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Growing Confidence and Remaining Uncertainty About Animal Consciousness

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Louis Irwin[1]

1. Department of Biological Sciences, University of Texas at El Paso, United States

While the study of consciousness has had a controversial history and, until recently, a pessimistic prognosis, recent views within the neuroscientific community suggest that a maturing if incomplete scientific understanding of consciousness is close at hand. Most published definitions of consciousness boil down to a focus on it as a process arising in a nervous system engaged with a body and its environment, giving rise to subjective (personal) experience. A broad consensus on the phenomenology of consciousness sees it consisting at a minimum of (1) awarenessand focused attention, (2) unity of perception, (3) qualitative variations in content, (4) mental causation, and (5) a sense of self. There is also broad agreement that the substrate of consciousness requires sizeable, complex nervous systems organized into several hierarchical levels of processing. Further insight is gained by reconstructing the evolution of subjective phenomenological experience — most likely from multiple origins, hosted by a diversity of body and brain architectures, and diverging into markedly different forms across the animal kingdom. The three major mysteries that remain about phenomenological experience are (1) the neurological correlates of consciousness, (2) the apparent gap between phenomenology and mechanism, and (3) the agent that monitors the brain activity admitted into consciousness.

Corresponding author: Louis Irwin, lirwin@utep.edu

Introduction

As neurobehavioral and cognitive scientists have increasingly turned their attention to the study of consciousness in humans and other animals, the mysteries of what was long considered by many to be scientifically impenetrable (Storm et al., 2017) have begun to recede in the face of growing consensus around some of the major concepts and assumptions in that field of study (Graziano et al., 2020). The literature on consciousness in humans and other animals is vast, and this viewpoint makes no attempt to cover it comprehensively. Rather, it focuses on those aspects of consciousness about which there is a growing body of agreement in principle, if not in detail. Those include the issues of definition, ontology, and evolution. It also points out the remaining mysteries of animal consciousness: its neurological correlates, agency, and the apparent gap between mechanism and phenomenology. The assertions offered here are neither universally accepted nor uncontroversial (Francken et al., 2022), but are offered as rebuttable benchmarks for growing mainstream thinking in the field of animal consciousness studies at this time.

The Definitional Problem

Published definitions of consciousness number in the hundreds. In a carefully filtered list of publications between 2007 and 2017 alone, Sattin *et al* (2021) identified 29 different theories with 21 subcategories of consciousness. In their monumental review of the

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subject, Ginsburg and Jablonka referred to 12 different forms of consciousness in animals (Ginsburg and Jablonka, 2019). This multitude of ways to define consciousness reflects the variety of theoretical models put forth as explanations for its different aspects. Like 'intelligence' and 'personality,' the term 'consciousness' is turning into a word in folk psychology with limited utility unless further qualified with regard to the way it is measured and the specific aspects of the phenomenon under consideration.

Nonetheless, across a broad collection of definitions for consciousness, including the diversity of forms that consciousness takes, a few ideas consistently recur (Sattin et al., 2021). There is almost universal agreement that consciousness is subjective, or an awareness only accessible by and seemingly occurring within or to the individual organism. An emphasis on the phenomenological character of consciousness draws attention to how it feels, always in terms of sensory perception and often including emotional feeling as well. Above all, consciousness is acknowledged as and often taken to be synonymous with current experience. Ginsburg and Jablonka (2019) even use "subjective experiencing" as a synonym for consciousness. Often, but not always, explicit reference is also made to the fact that consciousness is a process arising within a nervous system. The need to define consciousness as precisely as possible in all communications about the subject is obvious (Francken et al., 2022).

For the purposes of this viewpoint, the definition offered by co-editors of a recent collection of papers on comparative animal consciousness will apply: Consciousness is "the process by which an animal has perceptual and affective experience or feelings, arising from the material substrate of a nervous system" (Irwin et al., 2022).

The Ontological Issues

The nature of consciousness – its essence, features, and substrate – as well as the interdependence among its different aspects, constitute the ontological issues of consciousness.

Phenomenal Features of Subjective Experience

Numerous authors have assembled a short list of the essential features of consciousness. Most commonly they include the following:

Focused Attention

Humans report and other animals behave as though they are attending to or aware of one thing at a time. This does not preclude the fact that awareness of peripheral or unrelated sensory perceptions are present, but that the organism's attention is focused on one particular subject or event at a given instant. This traditionally has been considered a major feature of consciousness (Dehaene and Naccache, 2001; Edelman et al., 2011; Baars and Edelman, 2012). "My experience is what I agree to attend to," in the words of William James (1890), who further defined consciousness as "the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought."

Mental Unity

Mental unity refers to that feature of consciousness that gives rise to a coherent perception of reality. All the individual sensations or fragments of memory appear as an integrated and meaningful rather than a fragmented target of attention (Tononi, 2004; Feinberg, 2012; Ginsburg and Jablonka, 2019; Miyahara and Witkowski, 2019).

Qualitative Content and Variation

Within a given modality, such as vision, conscious organisms with color vision discern the difference between red, blue, and yellow, and hundreds of shades in between. Different pitches of sound, exposure to variable temperatures, numerous forms of pain, and a variety of pleasurable sensations are distinguishable in the conscious state. The qualitative differences within perceptual modalities are referred to as *qualia* (singular, *quale*). All these different perceptual qualities reflect differences in the physical nature of the stimuli (wavelength of light, frequency of sound waves, *etc.*) and the neural mechanisms that transpose them into decipherable information within the nervous system (wavelength-sensitive photopigments, cochlear hair cells sensitive to different sound frequencies, *etc.*), and serve to enable high-order discriminations in a multidimensional space of signals (Edelman, 2003).

Mental Causation

Mental causation refers to the capacity for consciousness to initiate volitional activity, invoke imagery, or access memory (Feinberg and Mallatt, 2018). Humans can conjure images and recall memory from a state of idle thinking. The extent to which other animals do so is unclear, though the parallel evolution of imaginative consciousness among different vertebrates seems evident (Zachs et al., 2022). All motile organisms show goal-directed behavior, and the role of consciousness for carrying it out has frequently been noted (Sheets-Johnstone, 1999; Dehaene and Naccache, 2001; Frith, 2002; Koch, 2012; Fried et al., 2017; Williford et al., 2018; Ginsburg and Jablonka, 2019; Pennartz et al., 2019). Intentional movement is the way an organism interacts volitionally with its environment, and a consciousness of spatial orientation and extent is central to this ability (Merleau-Ponty, 1945; Clark, 2016; Stocker, 2016; Irwin and Irwin, 2020; Vallortigara, 2021). Furthermore, the behavioral versatility characteristic of volitional behavior is most effectively organized by conscious thinking (Griffin and Speck, 2004).

