

**Call for Commentary:** *Animal Sentience* publishes [Open Peer Commentary](#) on all accepted target articles. Target articles are peer-reviewed. Commentaries are editorially reviewed. There are submitted commentaries as well as invited commentaries. Commentaries appear as soon as they have been revised and accepted. Target article authors may respond to their commentaries individually or in a joint response to multiple commentaries.

**Instructions:** <http://animalstudiesrepository.org/animsent/guidelines.html>

## Insects have the capacity for subjective experience

Colin Klein<sup>1\*</sup> & Andrew B. Barron<sup>2\*</sup>

<sup>1</sup>Department of Philosophy, Macquarie University

<sup>2</sup>Department of Biological Sciences, Macquarie University

\*equal authorship contribution

**Abstract:** To what degree are non-human animals conscious? We propose that the most meaningful way to approach this question is from the perspective of functional neurobiology. Here we focus on subjective experience, which is a basic awareness of the world without further reflection on that awareness. This is considered the most basic form of consciousness. Tellingly, this capacity is supported by the integrated midbrain and basal ganglia structures, which are among the oldest and most highly conserved brain systems in vertebrates. A reasonable inference is that the capacity for subjective experience is both widespread and evolutionarily old within the vertebrate lineage. We argue that the insect brain supports functions analogous to those of the vertebrate midbrain and hence that insects may also have a capacity for subjective experience. We discuss the features of neural systems which can and cannot be expected to support this capacity as well as the relationship between our arguments based on neurobiological mechanism and our approach to the “hard problem” of conscious experience.

**Keywords:** subjective experience, primary consciousness, vertebrate midbrain, superior colliculus, invertebrate, insect



**Colin Klein** is Senior Lecturer in the Department of Philosophy at Macquarie University. He works on philosophy of neuroscience with a side interest in the perception of pain and other homeostatically relevant states. In 2014 he received an ARC Future Fellowship to look at interventionist approaches to cognitive neuroscience. <http://www.colinklein.org>

**Andrew B. Barron** is Associate Professor in the Department of Biological Sciences at Macquarie University. With his team at Macquarie, he is exploring the neurobiology of major behavioural systems such as memory, goal-directed behaviour and stress from a comparative and evolutionary perspective. In 2015 he was awarded an ARC Future Fellowship to develop a computational model of the honey bee brain. <http://bio.mq.edu.au/research/groups/cognitive-neuroethology/dr-andrew-barron/>



## **1. Introduction**

What follows is a synopsis of our argument in [Barron & Klein \(2016\)](#). Our intention here is both to summarize our arguments from comparative functional neurobiology that insects have subjective experience as well as to expand upon and clarify some points from our previous article. Here we provide some further discussion of why we believe the insect brain is capable of subjective experience and of the features of nervous system organization which do and do not have this capacity. We conclude with reflections on the relationship between our structural arguments and the so-called “hard problem of consciousness” (Chalmers, 1996).

## **2. Consciousness and Subjective Experience**

Consciousness is a complex, multifaceted phenomenon (Bayne, Hohwy, & Owen, 2016). Terminology to describe consciousness has proliferated more quickly than our understanding of the phenomenon. Most authors, however, mark off a very basic sense of “conscious” that refers to the basic capacity to have subjective experience (Morin, 2006). In Nagel’s (1974) familiar term of art, there is “something it is like” to be an organism with subjective experience. Organisms capable of subjective experience do more than merely react: they have a perspective on the world with a unique phenomenological feel.

We distinguish this minimal level of consciousness from more demanding conscious relations. We think it is possible to have subjective experience without higher-order thoughts (Edelman, 2003; Rosenthal, 2005), self-awareness of oneself as a subject (Christoff, Cosmelli, Legrand, & Thompson, 2011; Morin, 2006), or reportable access to one’s own phenomenal states (Block, 1995). We think, in short, that it is possible to simply be aware, with no further reflection.

Such a distinction is, of course, philosophically contentious. Some believe that subjective experience requires heavier capacities for self-reflection. We justify adopting this distinction in three ways. First, we think that this is the modal position among philosophers and consciousness scientists. Second, adopting such a distinction corrects for potential anthropocentric bias. Third, the distinction alone does not secure our conclusion. We argue that insects have the capacity for subjective experience. Even those who think that sentience without self-reflection is possible are wary of including insects on our side of the line. Hence work remains to be done.

In humans, the capacity for subjective experience is dissociable from the capacity for self-reflexive consciousness. While the latter is dependent on cortical and midbrain structures (Damasio, 1999), several authors have argued that the former is supported by the midbrain and subcortical structures (Damasio & Carvalho, 2013; Mashour & Alkire, 2013; Merker, 2005, 2007; B. Merker, 2013; Parvizi & Damasio, 2001; Penfield & Jasper, 1954). We rely especially on the work of Bjorn Merker (2007), who draws on evidence from anesthesia, vegetative state research, developmental disorders, brain damage and lesion studies to create a compelling argument that the integrated structures of the vertebrate midbrain are sufficient to support the capacity for subjective experience in humans.

Yet while cortical damage can profoundly affect the content of conscious experience, it seems that there is no part of the cortex upon which the capacity for consciousness reliably depends (Damasio, Damasio, & Tranel, 2012; Damasio & Van Hoesen, 1983; Friedman-Hill, Robertson, & Treisman, 1995; Herbet et al., 2014; Kapur et al., 1994; Merker, 2007; Penfield & Jasper, 1954; Philippi et al., 2012). By contrast, the basic capacity for subjective experience is sensitive to damage to midbrain structures (Merker, 2007). The primary locus of action of many global anesthetics is subcortical (Alkire, Hudetz, & Tononi, 2008; Gili et al., 2013). Emergence from anesthesia (Långsjö et al., 2012; Mashour & Alkire, 2013), and coma or vegetative state (Schiff, 2010) are similarly predicted by the reengagement of subcortical structures.

