a nerve plexus to inhibit the pacemaker ring neurons. Moreover, this is only one of four circuits that suffice to inhibit swimming. Each of these circuits results in different specific decisions.

In short, the decision-making mechanisms illustrated do not conform to a neat hierarchical structure. Instead, the behavior of modern Cnidarians is determined by a heterarchical network of distributed decision-making mechanisms.

### Decision-Making in a Bilateral Invertebrate

It might be assumed that in organisms exhibiting bilateral symmetry with a brain situated at one end, decisions would all be brought under central control. But this is not the case. We illustrate this with the example of decision-making in the medicinal leech (*Hirudo verbena*), which must select swimming or crawling to move about. The decision is made in 21 individual ganglia situated between what are referred as the *head* and *tail* brains. Within each ganglion, consisting of approximately 400 neurons, the decision is made through a complex dynamical interaction of a subset of the neurons in the ganglion (Briggman, Abarbanel, & Kristan, 2005). Since different ganglia can make different decisions, coordinated behavior in the whole leech is achieved through coupling between ganglia. In addition, other factors, such as concentrations of serotonin and dopamine, synthesized by

other control mechanisms, influence the probability of each behavior, with serotonin increasing the likelihood of swimming and dopamine of crawling (Puhl & Mesce, 2008; Crisp & Mesce, 2006).

In addition, some behavioral decisions, such as feeding, inhibit responses to stimuli that would otherwise elicit a response (e.g., swimming or crawling) in non-feeding animals. In these conditions, the motor response circuitry is still capable of eliciting swimming. The inhibition instead results when presynaptic terminals of pressure-sensitive mechanosensory neurons are prevented from eliciting motor responses. Although the details of the process of presynaptic inhibition are not known, Gaudry and Kristan (2009) showed that the effect can be mimicked by bath application of serotonin to the exposed nervous system and negated by applying anserine, known to block serotonergic inhibition in *C. elegans*.

The leech thus illustrates that even in bilateral organisms, decision-making mechanisms are highly distributed and structured heterarchically. They also illustrate that chemical control mechanisms are operative even in systems with neurons.

### Decision-Making in Vertebrate Brains

A notable difference between vertebrates and the other organisms discussed above is the presence of the notochord, which serves to centralize many control mechanisms in the head region. One consequence of this is to bring together what Arendt, Tosches, and Marlow (2016) refer to as the apical nervous system (which arose at the apical tip of the gastrula-shaped ancestors and integrated information about body physiology) and the blastoporal nervous system (involved in controlling muscle contractility). Although different neural processes were thereby collocated in what Tosches and Arendt (2013) termed a chimeric brain, they were not integrated into one hierarchically organized system. Rather, they gave rise to multiple specialized processing centers that form a heterarchical network. We focus on two regions within that network—the hypothalamus and the basal ganglia.

The hypothalamus is a collection of nuclei that collectively regulate a wide spectrum of animal activities, from metabolic processes to overt behaviors, often by releasing hormones and neuropeptides into the circulatory system via the adjacent pituitary gland. To do so, the different nuclei typically integrate information from multiple regions of the body. As one example, we consider the role of the arcuate nucleus in making decisions about feeding and metabolism.

The arcuate nucleus is located in the ventral medial hypothalamus near the median eminence. As there is no blood-brain barrier at this location, neurons in the arcuate nucleus can communicate with the rest of the organism using hormones. It contains two populations of neurons that respond to peripheral signals indicating the state of satiety of the organism. Pro-opiomelanocortin (POMC) neurons respond to leptin, a peptide released by adipocytes, signaling the accumulation of fat. POMC neurons are influential in

inhibiting feeding behavior: When POMC are knocked out, mice exhibit hyperphagia and obesity; when they are activated optogenetically, they suppress food intake. Neuropeptide Y/agouti-related peptide neurons, on the other hand, are inhibited by leptin but activated by ghrelin, a peptide synthesized in the stomach that signals a lack of food being digested. Acute activation of these neurons results in increased food intake (Sohn, 2015; Trivedi, 2014). Reciprocal connections between these neurons "determine how much an animal will eat" (Leng, 2018).

This account is highly simplified. The arcuate nucleus receives numerous other signals and acts on many other areas of the brain. Adipocytes, for example, release about 100 different proteins besides leptin, some of which also affect neurons in the arcuate nucleus. At the same time, other parts of the digestive system also release hormones and peptides that affect arcuate neurons. Many of these send signals to the brainstem and other areas, which then project to the arcuate nucleus (Cone & Elmquist, 2015). Moreover, both leptin and ghrelin act on other parts of the hypothalamus that also exercise control over feeding behavior. For example, leptin activates oxytocin neurons in the supraoptic nucleus of the hypothalamus at the anticipated time of feeding (Johnstone, Fong, & Leng, 2006).