Sense of Self

A central feature of consciousness is held to be a sense of self (Husserl, 1962; Humphrey, 1992; Searle, 1992; Feinberg, 2001; Churchland, 2002; Blanke and Metzinger, 2009; Godfrey-Smith, 2016; Ginsburg and Jablonka, 2019; Seth, 2021; Abdulkarim et al., 2023). This must have emerged in the course of evolution when an organism gained the ability to distinguish between external stimuli ("What is happening out there") and internally generated feelings ("What is happening to me") (Humphrey, 1992; Vallortigara, 2020; Jablonka and Ginsburg, 2022). "Animal evolution produced... subjectivity and agency. It also produced animals who handle their dealings with the world in a way that includes *a tacit sense of self."* (Godfrey-Smith, 2020). Arguments that it could be widespread have been numerous (Droege and Braithwaite, 2015; Barron and Klein, 2016; Kohda et al., 2019; Fernö et al., 2020; Chittka, 2022).

Other Features Favored by Some Authors

In addition to the five phenomenal features of consciousness listed above, a few others are occasionally invoked. They include (1) Referral: the perception that experience occurs outside the head (Thompson and Varela, 2001; Feinberg and Mallatt, 2016); (2) Temporal depth: the capacity to hold on to incoming information in a working memory, so the present has some duration (Varela, 1996; Droege and Braithwaite, 2015; Williford et al., 2018; Jablonka and Ginsburg, 2022); (3) Global accessibility and broadcast: the capacity to link and integrate information from perception, memory and evaluative systems and broadcast the output back to input and executive systems that lead to relevant actions (Dehaene and Naccache, 2001; Edelman, 2003; Jablonka and Ginsburg, 2022); (4) Value attribution: the capacity to alter and update the rewarding or punishing values of actions and sensory stimuli (Varela, 1996; Jablonka and Ginsburg, 2022); (5) Perceptual filling-in: the spontaneous completion of a percept into a unified whole despite the partial absence of some primary sensory input (Varela, 1996); and (6) Situatedness: the capacity for map-based and object-oriented spatial cognition (Buzsáki, 2019; Pennartz et al., 2019; Irwin and Irwin, 2020; Jablonka and Ginsburg, 2022).

Requisite Biological Substrate

Building on the phenomenological approach of Varela (1991; Thompson and Varela, 2001) and the ecological psychology of Gibson (1979), modern cognitive science tends to favor the 4E (embodied, embedded, extended, and enacted) paradigm of cognition (Bateson, 2000). The resulting view of consciousness as a phenomenon that is structured and shaped by dynamic interactions between the brain, body, and both the physical and social environments (Hanna and Thompson, 2003; Gallagher and Zahavi, 2008; Di Paolo et al., 2010; Silberstein and Chemero, 2012; Newen et al., 2018; Domasio, 2021) is both credible and useful (Irwin and Irwin, 2020). Which agents, alive or not, have consciousness — and if living, whether consciousness is reducible to neural processes or encompasses a more expansive phenomenological experience — are ongoing debates. But this essay is concerned only with neurally-based consciousness, so by definition pertains only to animals with a nervous system. That being the case, what are the characteristics of nervous systems in which consciousness is embedded (or from which it is enacted)?

Like most aspects of consciousness, the scientific approach to revealing the neural substrates of consciousness derive from what is known about it in humans, other primates, mammals, and birds. Since the middle of the last century, a background of maintained activity within an ascending reticular formation in the upper brain stem of mammals has been correlated with degrees of wakefulness (Moruzzi and Magoun, 1949; Butler and Hodos, 1996a; Merker, 2007). It has also long been recognized that thalamic components of the reticular formation connect with the telencephalon (forebrain) in all vertebrate classes, comprising a phylogenetically old and evolutionarily stable system (Butler and Hodos, 1996c). The complexity and details of these connections vary across the different vertebrate classes, with amniotes (mammals, birds, and reptiles) generally possessing more numerous and dispersed neuronal connections than those of anamniotes (the other vertebrate classes). Nonetheless, a hierarchical organization is clear in all vertebrate nervous systems that distinguishes higher, more centralized centers from those that are lower, more peripheral, and closer to sensory input and motor output.

The nervous systems of invertebrates differ radically in many anatomical details from those of vertebrates, but complex hierarchical organization consisting of multiple layers or relays in both sensory and motor pathways can be discerned in several taxa, including the polychaete annelids, coleoid cephalopods (cuttlefish, squid, and octopi), and arthropods (Bullock, 1977).

Feinberg and Mallat (2020) have promoted the commonly-held view that consciousness is an evolved product of complex brains in complex bodies, so it is an emergent feature of a complex physical system. They have argued that animals with sensory hierarchies can be conscious if they have four or more levels of neurons projecting to (and including) the highest processing area, or in some cases, just three levels (Feinberg and Mallatt, 2016). Their reasoning is that consciousness is *structurally* complex because its neural circuits combine diverse details and types of sensory input into one unified experience. Complexity frequently takes the form of hierarchy (Simon, 1962), and hierarchies gain their complexity, among other ways, by gaining more levels, by increasing the number and specialization of components in each level, and by more interaction among the levels. From this growing complexity emerges more-sophisticated behaviors and consciousness. Other authors essentially agree (Tononi and Edelman, 1998; Koch, 2012; Campana et al., 2016; King and Wyart, 2021; Siegle et al., 2021; Chittka, 2022). The minimal number of layers required for consciousness was set initially at four because the neural substrates of most sensory processing which leads to perception in humans is four.

Though differing dramatically in anatomical detail, brains that fit this description can be found in all vertebrates and arthropods. While the coleoid cephalopods likewise share this description, they also have the unique feature of having complex neural centers peripherally located from their centrally-organized brains. Particularly in octopi, more neural tissue is found at the base of their eight arms than in their brains, raising the prospect that conscious experiences may be simultaneously multiple and diversely situated in those animals (van Woerkum, 2020; Carls-Diamante, 2022).

Significant variation in brain complexity is repeatedly observed, often within narrow taxonomic bounds as well as across broadly separated clades (Bullock, 1984; Northcutt, 1985; Butler and Hodos, 1996b; Striedter, 2005), consistent with the probability of the independent origin and diverse parallel evolution of different forms of neural complexity (Godfrey-Smith, 2020). Given that fact and the apparent ancient origins of at least sensory consciousness, it seems highly likely that consciousness itself had multiple independent origins and is mediated by a variety of independently evolved neural architectures (Feinberg and Mallatt, 2016; Irwin, 2020; Mallatt and Feinberg, 2021). However, the alternative of a single origin early in the evolution of animals, followed by divergence and loss in some clades cannot be ruled out.