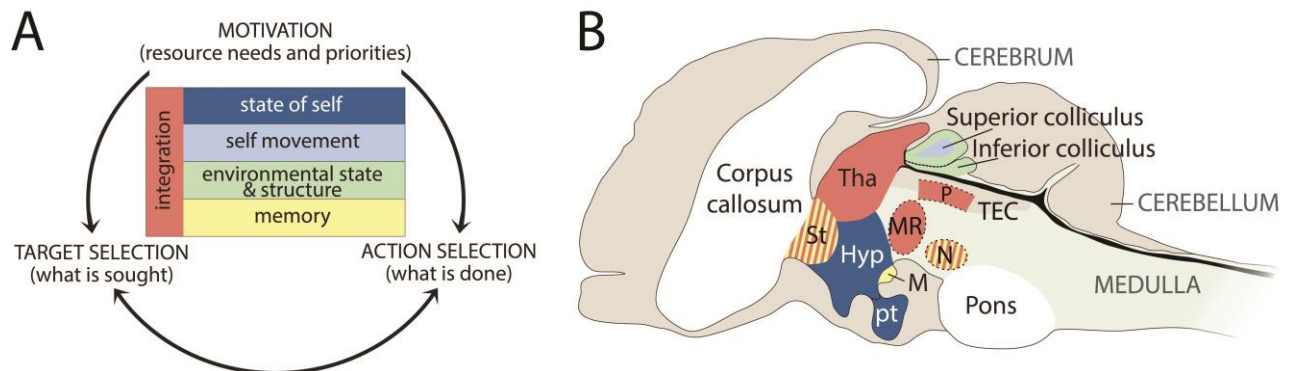
Note here the important distinction between the capacity for subjective experience and the particular contents of experience at a given time. The human cortex obviously makes a considerable contribution to *what* we are aware of. Cortical damage may appear to remove whole categories of conscious content, but determining the actual effects of such damage requires careful investigation, given the complexity of inhibitory interactions with sub-cortical regions (Sprague, 1966). Similarly, there ought to be considerable variation in conscious content across phyla. Yet these are all variations which require the capacity for subjective experience in the first place.

The evidence is thus that the basic capacity for subjective experience is supported by subcortical structures. Why might this be the case? We adopt a proposal put forward by Merker (2007), who offers a functional proposal for the midbrain and subcortical basal ganglia structures that explains their role in subjective experience. These structures combine processed sensory information on the state and structure of the environment with processed information on the homeostatic needs of the organism. The outcome is a unified multimodal neural model of the agent within its environment, which is weighted by the current needs and state of the agent. Within the midbrain, different structures perform different roles in this information economy (**Figure 1**). This modeling gives the organism a unique, unified perspective on the world. This, argues Merker, is what makes subjective experience possible.

Two features of this proposal are particularly relevant for our argument. First, the integrated processing of spatial information in the midbrain enables a mobile animal with spatial senses to solve the so-called *re-afference problem* (von Holst & Mittelstaedt, 1950). A moving animal must disambiguate environmental movement from the sensory input caused by its own motion relative to the environment. For active animals with well-developed spatial senses, it is computationally more effective to resolve the re-afference problem once in a unified sensory model than to resolve it in a dispersed and peripheral way for each sense independently. In addition, different senses contribute different information on how the body is moving; thus re-afference can be resolved with greater accuracy and precision by integrating information from multiple senses (Merker, 2005).

In vertebrates, the layered tectum (or superior colliculus (SC) in mammals) of the roof of the midbrain receives processed and topographically organized input from all spatially structured senses, including vision, auditory, and somatosensory inputs (Damasio & Carvalho, 2013; Harting, Updyke, & Van Lieshout, 1992; Klier, Wang, & Crawford, 2001;

McHaffie, Stanford, Stein, Coizet, & Redgrave, 2005; Merker, 2007). In mammals, inputs to the SC include inputs from the vestibular system (Frens, Suzuki, Scherberger, Hepp, & Henn, 1998), information on eye position (Groh & Sparks, 1996; Knox & Donaldson, 1995; Van Opstal, Hepp, Suzuki, & Henn, 1995), and somatosensation (Merker, 2007). This allows the influence of self-motion on the sensory fields to be factored out of the constructed sensory model of the environment (Sparks, 1988). Hence the SC is vital for organizing motion in space, for directed attention, and for reaching and grasping for targets (Horowitz & Newsome, 1999; Krauzlis, Liston, & Carello, 2004; McPeck & Keller, 2004; Zenon & Krauzlis, 2012).



**Figure 1: The vertebrate behavioral core control system.** Following Merker (2007), autonomous animal decision making can be considered to involve three related domains: motivation, target selection, and action selection (A). These domains can be resolved and decisions can be made by an integrated neural system that contains information on the state of self, self-movement, environmental state, and structure and memory of prior experience. These capacities are supported by different midbrain structures (B – shown here not to scale). As a simplification, regions are colored according to their primary function(s) described in A. The superior colliculus (part of the tectum (TEC) forming the roof of the midbrain) processes multisensory spatial information (Merker 2007). Hypothalamic structures (Hyp) and associated nuclei, the pituitary (pt) and mammillary bodies (M) collate information on the physiological status of the organism referenced with prior experience, to identify needs to maintain a homeostatic optimum (Damasio & Carvalho, 2013; Swanson, 2000). Integrative structures within the midbrain and basal ganglia, including the periaqueductal grey (P), substantia nigra (N), thalamus (Tha), striatum (St) and midbrain reticular formation (MR), integrate these sources of information with forms of memory to update relevance to the organism according to prior experience (McHaffie et al., 2005; Merker, 2007).

The mammalian SC thus acts as a point of convergence for spatially structured sensory information, including information about the position, orientation, and movement of the body (Masino, 1992; May, 2006; Merker, 2005; Sparks, 1988; Zenon & Krauzlis, 2012). Processing within the SC creates a neural model of the mobile animal in space, which is essential for resolving decisions about how to react to resources around the animal.

The second relevant feature of the midbrain is that information integration within it allows for efficient action selection in complex environments. Merker (2007) has described the functions of the vertebrate midbrain as a “behavioral core control system.”

The midbrain supports autonomous decision making, as well as serving as the “final common pathway” for action planning. This is important, since adaptive behavior requires the ability to select between competing drives in rapidly changing environments (Jékely, Keijzer, & Godfrey-Smith, 2015).