This sketch suffices to reveal the complexity of feeding regulation. Decisions about feeding are made by a distributed, heterarchical network of decision-making mechanisms that employ both electrical and chemical signaling.

We turn now to the basal ganglia, a network of subcortical nuclei. As we noted above, many cognitive scientists now recognize the role the basal ganglia play in decision-making. We contend, however, that their treatment of the basal ganglia is highly selective. The basal ganglia do not merely augment cognitive decision-making carried out in the frontal cortex; they provide an architecture that is used in collaboration with many other brain regions to facilitate making a wide range of decisions.

We begin with what has drawn the attention of researchers interested in decision-making to the basal ganglia—the loops between cortical areas, the basal ganglia, and the thalamus. These loops tend to be highly specific—when inputs to the basal ganglia originate in the frontal cortex, outputs project back to the same region of the frontal cortex. This allows the basal ganglia to act as a control mechanism on the processing in these cortical areas.

It is the architecture of the basal ganglia themselves that implicate these loops in decision-making. Inputs arrive at the striatum, which is laid out topographically so that inputs from the same region often arrive at the same part of the striatum. Inputs to the striatum, project through one of two pathways to the output regions of the basal ganglia—the substantia nigra pars reticulata and the globus pallidus internus. By default, neurons in the output regions send out inhibitory signals to their targets. When they receive inputs along what is known as the *indirect pathway*, this inhibitory output is enhanced. When, however, they received inputs along the

*direct pathway*, inhibition is reduced. There is competition between input neurons in the striatum to send projections along the direct or indirect pathways. Winning the competition enables the region from which the input was received to be released from inhibition and continue its processing while nearby areas are inhibited. The basal ganglia thus perform the activity of selecting between alternatives—important to making decisions.

There are two important qualifications to the account we just presented: First, much of the attention has been directed at loops originating and terminating in the prefrontal cortex as this is taken to be the locus of high-level cognitive activity. But the basal ganglia perform the function of decision-making far more broadly. Similar loops originate and terminate in other cortical areas, including sensory and motor processing areas. The basal ganglia thus contribute to perceptual and motor decisions. Additionally, and critical from our perspective, similar loops link the basal ganglia to many non-cortical brain areas, including mesencephalic (the cuneiform nucleus, the pedunculopontine nucleus, and surrounding structures) and diencephalic regions that sequence commands sent to central pattern generators in the brainstem and spinal cord. Through these loops, the basal ganglia contribute to decision-making involving these lower-level brain regions, and can do so potentially independently of the cortex.

To support our contention that the role of the basal ganglia figures in decision-making that goes far beyond what it does in conjunction with the cortex, we point to two lines of research. First, the basal ganglia are found across vertebrates from the lamprey to humans, suggesting it was present at the root of vertebrate evolution (Stephenson-Jones, Ericsson, Robertson, & Grillner, 2012). In lamprey and presumably early mammals, the pallium, from which cortex later evolved, is small, suggesting that its inputs to the basal ganglia were relatively minor and other inputs predominated. This is supported by research in the 20th century that showed decorticate cats exhibited many locomotor and other behaviors of ordinary cats as long as the basal ganglia and thalamus were spared. They ate and drank, responded to stimuli, groomed themselves, moved about in their environment, and made the decisions necessary to engage in these activities. Without the basal ganglia and thalamus, however, they are unable to initiate these activities (Bard & Macht, 1958); Whelan (1996). These two lines of evidence point to a central role of the basal ganglia in decision-making in a multitude of contexts, not just in coordination with the cortex.

Second, when we look into further details of the basal ganglia mechanism, a different, and even more radically distributed picture of decision-making emerges. Regions in the striatum that figure in loops with the prefrontal cortex also receive inputs from many other cortical and non-cortical regions, indicating that they integrate diverse information when selecting between prefrontal activities (e.g., shifting attention). The other relevant fact is that the evaluation processes involved in decision-making do not happen

entirely within the bounds of the basal ganglia. There is no evidence that the inputs to the basal ganglia encode the content of what is processed in other brain areas. Rather, the strength of the signals received on the various inputs to the striatum reflects evaluations already performed in the various cortical and non-cortical areas that contribute inputs. That is, the basal ganglia merely receive and integrate the evaluations to select the strongest options. The relevant decision-making systems are composites of the basal ganglia and the brain regions from which inputs originate. Thus, even in the cases in which the basal ganglia are implicated in decision-making, the actual decision-making mechanism is a radically distributed network of component mechanisms.