The Evolutionary Imperative

The ontology of consciousness (subjective experiencing) as laid out in the previous section provides a framework for exploring the question of its evolutionary origins and subsequent evolution.

Given the need to integrate multiple sensory inputs with ongoing motor responses in a unified and coherent manner, some level of consciousness must have arisen “when simple reflexives evolved into a unified 'inner world,' or 'qualia,' or the subjective feeling of things” (Feinberg and Mallatt, 2016; Feinberg and Mallatt, 2020). A number of authors agree with this assumption (Edelman, 2003; Griffin and Speck, 2004; Lacalli, 2020, 2022).

Consciousness became necessary especially once animals started moving about, in order to solve the logistical problems of decision making while in motion (Merker, 2005; Chittka and Wilson, 2019; Irwin, 2020; Vallortigara, 2021).

The simplest multicellular organisms that became fully motile emerged during the Precambrian, but the simplicity of their nervous systems leaves their capacity for consciousness in question. By the time arthropods became a dominant feature of the Cambrian seascape, however, neural complexity had advanced to the level of hierarchical organization deemed necessary for consciousness; so some form of consciousness has likely existed for close to half a billion years (Feinberg and Mallatt, 2016). Arising somewhat later and independently were the vertebrates (Cowen, 1995) and coleoid cephalopods (Nixon and Young, 2003)—groups that also have nervous systems sufficiently hierarchical and complex for consciousness. The earliest vertebrates probably had concentrated sensory centers in their midbrains, hence consciousness may have been mediated by the midbrain in that group (Lacalli, 2018). Subsequent evolution relocated details of sensory perception and motor control to higher brain centers, now considered a neuroanatomical necessity for animals that perceive qualia at a high level of resolution and manage motion with fine motor control. This includes all mammals.

Credible arguments in fact have been advanced for some level of consciousness in all other vertebrates as well (Feinberg and Mallatt, 2018). The evidence is particularly strong for birds (Edelman et al., 2005; Butler, 2008; Herculano-Houzel, 2020; Nieder et al., 2020; Pepperberg, 2020; Gunturkun, 2021; Ehret and Romand, 2022), but has also been advanced for reptiles (Learmonth, 2020), amphibians (Berry and Mendelson, 2019), and fishes (Kohda et al., 2019; Fernö et al., 2020; Akinrinade et al., 2023), including Agnatha (Lacalli, 2018; Suzuki, 2021), the class basal to the evolution of all vertebrates.

Among invertebrates, plausible evidence for cognition complex enough to imply consciousness has been reported for insects (Menzel, 2012; Stopfer, 2014; Barron and Klein, 2016; Wilson, 2018; Chittka and Wilson, 2019), arachnids (Cross and Jackson, 2019), decapod crustaceans (Elwood, 2019; de Souza Valente, 2022), and cephalopods (Mather, 2008; Edelman and Seth, 2009; Godfrey-Smith, 2016; Schnell and Clayton, 2020; Ponte et al., 2022), though smaller brains with an (undetermined) insufficiency of neurons may limit the capacity for consciousness in some members of those groups. A fair critique of this list is that these are simply the best studied cases. Further research may disclose similar evidence in other invertebrates.

Ginsburg and Jablonka (2010) agree that the origin of consciousness was ancient, likely arising during the great Cambrian diversification. They propose that one of the key factors driving this diversification was associative learning, and propose that the emergence of unlimited associative learning (UAL) marked the transition point in evolution from the absence of consciousness to its minimal presence (Ginsburg and Jablonka, 2019), although an evolutionary transition that is completed or mature rather than minimal may be a more appropriate construal of their argument for the importance of UAL (Metzinger, 2020; Irwin, 2022).

Summarizing the implications for comparative animal consciousness provided by the arguments above, the general consensus appears to be that the dramatic diversification of animal forms and interactions during the Cambrian over 500 million years ago led to natural selection for more complex nervous systems. These were required for discerning qualitative variations in sensory inputs, integrating various modes of information, controlling goal-directed motor behavior, and facilitating learning. In two major clades (arthropods and vertebrates) and at least one subclass of mollusks (coleoids), arguments for the capacity for consciousness are widely accepted.

Remaining Uncertainties

Broad agreement in principle has been reached among neuroscientific researchers concerning the definitional outlines of primary (sensory) consciousness and the ontological features of phenomenal experience across the animal kingdom. Also, complex nervous systems with multilayered processing capability are widely (though not universally) believed to be a minimal requirement for consciousness. The major uncertainties remaining are three-fold: (1) What are the neurological correlates of consciousness? (2) How can the gap between mechanism and phenomenology be bridged? (3) What is the monitoring mechanism for those processes?

The Neurological Correlates of Consciousness (NCCs)

While conceding once again that a full account of animal consciousness entails more than the neural processes that give rise to it, no one doubts that neural processes are a necessary part of the account. The time may come when components of machines may serve as well as neurons for the generation of consciousness, but for now the only substrates for consciousness of which we can be certain are the complex nervous systems of animals. But what exactly are the neural circuits and processes that underlie phenomenal consciousness?

Underlying the ontology of consciousness is the assumption that fragments of experience are coextensive with specific patterns of neuronal activity. The circuits that mediate this activity have variously been called ‘cell assemblies’ (Hebb, 1949; Restivo et al., 2015), ‘structured neuronal groups’ (Edelman, 1978), or ‘selector circuits’ (Lacalli, 2022), among others, and are assumed to be local neuronal ensembles whose pattern of activity varies for different qualia or for diverse units of perception. These would be the elementary, or primary, neuronal correlates of consciousness, though are not assumed to be sufficient for consciousness alone.

Different theories of consciousness propose different mechanisms for raising the primary NCCs to conscious awareness, and there is no consensus on which theory or mechanism is likely to provide the most accurate account of how consciousness is generated. However, the three following models are among those frequently advanced as being most promising (Francken et al., 2022). All three were proposed in the context of mammalian (and largely human) neuroanatomy, but their characteristics are generalizable enough to be applicable to any animal with a sufficiently complex nervous system.