The interacting systems of the midbrain and basal ganglia support resolution of competing behavioral options by compiling information on the location and availability of resources, the meaning and relevance of stimuli to the organism, and its physiological needs (**Figure 1**). The hypothalamic structures and associated nuclei that form the floor of the midbrain collate information on the physiological status of the organism (Swanson, 2000). These nuclei motivate and participate in the initiation of behavior directed at maintaining the animal in optimal physiological condition (Damasio & Carvalho, 2013; Swanson, 2000). The integrative structures of the basal ganglia and midbrain utilize the information on the status and needs of the animal together with information on where the animal is situated relative to available resources in order to prioritize resource seeking, resolve competing needs, and select targets and actions (McHaffie et al., 2005; Merker, 2007; Gurney, Prescott, & Redgrave, 2001; Redgrave, Prescott, & Gurney, 1999).

Possible actions are set in competition, and the winner of the competition gains effective control of action (Gurney et al., 2001; Merker, 2007; Redgrave et al., 1999). This in turn feeds back into topographically oriented spatial information generated by the SC, generating “task-relevance maps” (Navalpakkam, Arbib, & Itti, 2005) which further guide active exploration of the environment. The motivational and physiological states of the organism prioritize target and action selection, but the location and availability of targets is also a key factor influencing what is targeted and what next action will be taken (Merker, 2007).

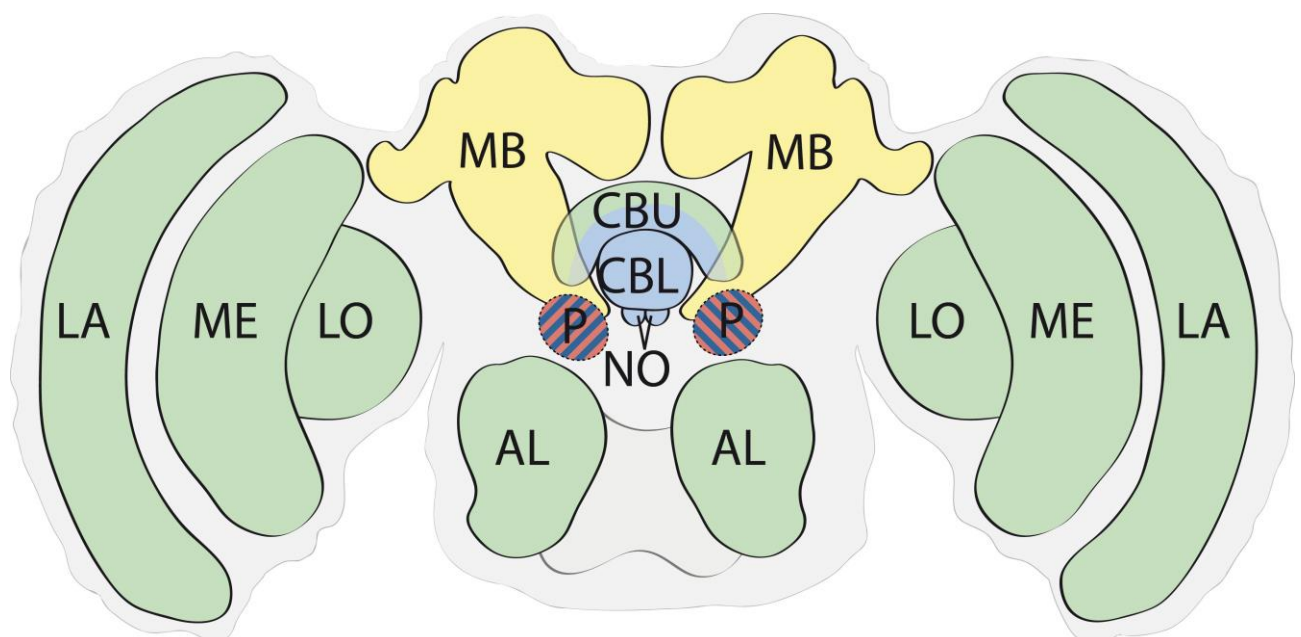
The midbrain thus allows for unified sensory processing and decision making without invoking a separate control system utilizing the information to make a decision (McHaffie et al., 2005; Redgrave et al., 1999) or regressing to a “Cartesian Theatre” (Dennett, 1991). Merker’s (2007) conceptual behavioral core control system emphasizes how domains critical to decision making, target selection, action selection and motivation must interact since the interactions are critical to effective decision making. Crucially, the midbrain integrates particular *types* of information into a unified model. Thus it is not integration *per se* that matters (as suggested, for example, by Tononi (2004, 2008; Tononi & Koch, 2015), but the dynamic and ongoing connection between perception, interoception, associative memory, and motor feedback.

### **3. Parallels Between Vertebrate and Insect Brains**

The functional parallels between the vertebrate midbrain and insect brains form the centerpiece of our argument. While there is no obvious similarity in the gross anatomy (**Figure 2**), there is an overall similarity in functional architecture between the vertebrate midbrain and the insect brain as a whole. (A full presentation may be found in Barron & Klein, 2016).

In the insect brain, the central complex (CX) is specialized for the processing of spatial information and the organization of movement (Heinze & Homberg, 2007; Pfeiffer &

Homberg, 2014; Plath & Barron, 2015). The CX is functionally analogous to the SC in many respects. The CX processes multiple sources of spatial information drawn from different senses to locate the moving animal in space. This includes spatially structured information on plane-polarized light (Bockhorst & Homberg, 2015; Heinze & Homberg, 2007; Lin et al., 2013; Pfeiffer & Homberg, 2014); spatially structured visual information on moving objects (Kathman, Kesavan, & Ritzmann, 2014; Rosner & Homberg, 2013; Seelig & Jayaraman, 2013; Weir, Schnell, & Dickinson, 2014) corrected for self-motion to resolve the re-orientation problem (Seelig & Jayaraman, 2013); and spatially structured mechanosensory and proprioceptive information in cockroaches (Guo & Ritzmann, 2013), *Drosophila* (Seelig & Jayaraman, 2015), and crickets (Kai & Okada, 2013). Like the mammalian SC, the insect CX is necessary for targeting, reaching, orientation, and directed movement (Kai & Okada, 2013; Kathman et al., 2014; Pfeiffer & Homberg, 2014). Processing within the CX enables the insect to maintain a course using either visual or proprioceptive information (Seelig & Jayaraman, 2015).