To sum up, the basal ganglia are central to many decision-making activities, whether in collaboration with cortex or not. In cases in which the loops originate and return to the prefrontal cortex, they are involved in decisions, such as gating and maintaining working memory, that are traditionally recognized as "cognitive." But these are only some of the decision-making activities in which they are involved. And these do not exhaust decision-making in vertebrates as we also noted the role of various parts of the hypothalamus in decision-making.

## Implications for Studying Human Decisions

Decision-making is a fundamental activity of all living organisms, not just humans. Adopting a phylogenetic perspective makes it clear just how radically distributed decision-making mechanisms are. Rather than a pyramid structure in which all decisions are made by a hierarchy of cortical decision-making mechanisms, the phylogenetic perspective suggests that many different control mechanisms, neural and otherwise, are involved in decision-making. Many of these interact with each other in a complex manner, resulting in a heterarchical network, not a hierarchy. Ignoring these and attributing all decision-making to one mechanism seriously misrepresents how humans and other organisms make decisions.

To illustrate the implications of adopting a heterarchical framework over a hierarchical one, consider how the two frameworks address the phenomenon of weakness of will—exhibited, for example, when one judges that it is the best to refrain from drinking one more glass of wine, but nevertheless goes on to drink it. On the hierarchical model of the mind, coherence of an agent's behaviors is provided either by the single decision-making mechanism or the one at the highest level. Because all other "bureaucratic" mechanisms function to serve its agenda, there should be no genuine conflicts. This makes it challenging to explain weakness of will as there is little theoretical resource for accounting for the decision to have the drink (Haas, 2018). At best, it must be judged to be irrational.

In contrast, the heterarchical model recognized multiple decision-making mechanisms and does not assume coherence of decision-making and so of resulting behaviors; instead, coherence is something to be achieved (with varying degrees of success) by coordinating different, autonomous decision

mechanisms. The coordination is performed again by various control mechanisms, both internal to the organism, as we discussed above (Huang, 2017), as well as external, which we will touch on briefly soon. Thus, under the heterarchy framework, weakness of will and other forms of more subtle internal conflicts are explained as resulting from less than perfect coordination of the conflicting autonomous decision-making mechanisms. Of course, the conflicting mechanisms usually constrain and coordinate each other to a high degree. This is why weakness of will is the exception, rather than the norm.

Some cognitive scientists might acknowledge that decision-making is heterarchical but insist that cognitive science should still focus only on distinctively human decisions. We conclude by identifying two benefits for extending the approach to decision-making as we have done in this paper. First, once we recognize that all decision-making mechanisms are control mechanisms, we can explore whether there are some shared design principles between different decision-making mechanisms as well as differences between them that are appropriate for making different types of decisions. Second, adopting a concept of decision-making that does not privilege explicit reasoning, we are in a better position to see, through contrast, the unique features of distinctively human decision-making that has been the focus of much of cognitive science.

While all decision-making mechanisms, as control mechanisms, must collect, process, and evaluate information, they do so in different specialized ways. For example, cortical decision mechanisms typically receive their information and communicate control signals via fast synaptic transmission through highly organized, layered structures. These features enable neocortical areas to specialize in tracking relatively fast-changing contexts (e.g., the movement of objects), extract complex patterns from the inputs (e.g., languages and social norms), as well as produce appropriate control signals in response to them. On the other hand, hypothalamic control mechanisms collect, among others, chemical signals released from a wide range of bodily sources through the circulatory system; and they often broadcast their control chemically. Due to the relatively slower transmission, they often specialize in tracking regularities that change more slowly, such as daily cycles in the environment and hunger, but regulate a wider range of targets in response to them.

One dramatic form of specialization is realized when humans make decisions based on explicitly represented information and norms. As developed in interactionist accounts of explicit reasoning (Heyes, 2018) explicit representation allows people to communicate the reasons for their actions to others and thereby allows others to understand them. Insofar as these explicit representations constitute commitments, others can predict their actions. Explicit reasoning facilitates social coordination in which social norms, institutions, and knowledge (as well as myths and confabulations) figure in control of individual actions. They also allow individuals to exert some control over other agents or social groups.