Not surprisingly, many current hypotheses about the neural basis for consciousness focus particularly on the thalamocortical circuitry well understood in mammals (Frith, 2002; Butler, 2008; Edelman and Seth, 2009; Aru et al., 2019). Alignment of the arousal function of the brainstem reticular formation with the feedforward and feedback relationship between the thalamus and higher brain regions fits nicely with the view of Gerald Edelman (1989) that consciousness is a form of awareness that arises from integration of many inputs by reentrant interactions in the *Dynamic Thalamocortical Core* (Edelman, 2003). Empirical evidence in support of this view includes the observation that human consciousness involves widespread, relatively fast low-amplitude interactions in the thalamocortical core of the brain (Seth et al., 2005); that the descent to sleep is subserved by reduced thalamocortical connectivity (Spoormaker et al., 2010); that transcranial magnetic stimulation and high-density EEG can detect clear-cut changes in the ability of the thalamocortical system to integrate information when the level of consciousness fluctuates across the sleep-wake cycle (Massimini et al., 2009); and that activity of the thalamus with specific cortical regions is fundamental for human consciousness (Scheinin et al., 2021).

A related hypothesis is that of the *Global Neuronal Workspace* (GNW) that views access to consciousness when incoming information is made globally available to multiple brain systems through a network of neurons with long-range axons densely distributed in the cerebral cortex (Dehaene and Naccache, 2001; Dehaene and Changeux, 2011). Evidence supporting this model includes source-reconstructed data from frontal and parietal cortices during normal wakefulness, propofol-induced mild sedation, and loss of consciousness that demonstrate the importance of recurrent corticocortical communication in the maintenance of consciousness (Boly et al., 2012); data showing that coactivation of the somatosensory cortex and ventral premotor cortex was more frequent in conscious than in unconscious states (Noel et al., 2019); and the finding that alterations in long-distance connectivity were associated with psychotic symptoms, supporting the hypothesis that long-distance structural connectivity within the GNW plays a crucial role in conscious access (Berkovitch et al., 2021). The GNW model is particularly attractive in view of the unitary and multimodal nature of phenomenology.

A distinct but compatible concept is that of *Higher-Order Thought (HOT),* which proposes that conscious awareness occurs when nonconscious primary sensory information is cognitively re-represented in a higher-order mental state (Rosenthal, 2000). Inherently invoking hierarchical processing, HOT is compatible with known features of sensory processing (Campana et al., 2016; King and Wyart, 2021), executive functions (Marino, 2005; Merker, 2007; Bobrowicz et al., 2020), and emotion (LeDoux and Brown, 2017; Brown et al., 2019). Though exemplified most often in the case of visual perception in mammals (LeDoux, 2019), HOT could apply to any perception arising from hierarchical processing of sensory information.

The Dynamic Thalamocortical Core, GNW, and HOT models of consciousness share a number of overlapping features, and generally reinforce one another (Edelman et al., 2011; LeDoux, 2019; Noel et al., 2019). No single model, however, covers the full spectrum of the phenomenal features of conscious experience (Seth et al., 2006). And some researchers have reported data inconsistent with the GNW and HOT models. For instance, stimulation of anterolateral prefrontal sites, often considered crucial in GNW and HOT theories of consciousness, seldom elicits any reportable alterations in consciousness (Raccah et al., 2021). Also, evidence that anesthetics can dissociate an animal's level of consciousness from cortical connectivity (Pal et al., 2020) raises questions about the role of cortical connectivity in consciousness. Furthermore, the applicability of currently proposed NCCs to animals with neural architectures very different from those on which most models are based will remain in question until mechanisms compatible with the diversity of nervous systems over a broader range of the animal kingdom are explored (Storm et al., 2017).

Bridging the Gap Between Mechanism and Phenomenology

Even if the neural correlates of consciousness could be decisively determined, an explanatory gap would remain between the bioelectrical and neurochemical dynamics of the relevant circuits, and the phenomenological manifestation of those dynamics.

David Chalmers, the philosopher most commonly associated with the 'hard problem' of the disconnect between mechanism and phenomenology, argued that "the explanation of functions does not suffice for the explanation of experience" (Chalmers, 1995). Gerald Edelman (2003) agreed, but said it doesn't have to: "A scientific theory cannot presume to replicate the experience that it describes or explains; a theory to account for a hurricane is not a hurricane." He goes on to argue that "differences in qualia correlate with differences in the neural structure and dynamics that underlie them." Related notions are numerous (Searle, 1992; Thompson and Varela, 2001; Dehaene and Changeux, 2011; Feinberg, 2012). Churchland (2007) wrote that "... what we call 'the mind' is in fact a level of brain activity...."

Lahav & Neemeh (2021) argue that phenomenology (the experience of consciousness) and the neural processes that give rise to the experience are two different ways the same phenomenon appears based on the perspective of the observer. That perspective is either from within the cognitive system (the first-person perspective) or outside of it (the third-person perspective). A similar distinction was earlier made between "auto- and allo-ontological irreducibilities," contrasting the first-person and third-person accounts of the same reality (Feinberg and Mallatt, 2018).

Related to the argument of differing perspectives is the case for different levels of resolution between dynamics of particular patterns of neural activity and the holistic perception of those processes as they emerge in consciousness (Searle, 2004). The granular details of the neural substrate of consciousness are analogous to the pixels of a display on a computer screen. Though actually based on the sum of all the pixels on the screen, the pixels are not perceived individually but their overall effect is perceived as a complex, holistic gestalt. In like manner, an image emerges in consciousness from the collective activity of millions of neurons as a unified and meaningful holistic image. Another example would be the sensation arising from water in contact with the skin. The perception of "wetness" (a combination of temperature and texture) arises from contact with a massive number of water molecules detected by particular receptors that generate action potentials in specific neuronal circuits. The granular details of the neural dynamics are not individually detectable by the cognitive system, which instead perceives their overall effect as "water in contact with the skin." In these cases, the differences in perspective are based on different levels of resolution. In all likelihood, the greater the number of neurons involved in neural processing of the stimulus, the higher will be the level of resolution of the resulting perceptual content (Herculano-Houzel, 2017).

Most neuroscientists agree with the argument that consciousness arises from a physical substrate in a manner that will be uncovered in time, when newer data and insights conveyed through a more suitable vocabulary will clarify the link between mechanism and experience (P.S. Churchland, 1982; P.S. Churchland and Sejnowski, 1988; P.M. Churchland, 2013). We are not there yet though.

The Monitoring Mechanisms of Consciousness

In the previous section, two possible explanations were offered that sought to reconcile the action of local neuronal circuits with the holistic phenomenological experience that activity in those circuits gives rise to. But widespread vigorous neuronal activity is occurring constantly throughout the brain, in all states of awareness, *without* giving rise to conscious experience (Batterink and Neville, 2013). So what is the filter that determines which neural processes will make their way into consciousness? What is the nature of the agent that focuses on only those neural events of which we are conscious, and where in the nervous system (or body) does it reside?