**Figure 2: Basic functional anatomy of the insect brain** (not to scale). The structures of the insect brain are functionally analogous to those functions of the vertebrate midbrain described in **Figure 1**. (Regions are colored to highlight the functional analogy with **Figure 1A**.) Sensory lobes, of the antennae (AL) and visual system (lamina (LA), medulla (ME) and lobula (LO)) contribute information on environment state and structure (Galizia, 2014; Horridge, 2005). The mushroom bodies (MB) support learning and memory (Bazhenov et al., 2013; Heisenberg, 2003; Huerta, Nowotny, Garcia-Sanchez, Abarbanel, & Rabinovich, 2004; Menzel, 2001; Schwaerzel et al., 2003). The central complex (CX) is anatomically variable between insect orders, but is typically composed of the central body upper (CBU), central body lower (CBL), and noduli (NO). It is specialised for processing spatial information (Kathman et al., 2014; Pfeiffer & Homberg, 2014; Pfeiffer & Crailsheim, 1998; Plath & Barron, 2015; Seelig & Jayaraman, 2015). The protocerebrum (P) is large and anatomically complicated region, and connects these other regions. It is premotor and serves as a final common path for all sensory information either directly from the lobes, or via the MB and CX pathways. Modulatory and inhibitory connections to and within the protocerebrum convey information on physiological state (Galizia, 2014; Parnas

et al., 2013). The region is involved in both integration of information and processing of state of self, hence the hatched shading.

The CX sends outputs to and receives inputs from protocerebral structures, particularly the bulb and lateral accessory lobe (Pfeiffer & Homberg, 2014) (**Figure 2**). The protocerebrum is composed of a number of interconnected subregions that are both premotor and a point of convergence for outputs from the sensory lobes, the CX, and the mushroom bodies (MB) (Ito et al., 2014; Strausfeld, 1976, 2012; Strausfeld & Hirth, 2013).

In the vertebrate midbrain and basal ganglia, there are several integrative loci that support learning and memory so that the organism can update its responses to stimuli according to its experience (**Figure 1A**). In insects, this capacity is supported by the MB (Bazhenov, Huerta, & Smith, 2013; Fahrbach, 2006; Galizia, 2014). Connectivity between the intrinsic neurons that make up the MB (Kenyon cells) and their inputs and outputs is plastic, supporting experience-dependent changes in how stimuli are represented by the population of neurons in the MB, and the downstream neurons that are activated or inhibited (Barron, Gurney, Meah, Vasilaki, & Marshall, 2015; Galizia, 2014).

Within the protocerebrum, and connecting to the CX and MB, there are highly specialized modulatory neuron clusters that modify neural activity according to the physiological and motivational state of the insect (Andretic, van Swinderen, & Greenspan, 2005; Burke et al., 2012; Krashes et al., 2009; Søvik, Perry, & Barron, 2015). These specialized circuits modify how the insect responds to events according to its subjective internal state such as arousal, sleep, satiation, hunger, and reward (Andretic et al., 2005; Burke et al., 2012; Krashes et al., 2009; Liu, Liu, Kodama, Driscoll, & Wu, 2012; Søvik et al., 2015). This is functionally parallel to the hypothalamic nuclei in vertebrates.

Competitive processing within the protocerebrum contributes to effective decision making and action selection utilizing all available sensory information as well as information on the state of the insect (Barron et al., 2015; Galizia, 2014; Liang et al., 2013; Parnas, Lin, Huetteroth, & Miesenböck, 2013). Hence competitive processing within the protocerebrum is functionally similar to the vertebrate basal ganglia system.

The insect classifies and weights environmental stimuli according to their relevance to the insect (Strube-Bloss, Nawrot, & Menzel, 2011). In addition, insects selectively filter the processing of sensory information to prioritize the stimuli of the greatest immediate relevance and discount stimuli of no subjective relevance. This has been demonstrated for both honey bees (*Apis mellifera*) and *Drosophila* (Paulk et al., 2014; Sareen, Wolf, & Heisenberg, 2011; van Swinderen, 2005; van Swinderen & Greenspan, 2003) in which the neural representation of the environment is both subjective and egocentric.

In summary, there are significant parallels between the functional organization of the insect brain and that of the vertebrate midbrain behavioral core control system. Both systems have specialized regions for processing the position of the moving animal in space. In both systems action selection is resolved by combining information on position with information on the environment, the relevance of stimuli in the environment to the animal, and the state of the animal (**Figures 1, 2**). In vertebrates the channels of

information are sufficiently unified such that the system as a whole creates a functional representation of the state of the mobile animal in space as a solution for effective decision making.

As we have argued, processing of this kind supports the capacity for a subjective experience of the environment. Processing in the insect brain is unified to a similar degree, for similar reasons. Hence we propose that the insect brain can also support a capacity for subjective experience.

#### **4. The Evolutionary Origins of Subjective Experience**

We have argued that subjective experience arose as a consequence of the integrated behavioral control systems for effective decision making and action selection. In both vertebrate and insect lineages, the control systems we have described are highly conserved and basal to the groups (Feinberg & Mallatt, 2016; Strausfeld, 2012). The early evolution and high degree of conservation of these neural systems is understandable given that they resolve fundamental problems for mobile animals. But if these unified behavioral control systems are ancient, then it is possible that subjective experience itself is similarly ancient.

The key structural elements of the vertebrate behavioral core control system are all present and functional in lampreys (extant, primitive jawless fish) (Feinberg & Mallatt, 2013; Grillner, Robertson, & Stephenson-Jones, 2013; Merker, 2005; Stephenson-Jones, Samuelsson, Ericsson, Robertson, & Grillner, 2011; I. C. Zompa & Dubuc, 1996; Iolanda C. Zompa & Dubuc, 1998). These structures are present in the basal vertebrates and conserved across all extant groups. It has also been proposed that similar structures might have been present in the fossil vertebrate *Haikouichthys* from the Cambrian (Feinberg & Mallatt, 2013; Feinberg & Mallatt, 2016). *Haikouichthys* is reconstructed as a fish-like active swimmer with large image-forming eyes (Shu et al., 2003). If so, then subjective experience in vertebrates is at least as old as the Cambrian (Feinberg & Mallatt, 2013; Feinberg & Mallatt, 2016).

The insect behavioral core control system has similarly ancient origins. The CX is basal to insects. It almost certainly predates the divergence of insects, crustaceans and arachnids since homologous structures are found in all three groups (Homberg, 2008; Loesel, Nässel, & Strausfeld, 2002; Pfeiffer & Homberg, 2014). Some Cambrian arthropods had well-developed cephalic ganglia with structural similarities to extant crustacean and insect brains (Ma, Hou, Edgecombe, & Strausfeld, 2012). It is reasonable to suppose that a version of the extant insect behavioral core control system was present in at least some Cambrian arthropods to support their presumed active foraging and hunting lifestyles (Trestman, 2013).