As powerful as social control is over individual behavior, individuals still make decisions as to what norms and information to accept from their society or borrow from others. Most individuals follow the norms of their society, but all societies witness dissenters. Understanding the heterarchical, distributed nature of decision provides some insight into this process. The decision to adopt one set of evaluative norms rather than another relies on the more basic, highly-distributed, heterarchically-organized decision mechanisms embodied in humans as a result of evolution, development, and prior social and cultural engagement. Once adopted, control mechanisms trafficking in explicitly represented norms, knowledge, and myths act on other control mechanisms, resulting often in them also making decisions in accord with these explicit representations. When explicit norms and knowledge succeed in controlling other decision-making mechanisms, individuals end up acting in accordance with the norms of society; when they fail to do so, individuals act in violation of these norms.

We recognize, therefore, that in explicit decision-making humans can rise above their biological endowments, drawing upon specialized capacities made possible by the frontal cortex that enable them to be affected by their society and culture. We insist, however, that humans do so only to a limited extent and that much of their decision-making relies on a multitude of decision-mechanisms located outside the frontal cortex and shared with other animals. Moreover, even in our distinctively human decision-making, we rely on these more basic mechanisms in selecting, adopting, and acting on explicit norms.

## Acknowledgment

This work is supported in part by a fellowship to Dr. Linus Ta-Lun Huang, sponsored by Academia Sinica, Taiwan.

## References

- Arendt, D., Tosches, M. A., & Marlow, H. (2016). From nerve net to nerve ring, nerve cord and brain--evolution of the nervous system. *Nature Reviews Neuroscience*, 17(1), 61-72. doi:10.1038/nrn.2015.15
- Arkett, S. A., Mackie, G. O., & Meech, R. W. (1988). Hair Cell Mechanoreception in the Jellyfish *Aglantha-Digitale*. *Journal of Experimental Biology*, 135, 329-342.
- Bard, P., & Macht, M. B. (1958). The behaviour of chronically decerebrate cats. In *Ciba Foundation Symposium - Neurological Basis of Behaviour* (pp. 55-71). London: Little, Brown.
- Bechtel, W., & Abrahamsen, A. (2005). Explanation: A mechanist alternative. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 36(2), 421-441.
- Briggman, K. L., Abarbanel, H. D. I., & Kristan, W. B. (2005). Optical imaging of neuronal populations during decision-making. *Science*, 307(5711), 896-901. doi:10.1126/Science.1103736
- Carruthers, P. (2008). *Precis of The architecture of the mind: Massive modularity and the flexibility of thought*. *Mind &*