A reasonable assumption is that the agency of consciousness — the 'witness' to the relevant neural processes — is itself a specific neural process. What that filter or witness or focusing mechanism is has not been determined for humans, much less for any other animal. Dennett (1991, 2017) has been adamant in laying to rest any dualistic explanations of consciousness. In so doing, he has derided the notion of a 'Cartesian Theater' where neural activity giving rise to consciousness is put on display. However, his own Multiple Drafts model in which multitrack processes of interpretation and elaboration of sensory inputs are under continuous 'editorial revision' leaves open the question of what is doing the editing and revising. Therefore, it seems clear that some compartment of the brain (Crick, 1984; Slagter et al., 2017; Aru et al., 2019) or of brain activity (Goldman et al., 2019) admits some neural activity into consciousness while all other activity in that moment is excluded. Metaphorically, at least, a screening room (Cartesian Theater) in which or by which such a process takes place may be a fit analogy.

Summary and Conclusions

A comprehensive and credible scientific explanation of consciousness across the full range of animal phylogeny is not yet agreed upon by those who have studied it intensively in humans and other animals. But there appears to be growing agreement on several critical elements of phenomenological consciousness across the animal kingdom. The following elements of broad agreement are offered as rebuttable assertions about the current state of animal consciousness research:

1. Animal consciousness can minimally be defined as the *process* by which an animal has *perceptual and affective experience or feelings*, arising from the material *substrate of a nervous system.*
2. The experience of being conscious entails, at a minimum, (1) being aware and capable of focusing attention, (2) perceiving reality in a unified and coherent manner, (3) distinguishing qualitative details and variations in the content of what is being experienced, (4) being able to initiate mental imagery and volitional activity, and (5) having a sense of self. Beyond this baseline of features that all conscious animals experience, some must also perceive temporal depth, emotion, a sense of place, and be capable of perceptual infilling, mental causation, and value attribution.
3. Animal consciousness is implemented by complex nervous systems that process information through neural circuits encompassing at least three hierarchical levels. All vertebrates, most if not all arthropods, and the coleoid cephalopods have nervous systems that meet these criteria. Future research will likely lead to expansion of this list.
4. Animal consciousness first arose about 500 million years ago under the selective pressure to integrate multiple modalities of information involving larger, more dynamic, motile organisms. It probably evolved independently in different branches of the animal kingdom in a number of different neural architectures. The nature of conscious experience therefore varies greatly according to the neural peculiarity, body form, and ecological function of different species in diverse habitats.

Uncertainty remains about three aspects needed for a comprehensive understanding of how animals generate consciousness:

1. Of the many theories about the mechanism by which animals create phenomenological experience, no single theory is agreed upon. A few models, like the Dynamic Thalamocortical Core, Global Neuronal Workspace, and Higher Order Thought have many adherents. Most theories about the neurological correlates of consciousness have overlapping features, and the reality may consist of different combinations of various aspects of multiple theories unique to different species.
2. The gap between the phenomenological experience of consciousness and its neurological correlates remains controversial, but plausible explanations relating mechanism to phenomenology are arising as the neuroscientific study of consciousness matures.
3. The agency of consciousness — the 'witness' to the neural processes that give rise to phenomenological experience, as opposed to all the other neural activity that simultaneously remains unconscious — has not been determined for humans, much less for any other animal. What that filter or witness or focusing mechanism is in different species is a major challenge in consciousness research. The notion of a 'Cartesian Theater' where neural activity giving rise to consciousness is put on display has been derided by Dennett (1991), but may in fact be a fitting metaphor.

References

- Abdulkarim Z, Guterstam A, Hayatou Z, Ehrsson HH (2023) Neural substrates of body ownership and agency during voluntary movement. J Neurosci 43:2362-2380.
- Akinrinade I, Kareklas K, Teles MC, Reis TK, Gliksberg M, Petri G, Levkowitz G, Oliveira RF (2023) Evolutionarily conserved role of oxytocin in social fear contagion in zebrafish. Science 379:1232-1237.
- Aru J, Suzuki M, Rutiku R, Larkum ME, Bachmann T (2019) Coupling the state and contents of consciousness. Front Syst Neurosci 13.
- Baars BJ, Edelman DB (2012) Consciousness, biology and quantum hypotheses. Physics of life reviews 9:285-294.
- Barron AB, Klein C (2016) What insects can tell us about the origins of consciousness. Proc Natl Acad Sci U S A 113:4900-4908.
- Bateson G (2000) Steps to an Ecology of Mind, 2nd Edition. Chicago: Univ. of Chicago Press.