It is presently unclear whether the insect and vertebrate behavioral core control systems evolved independently. Strausfeld and Hirth (2013) have argued for a deep homology between the insect CX and associated structures and vertebrate basal ganglia. If this interpretation is correct, it would imply that a form of behavioral core control system may even predate the divergence of these groups.



## 5. Defending the Insect Brain

Our argument depends on functional claims about the insect brain. Much of this is recent science. Insect brains have been consistently underestimated, and it is worth addressing some of those misunderstandings.

Some have denied that insects have the requisite functional organization for subjective experience. This includes Merker himself, (2007), who cites Altman's (1989) characterization of the insect brain as a decentralized system with the cephalic ganglion a locus for sensory input but with action selection resolved locally at the motor systems of the segmental ganglia. Altman's (1989) view of the insect nervous system was itself inspired by Brooks's (1989) subsumption architectures for behavioral control of a walking robot.

This view of the insect brain is outdated. The cephalic ganglion clearly executes a command function over the behavioral system since reasonably small and neurochemically specific lesions of the protocerebrum proximal to the CX can completely incapacitate an insect by removing volitional behavioral control (Libersat & Gal, 2014).

Others have focused not on organization but on neuron number. The gulf between the size of insect and mammalian brains is indeed enormous. The honey bee has less than a million neurons in the cephalic ganglion – and this is a very large brain for an insect. By comparison, a mouse (*Mus musculus*) has 68 million neurons in the brain, a rhesus monkey (*Macaca mullata*) 6.4 billion and a human 86 billion (Herculano-Houzel, 2016).

Many writers on insects have thus focused on the limitations imposed by their comparatively tiny brains. Feinberg and Mallatt (2013) have argued that most of the vertebrates have a capacity for subjective experience. Yet they are equivocal on whether insects have the capacity, precisely because of neuron number (Feinberg & Mallatt, 2016).

We believe it is inappropriate to focus on neuron number alone. Functional organization is what matters. Neuron number is important only insofar as it might affect functional organization. Insect brains are small, but they have enough neurons to do the job, and that is all that matters.

Insect brains are also extremely economical in their use of neurons. While higher vertebrates have large neural loci for processing internal states and motivations, insects perform analogous functions with clusters of just a few neurons (Andretic et al., 2005; Burke et al., 2012; Krashes et al., 2009; Sjøvik et al., 2015). The human nucleus accumbens (part of the reward system of the vertebrate brain) is larger than the whole honey bee brain, but honey bees organize analogous reinforcing functions of the nucleus accumbens with clusters of just a few broad-field neuromodulatory neurons (Perry & Barron, 2013; Sjøvik et al., 2015).

The larger vertebrate brains are very likely more robust, degenerate, and precise, and have greater capacities for storage and parallel processing than the small and

economical insect brains (Chittka & Niven, 2009). But we agree with Chittka and Niven (2009) that the qualitative differences in processing capacity of brains at the insect and vertebrate scales are not as great as they might seem given the differences in neuron number.

## **6. Why There Is a Lower Bound**

Finally, some have postulated subjective experience in insects because they think that consciousness is even *more* widespread. For example, authors have postulated subjective experience in plants (Pelizzon & Gagliano, 2015), in any reasonably complex system (see Tononi, 2004), or even that it is a fundamental feature of the universe akin to spin and electric charge (Strawson, 2006). Such views would obviously imply that insects are conscious (though that is far from their most striking prediction).

We disagree. We think there is a cutoff. Many animals, all plants, and (as far as we know) all currently existing man-made artifacts fall below the line. Without the right kind of centralized integration and modeling, an organism cannot be conscious.

Box jellyfish, for example, are highly mobile and use well-developed lensed eyes and chemosensors to actively hunt prey (Garm, Oskarsson, & Nilsson, 2011; Kingsford & Mooney, 2014). Yet they (like all Cnidarians) have a decentralized nervous system, and a completely decentralized behavioral control system. Sense organs independently modulate activity in local regions of the sensory net and muscle walls to steer the animal (Petie, Garm, & Nilsson, 2011).

While centralized processing of all available exteroceptive and interoceptive sensory information is necessary for subjective experience, centralization alone is not sufficient. What is processed, and how it is processed, also matters. This requirement may itself seem churlish. Having gone so far, why deny conscious experience to (say) worms?

We think the answer is instructive. Consider the nematode *Caenorhabditis elegans*. The nervous system of the nematode is centralized, and famously well characterized. It includes thermo-, mechano-, chemo-, and nociceptors, and interoceptive senses related to physiological state (Gordus, Pokala, Levy, Flavell, & Bargmann, 2015) and the passing of time (de Bono & Maricq, 2005). These are integrated at the level of an array of interneurons that activate motor neurons (de Bono & Maricq, 2005; Kato et al., 2015). Nematodes are thus able to integrate multiple forms of sensory input using a centralized nervous system. Action selection in nematodes is driven by shifts in global brain dynamics (Kato et al., 2015).

Nematodes can learn, and hence can change how they react to stimuli (Gordus et al., 2015). They also have basic memory and can retain learned behavioral changes (Ardiel & Rankin, 2010). But nematodes have no spatial senses. They have no capacity to locate themselves in their environment or to detect the relative position of objects around them. This has significant consequences. Because there are no spatial dimensions to a nematode's sensory world, the only way nematodes can interrelate sensory information is by contiguity. This is supported by their neural network and basic forms of learning and memory (Ardiel & Rankin, 2010; Gordus et al., 2015).

Nematodes cannot perform the integrated spatiotemporal modeling that characterizes the vertebrate midbrain and the insect brain. All nematode behavior is a direct reaction to their immediate state. There is no evidence of planning in nematodes, nor structured search behavior. Hungry nematodes respond to starvation with increased locomotion and dispersal in a random rather than directed search (Artyukhin, Yim, Cheong, & Avery, 2015; Lüersen, Faust, Gottschling, & Döring, 2014).