- Language*, 23(3), 257-262. doi:10.1111/j.1468-0017.2008.00340.x
- Cisek, P. (2019). Resynthesizing behavior through phylogenetic refinement. *Attention, Perception, & Psychophysics*. doi:10.3758/s13414-019-01760-1
- Clark, A. (1997). *Being there: Putting brain, body, and world together again*. Cambridge, MA: MIT Press.
- Cone, R. D., & Elmquist, J. K. (2015). Neuroendocrine control of energy stores. In S. Melmed, K. S. Polonsky, P. R. Larsen, & H. M. Kronenberg (Eds.), *Endocrinology* (pp. 1608-1632): Elsevier.
- Crisp, K. M., & Mesce, K. A. (2006). Beyond the central pattern generator: amine modulation of decision-making neural pathways descending from the brain of the medicinal leech. *Journal of Experimental Biology*, 209(Pt 9), 1746-1756. doi:10.1242/jeb.02204
- Delgado, M. R., & Tricomi, E. (2011). Reward processing and decision making in the human striatum. *Neuroscience of Decision Making*, 145-172.
- Dennett, D. C. (1991). *Consciousness explained*. New York: Little, Brown.
- Evans, J., & Frankish, K. (2009). *In two minds: Dual processes and beyond*. Oxford: Oxford University Press.
- Falke, J. J., & Piasta, K. N. (2014). Architecture and signal transduction mechanism of the bacterial chemosensory array: Progress, controversies, and challenges. *Current Opinion in Structural Biology*, 29, 85-94. doi:doi.org/10.1016/j.sbi.2014.10.001
- Gaudry, Q., & Kristan, W. B. (2009). Behavioral choice by presynaptic inhibition of tactile sensory terminals. *Nature Neuroscience*, 12(11), 1450-1457. doi:10.1038/nn.2400
- Glimcher, P. W., & Fehr, E. (2014). *Neuroeconomics: Decision making and the brain* (Second edition. ed.). Amsterdam: Elsevier.
- Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annual Review of Neuroscience*, 30, 535-574. doi:10.1146/annurev.neuro.29.051605.113038
- Gonzalez, C. (2017). Decision-making: A cognitive science perspective. In S. E. F. Chipman (Ed.), *The Oxford Handbook of Cognitive Science*: Oxford University Press.
- Haas, J. (2018). An empirical solution to the puzzle of weakness of will. *Synthese*, 195(12), 5175-5195. doi:10.1007/s11229-018-1712-0
- Heyes, C. M. (2018). *Cognitive gadgets The cultural evolution of thinking*. Cambridge, MA: Harvard University Press.
- Holland, N. D. (2003). Early central nervous system evolution: An era of skin brains? *Nature Reviews Neuroscience*, 4(8), 617-627. doi:10.1038/nrn1175
- Huang, L. T. (2017). *Neurodemocracy: Self-organization of the embodied mind* (Ph.D. dissertation), University of Sydney.
- Hurley, S. (2001). Perception and action: Alternative views. *Synthese*, 129(1), 3-40. doi:doi.org/10.1023/A:1012643006930
- Keijzer, F., van Duijn, M., & Lyon, P. (2013). What nervous systems do: early evolution, input-output, and the skin brain thesis. *Adaptive Behavior*, 21(2), 67-85. doi:doi.org/10.1177/1059712312465330
- Leng, G. (2018). *The heart of the brain: The hypothalamus and its hormones*. Cambridge: MIT Press.
- Machamer, P., Darden, L., & Craver, C. F. (2000). Thinking about mechanisms. *Philosophy of Science*, 67, 1-25.
- Mackie, G. O. (1980). Slow Swimming and Cyclical "Fishing" Behavior in *Aglantha Digitale* (Hydromedusae: Trachylina). *Canadian Journal of Fisheries and Aquatic Sciences*, 37(10), 1550-1556. doi:10.1139/f80-200
- Mackie, G. O. (2004). Central neural circuitry in the jellyfish *Aglantha* - A model 'simple nervous system'. *Neurosignals*, 13(1-2), 5-19. doi:10.1159/000076155
- Mackie, G. O., Meech, R. W., & Spencer, A. N. (2012). A new inhibitory pathway in the jellyfish *Polyorchis penicillatus*. *Canadian Journal of Zoology*, 90(2), 172-181. doi:10.1139/Z11-124
- McCulloch, W. S. (1945). A heterarchy of values determined by the topology of nervous nets. *The bulletin of mathematical biophysics*, 7(2), 89-93. doi:10.1007/BF02478457
- Moreno, A., & Mossio, M. (2014). *Biological autonomy: A philosophical and theoretical inquiry*. Dordrecht: Springer.
- Prindle, A., Liu, J., Asally, M., Ly, S., Garcia-Ojalvo, J., & Süel, G. M. (2015). Ion channels enable electrical communication in bacterial communities. *Nature*, 527(7576), 59-63. doi:10.1038/nature15709
- Puhl, J. G., & Mesce, K. A. (2008). Dopamine activates the motor pattern for crawling in the medicinal leech. *Journal of Neuroscience*, 28(16), 4192-4200. doi:10.1523/JNEUROSCI.0136-08.2008
- Satterlie, R. A. (2018). Jellyfish locomotion. In *Oxford Research Encyclopedia, Neuroscience*. New York: Oxford University Press.
- Sohn, J. W. (2015). Network of hypothalamic neurons that control appetite. *BMB reports*, 48(4), 229-233. doi:10.5483/BMBRep.2015.48.4.272
- Sourjik, V., & Wingreen, N. S. (2012). Responding to chemical gradients: bacterial chemotaxis. *Current Opinion in Cell Biology*, 24(2), 262-268. doi:doi.org/10.1016/j.ceb.2011.11.008
- Stephens, C. (1998). Bacterial sporulation: A question of commitment? *Current Biology*, 8(2), R45-48. doi:10.1016/s0960-9822(98)70031-4
- Stephenson-Jones, M., Ericsson, J., Robertson, B., & Grillner, S. (2012). Evolution of the basal ganglia: Dual-output pathways conserved throughout vertebrate phylogeny. *Journal of Comparative Neurology*, 520(13), 2957-2973. doi:10.1002/cne.23087
- Tosches, M. A., & Arendt, D. (2013). The bilaterian forebrain: an evolutionary chimaera. *Current Opinion in Neurobiology*, 23(6), 1080-1089. doi:https://doi.org/10.1016/j.conb.2013.09.005
- Trivedi, B. P. (2014). Neuroscience: Dissecting appetite. *Nature*, 508(7496), S64-S65. doi:10.1038/508S64a
- Whelan, P. J. (1996). Control of locomotion in the decerebrate cat. *Prog Neurobiol*, 49(5), 481-515.