- Batterink L, Neville H (2013) The human brain processes syntax in the absence of conscious awareness. J Neurosci 33:8528-8533.
- Berkovitch L, Charles L, Del Cul A, Hamdani N, Delavest M, Sarrazin S, Mangin JF, Guevara P, Ji E, d'Albis MA, Gaillard R, Bellivier F, Poupon C, Leboyer M, Tamouza R, Dehaene S, Houenou J (2021) Disruption of conscious access in psychosis is associated with altered structural brain connectivity. J Neurosci 41:513-523.
- Berry SM, Mendelson JR (2019) Caudata cognition. In: Encyclopedia of Animal Cognition and Behavior. (Vonk J, Shackelford T, eds): Springer Cham.
- Blanke O, Metzinger T (2009) Full-body illusions and minimal phenomenal selfhood. Trends Cogn Sci 13: P7-13.
- Bobrowicz K, Johansson M, Osvath M (2020) Great apes selectively retrieve relevant memories to guide action. Sci Rep 10:12603.
- Boly M, Moran R, Murphy M, Boveroux P, Bruno MA, Noirhomme Q, Ledoux D, Bonhomme V, Brichant JF, Tononi G, Laureys S, Friston K (2012) Connectivity changes underlying spectral EEG changes during propofol-induced loss of consciousness. J Neurosci 32:7082-7090.
- Brown R, Lau H, LeDoux JE (2019) Understanding the higher-order approach to consciousness. Trends Cogn Sci 23:754-768.
- Bullock T (1977) Survey of animal groups. In: Introduction to Nervous Systems, 1st Edition (Bullock T, ed), pp 393-494. San Francisco: W. H. Freeman Co.
- Bullock TH (1984) Understanding brains by comparing taxa. Perspect Biol Med 27:510-524.
- Butler AB (2008) Evolution of brains, cognition, and consciousness. Brain Res Bull 75:442-449.
- Butler AB, Hodos W (1996a) The Reticular Formation, Chapter 13. In: Comparative Vertebrate Neuroanatomy: Evolution and Adaptation, pp 164-179. New York: Wiley-Liss.
- Butler AB, Hodos W (1996b) Comparative Vertebrate Neuroanatomy: Evolution and Adaptation. New York: Wiley-Liss.
- Butler AB, Hodos W (1996c) Dorsal Thalamus, Chapter 22. In: Comparative Vertebrate Neuroanatomy: Evolution and Adaptation, pp 307-327. New York: Wiley-Liss.
- Buzsáki G (2019) The Brain from Inside Out. New York: Oxford University Press.
- Campana F, Rebollo I, Urai A, Wyart V, Tallon-Baudry C (2016) Conscious vision proceeds from global to local content in goal-directed tasks and spontaneous vision. J Neurosci 36:5200-5213.
- Carls-Diamante S (2022) Where is it like to be an octopus? Front Syst Neurosci 16: DOI: 10.3389/fnsys.2022.840022
- Chalmers DJ (1995) Facing up to the problem of consciousness. Journal of Consciousness Studies 2:200-219.
- Chittka L (2022) The Mind of a Bee. Princeton, NJ: Princeton University Press.
- Chittka L, Wilson C (2019) Expanding consciousness. Amer Scientist 107:364-369.
- Churchland PM (2013) Matter and Consciousness, 3rd Edition. Cambridge, MA: MIT Press.
- Churchland PS (1982) Mind-brain reduction: new light from the philosophy of science. Neuroscience 7:1041-1047.
- Churchland PS (2002) Self-representation in nervous systems. Science 296:308-310.
- Churchland PS (2007) Neurophilosophy: the early years and new directions. Funct Neurol 22:185-195.
- Churchland PS, Sejnowski TJ (1988) Perspectives on cognitive neuroscience. Science 242:741-745.
- Clark A (2016) Surfing Uncertainty: Prediction, Action, and the Embodied Mind. New York: Oxford University Press.
- Cowen R (1995) History of Life, 2nd Edition. Boston: Blackwell.
- Crick F (1984) Function of the thalamic reticular complex: the searchlight hypothesis. Proc Natl Acad Sci U S A 81:4586-4590.
- Cross FR, Jackson RR (2019) Portia's capacity to decide whether a detour is necessary. J Exp Biol 222.
- de Souza Valente C (2022) Anaesthesia of decapod crustaceans. Vet Anim Sci 16:100252.
- Dehaene S, Naccache L (2001) Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. Cognition 79:1-37.
- Dehaene S, Changeux JP (2011) Experimental and theoretical approaches to conscious processing. Neuron 70:200-227.
- Dennett DC (1991) Consciousness Explained. Boston: Little, Brown & Co.
- Dennett DC (2017) From Bacteria to Bach and Back. New York: W.W. Norton & Co.
- Di Paolo EA, Rohde M, De Jaegher H (2010) Horizons for the enactive mind: values, social interaction, and play. In: Enaction: Toward a New Paradigm for Cognitive Science (Stewart J, Gapenne O, Di Paolo EA, eds), pp 33-87. Cambridge, MA: MIT Press.
- Domasio A (2021) Feeling and Knowing: Making Minds Conscious. New York: Pantheon.
- Droege P, Braithwaite VA (2015) A framework for investigating animal consciousness. Curr Top Behav Neurosci 19:79-98.

- Edelman DB, Seth AK (2009) Animal consciousness: a synthetic approach. Trends Neurosci 32:476-484.
- Edelman DB, Baars BJ, Seth AK (2005) Identifying hallmarks of consciousness in non-mammalian species. Conscious Cogn 14:169-187.
- Edelman GM (1978) Group selection and phasic reentrant signaling: A theory of higher brain function. In: The Mindful Brain: Cortical Organization and the Group-Selective Theory of Higher Brain Function, pp 51-100. Cambridge MA: MIT Press.
- Edelman GM (1989) The Remembered Present: A Biological Theory of Consciousness. New York: Basic Books.
- Edelman GM (2003) Naturalizing consciousness: a theoretical framework. Proc Natl Acad Sci U S A 100:5520-5524.
- Edelman GM, Gally JA, Baars BJ (2011) Biology of consciousness. Frontiers in psychology 2:4, doi: 10.3389/fpsyg.2011.00004.
- Ehret G, Romand R (2022) Awareness and consciousness in humans and animals – neural and behavioral correlates in an evolutionary perspective. Front Syst Neurosci 16.
- Elwood RW (2019) Discrimination between nociceptive reflexes and more complex responses consistent with pain in crustaceans. Philos Trans R Soc Lond B Biol Sci 374:20190368.
- Feinberg TE (2001) Altered Egos: How the Brain Creates the Self. New York: Oxford University Press.
- Feinberg TE (2012) Neuroontology, neurobiological naturalism, and consciousness: a challenge to scientific reduction and a solution. Physics of life reviews 9:13-34.
- Feinberg TE, Mallatt JM (2016) The Ancient Origins of Consciousness: How the Brain Created Experience. Cambridge, MA: MIT Press.
- Feinberg TE, Mallatt JM (2018) Consciousness Demystified. Cambridge, MA: MIT Press.
- Feinberg TE, Mallatt J (2020) Phenomenal consciousness and emergence: Eliminating the explanatory gap. Frontiers in psychology 11:1041.
- Fernö A, Folkedal O, Nilsson J, Kristiansen TS (2020) Inside the Fish Brain: Cognition, Learning and Consciousnes. In: The Welfare of Fish. Animal Welfare, vol 20 (Kristiansen T, Fernö A, Pavlidis M, van de Vis H, eds), pp 149-183. Cham.: Springer.
- Francken JC, Beerendonk L, Molenaar D, Fahrenfort JJ, Kiverstein JD, Seth AK, van Gaal S (2022) An academic survey on theoretical foundations, common assumptions and the current state of consciousness science. Neuroscience of consciousness 2022.
- Fried I, Haggard P, He BJ, Schurger A (2017) Volition and action in the human brain: processes, pathologies, and reasons. J Neurosci 37:10842-10847.
- Frith C (2002) Attention to action and awareness of other minds. Conscious Cogn 11:481-487.
- Gallagher S, Zahavi D (2008) The Phenomenological Mind: An Introduction to Philosophy of Mind and Cognitive Science, 1st Edition. New York: Routledge.
- Gibson JJ (1979) The Ecological Approach to Visual Perception. Boston: Houghton Mifflin.
- Ginsburg S, Jablonka E (2010) The evolution of associative learning: A factor in the Cambrian explosion. J Theor Biol 266:11-20.
- Ginsburg S, Jablonka E (2019) The Evolution of the Sensitive Soul: Learning and the Origins of Consciousness. Cambridge, MA: MIT Press.
- Godfrey-Smith P (2016) Other Minds: The Octopus, the Sea, and the Deep Origins of Consciousness. New York: Farrar, Straus and Giroux.
- Godfrey-Smith P (2020) Metazoa: Animal Minds and the Birth of Consciousness. London: William Collins.
- Goldman JS, Tort-Colet N, di Volo M, Susin E, Bouté J, Dali M, Carlu M, Nghiem T-A, Górski T, Destexhe A (2019) Bridging single neuron dynamics to global brain states. Front Syst Neurosci 13.
- Graziano MSA, Guterstam A, Bio BJ, Wilterson AI (2020) Toward a standard model of consciousness: Reconciling the attention schema, global workspace, higher-order thought, and illusionist theories. Cogn Neuropsychol 37:155-172.
- Griffin DR, Speck GB (2004) New evidence of animal consciousness. Anim Cogn 7:5-18.
- Gunturkun O (2021) The conscious crow. Learn Behav 49:3-4.
- Hanna R, Thompson E (2003) Neurophenomenology and the spontaneity of consciousness. In: The Problem of Consciousness: New Essays in Phenomenological Philosophy of Mind (Thompson E, ed), pp 133-162. Calgary, Canada: Univ. of Calgary Press.
- Hebb DO (1949) The Organization of Behavior: A Neuropsychological Theory. New York: John Wiley.
- Herculano-Houzel S (2017) The Human Advantage: How Our Brains Became Remarkable. Cambridge, MA: MIT Press.
- Herculano-Houzel S (2020) Birds do have a brain cortex -- and think. Science 369:1567-1568.
- Humphrey N (1992) A History of the Mind: Evolution and the Birth of Consciousness. New York: Copernicus - Springer-Verlag.
- Husserl E (1962) Phenomenological Psychology, 1972 Edition. The Hague: Nijhoff.