That immediate reactivity is in sharp contrast to the behavior of hungry rodents, ants, and bees, who will navigate to places where they have previously encountered food when hungry (Oades & Isaacson, 1978; Seeley, 1995; Wehner, 2013). Hence, in mammals and insects, homeostatic drives direct behavior to where resources are expected to be, even if they are not currently there. Such anticipatory behavior is not possible for nematodes, who have no capacity to form any spatial relations between arbitrary objects.

The final point is important. The key feature of the integrated core control system is that it allows the interaction of diverse and novel elements in a single process. That is what makes sensation and action integrated. That is why the basic capacity for subjective experience can be extended to include ever more complicated contents as brains expand. It allows organisms to extract synthetic interrelations between elements. And of course that is what allows the organism to represent itself and its place within a broader representation of the world.

We have emphasized the importance of mechanisms that support integrated modeling of the environment. The sense of “modeling” we have in mind is a relatively lightweight one. It is important to note that it does not require the construction of offline, non-dynamic representations. Models can be constructed dynamically rather than stored statically. The important thing for our purposes is the process of integration rather than static representation. Our view is thus compatible with (for example) Barbara Webb’s (2004, 2006) critiques of representationalist thinking in insect neuroscience.

That said, we believe that this integrative process is representational in a straightforward sense. We have little interest in arguing about the *terms* “representation” and “model.” The important fact for present purposes is that organisms like nematodes *lack* any such ability. As a consequence, a nematode cannot locate itself in space, nor position itself relative to things around it, nor relate itself to its own distant past, nor relate its current needs in arbitrary ways to any of this in order to give them meaning and context. The nematode nervous system just transforms the immediate sensory environment into immediate motor responses. Of course, for the simple environments that nematodes are bound to, and for the simple responses they can enact, this form of behavioral control system is more than sufficient. But we do not believe that with almost no capacity to interrelate sensory information the nematode nervous system supports a capacity for subjective experience.

## **7. Conclusion: Making Progress on Hard Problems**

We have emphasized throughout the importance of a mobile lifestyle in driving the evolution of consciousness. The importance of mobility for driving neural evolution is not a new idea, but it is worth emphasizing. Mobility presented a fundamentally new

sort of challenge to organisms, one that modern AI still finds extremely difficult (Brooks, 1999). As Moravec puts it (1984),

*I conclude that a mobile way of life favors general solutions that tend towards intelligence, while non-motion favors deep specializations. A fixed organism is repeatedly exposed to a limited set of problems and opportunities, and will do better in the long run if it becomes good at dealing with this limited range. A roving creature encounters fewer instances of a greater variety of different conditions, and does better with general methods, even if such generality is more expensive, or results in poorer performance in specific instances.*

*The cumulative effect of this difference in selection pressure is enormous, as evidenced by clams and octopus, or plants and animals. Trees are as successful and dominant in their niche as humans are in theirs, but the life of a tree does not demand high speed general purpose perception, flexible planning and precisely controlled action.*

Centralization in the service of action selection is, we have argued, the advance that allowed for the evolution of subjective experience.

Of course, we might be wrong. Many reject Merker's theory, or even the basic premise that the midbrain is key to subjective experience. Alternatives to Merker might fail to generalize to invertebrates. We have emphasized the importance of a unified perspective on the world as a key feature of subjective experience (Christoff et al., 2011). We might have left out other neural features that are necessary for subjective experience, such as an explicit representation of a temporal dimension (Kant, 1999). Insects may lack these (though see Skorupski & Chittka, 2006).

That said, we emphasize that disagreement of this sort should ultimately rest on empirical facts: that is, on structural, functional, and comparative hypotheses about brains. In that sense, our position is a thoroughly naturalistic one. We have not attempted to say anything about the hard problem of consciousness (Chalmers, 1996). Instead, we follow the advice of Penfield & Rasmussen (1950) to the effect that:

*...neurologists should push their investigations into the neurologic mechanism associated with consciousness and should inquire closely into the localization of that mechanism without apology and without undertaking responsibility for the theory of consciousness (Penfield & Rasmussen, 1950).*

We think that a contemporary study of consciousness resembles the study of vital forces before modern physiology (Cruse & Schilling, 2015). What seemed like a great gap between the organic and the inorganic was ultimately bridged by the development of appropriate scientific concepts.

We have a similar take on the hard problem: It is difficult because we don't yet have the concepts for assessing what a satisfying answer could even look like. The solution, however, is to press on as best we can with empirical inquiry, revising our concepts as

we go. We have offered an ostensive definition of the phenomenon we care about and we have given a mechanistic story about how that phenomenon is realized. The search for mechanisms does not require anything like a clear concept at the outset (Craver, 2007). Rather, a search for mechanisms can be the means of clarifying our concepts (Wimsatt, 2007) and thereby moving past seemingly intractable difficulties. We hope that this will also turn out to be the case for the study of consciousness. Insects, and invertebrates more generally, have often been overlooked as potential players in this story. We hope to correct that oversight.

### Acknowledgments

In addition to those thanked in [Barron & Klein \(2016\)](#), thanks to Bruno van Swinderen and attendees at the 2016 SydPP meeting for additional feedback. Figures 1 and 2 were created by Marcus J.A. Plath. This work was supported by Australian Research Council Future Fellowship project no. FT140100452 awarded to A.B.B. and Australian Research Council Future Fellowship project no. FT140100422 awarded to C.K.

**Call for Commentary:** *Animal Sentience* publishes [Open Peer Commentary](#) on all accepted target articles. Target articles are peer-reviewed. Commentaries are editorially reviewed. There are submitted commentaries as well as invited commentaries. Commentaries appear as soon as they have been revised and accepted. Target article authors may respond to their commentaries individually or in a joint response to multiple commentaries.

**Instructions:** <http://animalstudiesrepository.org/animsent/guidelines.html>

### References

- Alkire, M. T., Hudetz, A. G., & Tononi, G. (2008). Consciousness and anesthesia. *Science*, 322(5903), 876-880.
- Altman, J. S., & Kien, J. (1989). New models for motor control. *Neural Computation*, 1, 173-183.
- Andretic, R., van Swinderen, B., & Greenspan, R. J. (2005). Dopaminergic modulation of arousal in *Drosophila*. *Current Biology*, 15, 1165-1175.
- Ardiel, E. L., & Rankin, C. H. (2010). An elegant mind: Learning and memory in *Caenorhabditis elegans*. *Learning and Memory*, 17, 191-201.
- Artyukhin, A. B., Yim, J. J., Cheong, M. C., & Avery, L. (2015). Starvation-induced collective behavior in *C. elegans*. *Scientific Reports*, 5, 10647. doi: 10.1038/srep10647
- Barron, A. B., & Klein, C. (2016). [What insects can tell us about the origins of consciousness](#). *Proceedings of the National Academy of Science of the United States of America*, 113(18), 4900-4908.
- Barron, A. B., Gurney, K. N., Meah, L. F. S., Vasilaki, E., & Marshall, J. A. R. (2015). Decision-making and action selection in insects: inspiration from vertebrate-based theories. *Frontiers in Behavioral Neuroscience*, 9, 216. doi: 10.3389/fnbeh.2015.00216
- Bayne, T., Hohwy, J., & Owen, A. M. (2016). Are there levels of consciousness? *Trends in Cognitive Sciences*, 20(6), 405-413.
- Bazhenov, M., Huerta, R., & Smith, B. (2013). A computational framework for understanding decision making through integration of basic learning rules. *Journal of Neuroscience*, 33(13), 5686-5697.

- Block, N. (1995). On a confusion about a function of consciousness. *Behavioral and Brain Sciences*, 18(02), 227-287.
- Bockhorst, T., & Homberg, U. (2015). Amplitude and dynamics of polarization-plane signaling in the central complex of the locust brain. *Journal of Neurophysiology*, 113, 3291-3311.
- Brooks, R. A. (1989). A robot that walks; Emergent behaviors from a carefully evolved network. *Neural Computation*, 1, 253-262.
- Brooks, R. A. (1999). *Cambrian intelligence: The early history of the new AI*. Cambridge, MA: MIT Press.
- Burke, C. J., Huetteroth, W., Oswald, D., Perisse, E., Krashes, M. J., Das, G., Gohl, D., Silies, M., Certel, S., & Waddell, S. (2012). Layered reward signalling through octopamine and dopamine in *Drosophila*. *Nature*, 492(7429), 433-437. doi: 10.1038/nature11614
- Chalmers, D. (1996). *The conscious mind: In search of a fundamental theory*. New York: Oxford University Press.
- Chittka, L., & Niven, J. (2009). Are bigger brains better? *Current Biology*, 19, R995-R1008.
- Christoff, K., Cosmelli, D., Legrand, D., & Thompson, E. (2011). Specifying the self for cognitive neuroscience. *Trends in Cognitive Sciences*, 15(3), 104-112.
- Craver, C. F. (2007). *Explaining the brain*. New York: Oxford University Press.
- Cruse, H., & Schilling, M. (2015). Mental states as emergent properties: from walking to consciousness. *Open MIND*, 9, 1-38.
- Damasio, A. (1999). *The feeling of what happens: Body and emotion in the making of consciousness*. Orlando: Harcourt Inc.
- Damasio, A., & Carvalho, G. B. (2013). The nature of feelings: evolutionary and neurobiological origins. *Nature Reviews Neuroscience*, 14, 143-152.
- Damasio, A., & Van Hoesen, G. (1983). Emotional disturbances associated with focal lesions of the limbic frontal lobe. In P. Satz & K. M. Heilman (Eds.), *Neuropsychology of Human Emotion* (pp. 85-110). New York: Guilford Press
- Damasio, A., Damasio, H., & Tranel, D. (2012). Persistence of feelings and sentience after bilateral damage of the insula. *Cerebral Cortex*, 23(4), 833-846.
- De Bono, M., & Maricq, A. V. (2005). Neuronal substrates of complex behaviors in *C. elegans*. *Annual Review of Neuroscience*, 28, 451-501.
- Dennett, D. C. (1991). *Consciousness explained*. Boston: Little, Brown, & co.
- Edelman, G. M. (2003). Naturalizing consciousness: a theoretical framework. *Proceedings of the National Academy of Sciences*, 100(9), 5520-5524.
- Fahrbach, S. E. (2006). Structure of the mushroom bodies of the insect brain. *Annual Review of Entomology*, 51, 209-232.
- Feinberg, T. E., & Mallatt, J. (2013). The evolutionary and genetic origins of consciousness in the Cambrian Period over 500 million years ago. *Frontiers in Psychology*, 4(667), 1-27.
- Feinberg, T. E., & Mallatt, J. M. (2016). *The ancient origins of consciousness: How the brain created experience*. Cambridge, MA: MIT Press.
- Frens, M. A., Suzuki, Y., Scherberger, H., Hepp, K., & Henn, V. (1998). The collicular code of saccade direction depends on the roll orientation of the head relative to gravity. *Experimental Brain Research*, 120, 283-290.
- Friedman-Hill, S., Robertson, L. C., & Treisman, A. (1995). Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. *Science*, 269(5225), 853-855.
- Galizia, C. G. (2014). Olfactory coding in the insect brain: data and conjectures. *European Journal of Neuroscience*, 39, 1784-1795.