- Irwin LN (2020) Renewed perspectives on the deep roots and broad distribution of animal consciousness. Front Syst Neurosci 14:10.3389/fnsys.2020.00057.
- Irwin LN (2022) How minimal can consciousness be? Biosemiotics 16: https://doi.org/10.1007/s12304-022-09518-3
- Irwin LN, Irwin BA (2020) Place and environment in the ongoing evolution of cognitive neuroscience. J Cogn Neurosci 32:1837-1850.
- Irwin LN, Chittka L, Jablonka E, Mallatt J (2022) Comparative animal consciousness. Front Syst Neurosci 16:998421. doi: 998410.993389/fnsys.992022.998421.
- Jablonka E, Ginsburg S (2022) Learning and the evolution of conscious agents. Biosemiotics https://doi.org/10.1007/s12304-022-09501-y
- James W (1890) Principles of Psychology. New York: Henry Holt.
- King J-R, Wyart V (2021) The human brain encodes a chronicle of visual events at each instant of time through the multiplexing of traveling waves. J Neurosci 41:7224-7233.
- Koch C (2012) Consciousness: Confessions of a Romantic Reductionist. Cambridge, MA: MIT Press.
- Kohda M, Hotta T, Takeyama T, Awata S, Tanaka H, Asai JY, Jordan AL (2019) If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals? PLoS Biol 17:e3000021.
- Lacalli T (2018) Amphioxus neurocircuits, enhanced arousal, and the origin of vertebrate consciousness. Conscious Cogn 62:127-134.
- Lacalli T (2020) Evolving Consciousness: Insights From Turing, and the Shaping of Experience. Front Behav Neurosci 14:598561.
- Lacalli T (2022) On the origins and evolution of qualia: An experience-space perspective. Front Syst Neurosci 16:945722.
- Lahav N, Neemeh ZA (2021) A relativistic theory of consciousness. Front Psychol 12:704270.
- Learmonth MJ (2020) The matter of non-avian reptile sentience, and why it "matters" to them: a conceptual, ethical and scientific review. Animals (Basel) 10.
- LeDoux J (2019) The Deep History of Ourselves: The Four-Billion-Year Story of How We Got Conscious Brains. New York: Viking.
- LeDoux JE, Brown R (2017) A higher-order theory of emotional consciousness. Proc Natl Acad Sci U S A 114:E2016-E2025.
- Mallatt J, Feinberg TE (2021) Multiple routes to animal consciousness: constrained multiple realizability rather than modest identity theory. Front Psychol 12:732336.
- Marino L (2005) Big brains do matter in new environments. Proc Natl Acad Sci U S A 102:5306-5307.
- Massimini M, Boly M, Casali A, Rosanova M, Tononi G (2009) A perturbational approach for evaluating the brain's capacity for consciousness. Prog Brain Res 177:201-214.
- Mather JA (2008) Cephalopod consciousness: behavioural evidence. Conscious Cogn 17:37-48.
- Menzel R (2012) The honeybee as a model for understanding the basis of cognition. Nature reviews Neuroscience 13:758-768.
- Merker B (2005) The liabilities of mobility: a selection pressure for the transition to consciousness in animal evolution. Conscious Cogn 14:89-114.
- Merker B (2007) Consciousness without a cerebral cortex: a challenge for neuroscience and medicine. Behav Brain Sci 30:63-81; discussion 81-134.
- Merleau-Ponty M (1945) Phénoménologie de la perception (Phenomenology of Perception). London: Routledge & Kegan Paul, 1965.
- Metzinger T (2020) Minimal phenomenal experience: Meditation, tonic alertness, and the phenomenology of "pure" consciousness. Philosophy and the Mind Sciences 1:7.
- Miyahara K, Witkowski O (2019) The integrated structure of consciousness: phenomenal content, subjective attitude, and noetic complex. Phenom Cogn Sci 18:731-758.
- Moruzzi G, Magoun HW (1949) Brain stem reticular formation and activation of the EEG. Electroencephalography and clinical neurophysiology 1:455-473.
- Newen A, De Bruin L, Gallagher S (2018) 4E cognition: historical roots, key concepts, and central issues. In: The Oxford Handbook of 4E Cognition (Newen A, De Bruin L, Gallagher S, eds). New York: Oxford University Press.
- Nieder A, Wagener L, Rinnert P (2020) A neural correlate of sensory consciousness in a corvid bird. Science 369:1626-1629.
- Nixon M, Young JZ (2003) The Brains and Lives of Cephalopods. New York: Oxford University Press.
- Noel JP, Ishizawa Y, Patel SR, Eskandar EN, Wallace MT (2019) Leveraging nonhuman primate multisensory neurons and circuits in assessing consciousness theory. J Neurosci 39:7485-7500.
- Northcutt RG (1985) Brain phylogeny: speculations on pattern and cause. In: Comparative Neurobiology: Modes of Communication in the Nervous System

(Cohen MJ, Strumwasser F, eds), pp 351-378. New York: John Wiley.

- Pal D, Li D, Dean JG, Brito MA, Liu T, Fryzel AM, Hudetz AG, Mashour GA (2020) Level of consciousness is dissociable from electroencephalographic measures of cortical connectivity, slow oscillations, and complexity. J Neurosci 40:605-618.
- Pennartz CMA, Farisco M, Evers K (2019) Indicators and criteria of consciousness in animals and intelligent machines: An inside-out approach. Front Syst Neurosci 13:DOI:10.3389/fnsys.2019.00025.
- Pepperberg IM (2020) The comparative psychology of intelligence: Some thirty years later. Front Psychol 11:973.
- Ponte G, Chiandetti C, Edelman DB, Imperadore P, Pieroni EM, Fiorito G (2022) Cephalopod behavior: From neural plasticity to consciousness. Front Syst Neurosci 15.
- Raccah O, Block N, Fox KCR (2021) Does the prefrontal cortex play an essential role in consciousness? Insights from intracranial electrical stimulation of the human brain. J Neurosci 41:2076-2087.
- Restivo L, Niibori Y, Mercaldo V, Josselyn SA, Frankland PW (2015) Development of adult-generated cell connectivity with excitatory and inhibitory cell populations in the hippocampus. J Neurosci 35:10600-10612.
- Rosenthal DM (2000) Consciousness, content, and metacognitive judgments. Conscious Cogn 9:203-214.
- Sattin D, Magnani FG, Bartesaghi L, Caputo M, Fittipaldo AV, Cacciatore M, Picozzi M, Leonardi M (2021) Theoretical models of consciousness: A scoping review. Brain Sci 11.
- Scheinin A, Kantonen O, Alkire M, Langsjo J, Kallionpaa RE, Kaisti K, Radek L, Johansson J, Sandman N, Nyman M, Scheinin M, Vahlberg T, Revonsuo A, Valli K, Scheinin H (2021) Foundations of human consciousness: Imaging the twilight zone. J Neurosci 41:1769-1778.
- Schnell AK, Clayton NS (2020) Cephalopods: Ambassadors for rethinking cognition. Biochem Biophys Res Commun 564:27-36.
- Searle J (1992) The Rediscovery of the Mind. Cambridge, MA: MIT Press.
- Searle J (2004) Mind: A Brief Introduction. New York: Oxford University Press.
- Seth AK (2021) Being You: A New Science of Consciousness. New York: Penguin Random House.
- Seth AK, Baars BJ, Edelman DB (2005) Criteria for consciousness in humans and other mammals. Consciousness and cognition 14:119-139.
- Seth AK, Izhikevich E, Reeke GN, Edelman GM (2006) Theories and measures of consciousness: an extended framework. Proc Natl Acad Sci U S A 103:10799-10804.
- Sheets-Johnstone M (1999) The Primacy of Movement. Amsterdam: John Benjamins Publishing.
- Siegle JH et al. (2021) Survey of spiking in the mouse visual system reveals functional hierarchy. Nature.
- Silberstein M, Chemero A (2012) Complexity and extended phenomenological-cognitive systems. Topics Cogn Sci 4:35-50.
- Simon HA (1962) The architecture of complexity. Proc Am Philos Soc 106:467-482.
- Slagter HA, Mazaheri A, Reteig LC, Smolders R, Figee M, Mantione M, Schuurman PR, Denys D (2017) Contributions of the ventral striatum to conscious perception: An intracranial EEG study of the attentional blink. J Neurosci 37:1081-1089.
- Spoormaker VI, Schroter MS, Gleiser PM, Andrade KC, Dresler M, Wehrle R, Samann PG, Czisch M (2010) Development of a large-scale functional brain network during human non-rapid eye movement sleep. J Neurosci 30:11379-11387.
- Stocker K (2016) Place cells and human consciousness: a force-dynamic account. Journal of Consciousness Studies 23:146-165.
- Stopfer M (2014) Central processing in the mushroom bodies. Curr Opin Insect Sci 6:99-103.
- Storm JF, Boly M, Casali AG, Massimini M, Olcese U, Pennartz CMA, Wilke M (2017) Consciousness regained: Disentangling mechanisms, brain systems, and behavioral responses. J Neurosci 37:10882-10893.
- Striedter GF (2005) Principles of Brain Evolution, 1st Edition. Sunderland, MA: Sinauer Associates.
- Suzuki DG (2021) Consciousness in Jawless Fishes. Front Syst Neurosci 15:751876.
- Thompson E, Varela FJ (2001) Radical embodiment: neural dynamics and consciousness. Trends Cogn Sci 5:418-425.
- Tononi G (2004) An information integration theory of consciousness. BMC neuroscience 5:42.
- Tononi G, Edelman GM (1998) Consciousness and complexity. Science 282:1846-1851.
- Vallortigara G (2020) The rose and the fly. A conjecture on the origin of consciousness. Biochem Biophys Res Commun 564:170–174.
- Vallortigara G (2021) The efference copy signal as a key mechanism for consciousness. Front Syst Neurosci 15:765646.
- van Woerkum B (2020) Distributed nervous system, disunified consciousness? A sensorimotor

integrationist account of octopus consciousness. Journal of Consciousness Studies 27:149-172.

- Varela F (1996) Neurophenomenology: A methodological remedy for the hard problem. Journal of Consciousness Studies 3:330-349.
- Varela FJ, Thompson ET, Bosch E (1991) The Embodied Mind: Cognitive Science and Human Experience. Cambridge, MA: MIT Press.
- Williford K, Bennequin D, Friston K, Rudrauf D (2018) The projective consciousness model and phenomenal selfhood. Front Psychol 9:DOI: 10.3389/fpsyg.2018.02571.
- Wilson C (2018) Consciousness as a biological phenomenon: An alternative to panpsychism. Harvard Rev Philos.
- Zachs O, Ginsburg S, Jablonka E (2022) The futures of the past the evolution of imaginative animals. J Conscious Stud 29:29-61.

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