- Garm, A., Oskarsson, M., & Nilsson, D.-E. (2011). Box jellyfish use terrestrial visual cues for navigation. *Current Biology*, *21*, 798–803.
- Gili, T., Saxena, N., Diukova, A., Murphy, K., Hall, J. E., & Wise, R. G. (2013). The thalamus and brainstem act as key hubs in alterations of human brain network connectivity induced by mild propofol sedation. *The Journal of Neuroscience*, *33*(9), 4024–4031.
- Gordus, A., Pokala, N., Levy, S., Flavell, S. W., & Bargmann, C. L. (2015). Feedback from network states generates variability in a probabilistic olfactory circuit. *Cell*, *161*, 215–227.
- Grillner, S., Robertson, B., & Stephenson-Jones, M. (2013). The evolutionary origin of the vertebrate basal ganglia and its role in action selection. *Journal of Physiology*, *591*(22), 5425–5431.
- Groh, J. M., & Sparks, D. L. (1996). Saccades to somatosensory targets. III. Eye-dependent somatosensory activity in primate superior colliculus. *Journal of Neurophysiology*, *75*, 439–453.
- Guo, P., & Ritzmann, R. (2013). Neural activity in the central complex of the cockroach brain is linked to turning behaviors. *Journal of Experimental Biology*, *216*, 992–1002.
- Gurney, K. N., Prescott, T. J., & Redgrave, P. (2001). A computational model of action selection in the basal ganglia I: A new functional anatomy. *Biological Cybernetics*, *84*, 401–410.
- Harting, J. K., Updyke, B. V., & Van Lieshout, D. P. (1992). Corticotectal projections in the cat: Anterograde transport studies of twenty-five cortical areas. *Journal of Comparative Neurology*, *328*, 379–414.
- Heinze, S., & Homberg, U. (2007). Maplike representation of celestial E-vector orientations in the brain of an insect. *Science*, *315*, 995–997.
- Heisenberg, M. (2003). Mushroom body memoir: from maps to models. *Nature Reviews Neuroscience*, *4*, 266–275.
- Herbet, G., Lafargue, G., de Champfleury, N. M., Moritz-Gasser, S., le Bars, E., Bonnetblanc, F. C., & Duffau, H. (2014). Disrupting posterior cingulate connectivity disconnects consciousness from the external environment. *Neuropsychologia*, *56*, 239–244.
- Herculano-Houzel, S. (2016). *The human advantage: a new understanding of how our brain became remarkable*. Cambridge, MA: MIT Press.
- Homberg, U. (2008). Evolution of the central complex in the arthropod brain with respect to the visual system. *Arthropod Structure and Development*, *37*, 347–362.
- Horowitz, G. D., & Newsome, W. T. (1999). Separate signals for target selection and movement specification in the superior colliculus. *Science*, *284*, 1158–1161.
- Horridge, A. (2005). What the honeybee sees: a review of the recognition system of *Apis mellifera*. *Physiological Entomology*, *30*, 2–13.
- Huerta, R., Nowotny, T., Garcia-Sanchez, M., Abarbanel, H. D. L., & Rabinovich, M. I. (2004). Learning classification in the olfactory system of insects. *Neural Computation*, *16*, 1601–1640.
- Ito, K., Shinomiya, K., Ito, M., Armstrong, J. D., Boyan, G., Hartenstein, V., Harzsch, S., Heisenberg, M., Homberg, U., Jenett, A., Keshishian, H., Restifo, L. L., Rössler, W., Simpson, J. H., Strausfeld, N. J., Strauss, R., & Vosshall, L. B. (2014). A systematic nomenclature for the insect brain. *Neuron*, *81*(4), 755–765. doi: 10.1016/j.neuron.2013.12.017
- Jékely, G., Keijzer, F., & Godfrey-Smith, P. (2015). An option space for early neural evolution. *Philosophical Transactions of the Royal Society B*, *370*(1684). doi: 10.1098/rstb.2015.0181

- Kai, K., & Okada, R. (2013). Characterization of locomotor-related spike activity in protocerebrum of freely walking cricket. *Zoological Science*, *30*, 591-601.
- Kant, I. (1999). *Critique of pure reason: The cambridge edition of the works of Immanuel Kant* (P. Guyer & A. W. Wood, Eds.). Cambridge: Cambridge University Press.
- Kapur, N., Ellison, D., Parkin, A. J., Hunkin, N. M., Burrows, E., Sampson, S., & Morrison, E. (1994). Bilateral temporal lobe pathology with sparing of medial temporal lobe structures: Lesion profile and pattern of memory disorder. *Neuropsychologia*, *32*(1), 23-38.
- Kathman, N., Kesavan, M., & Ritzmann, R. (2014). Encoding wide-field motion and direction in the central complex of the cockroach *Blaberus discoidalis*. *Journal of Experimental Biology*, *217*, 4079-4090.
- Kato, S., Kaplan, H. S., Schrödel, T., Skora, S., Lindsay, T. H., Yemini, E., Lockery, S., & Zimmer, M. (2015). Global brain dynamics embed the motor command sequence of *Caenorhabditis elegans*. *Cell*, *163*, 1-14.
- Kingsford, M. J., & Mooney, C. J. (2014). The ecology of box jellyfishes (Cubozoa). In K. A. Pitt & C. H. Lucas (Eds.), *Jellyfish blooms* (pp. 267-303). New York: Springer
- Klier, E. M., Wang, H., & Crawford, J. D. (2001). The superior colliculus encodes gaze commands in retinal coordinates. *Nature Neuroscience*, *4*, 627-632.
- Knox, P. C., & Donaldson, I. M. L. (1995). The effect of afferent signals from extraocular muscles on visual responses of cells in the optic tectum of the pigeon. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *259*, 285-291.
- Krashes, M. J., DasGupta, S., Vreede, A., White, B., Armstrong, J. D., & Waddell, S. (2009). A neural circuit mechanism integrating motivational state with memory expression in *Drosophila*. *Cell*, *139*, 416-427.
- Krauzlis, R. J., Liston, D., & Carello, C. D. (2004). Target selection and the superior colliculus: goals, choices and hypotheses. *Vision Research*, *44*, 1445-1451.
- Långsjö, J. W., Alkire, M. T., Kaskinoro, K., Hayama, H., Maksimow, A., Kaisti, K. K., Aalto, S., Aantaa, R., Jääskeläinen, S. K., Revonsuo, A., & Scheinin, H. (2012). Returning from oblivion: imaging the neural core of consciousness. *The Journal of Neuroscience*, *32*(14), 4935-4943.
- Liang, L., Li, Y., Potter, C. J., Yizhar, O., Deisseroth, K., Tsien, R. W., & Luo, L. (2013). GABAergic projection neurons route selective olfactory inputs to specific higher-order neurons. *Neuron*, *79*, 917-931.
- Libersat, F., & Gal, R. (2014). Wasp voodoo rituals, venom-cocktails, and the zombification of cockroach hosts. *Integrative and Comparative Biology*, *54*(2), 129-142.
- Lin, C., Chuang, C. C., Hua, T., Chen, C. C., Dickson, B. J., Greenspan, R. J., & Chiang, A. S. (2013). A comprehensive wiring diagram of the protocerebral bridge for visual information processing in the *Drosophila* brain. *Cell Reports*, *3*, 1739-1753.
- Liu, Q., Liu, S., Kodama, L., Driscoll, M. R., & Wu, M. N. (2012). Two dopaminergic neurons signal to the dorsal fan-shaped body to promote wakefulness in *Drosophila*. *Current Biology*, *22*(22), R949-R951.
- Loesel, R., Nässel, D., & Strausfeld, N. (2002). Common design in a unique midline neuropil in the brains of arthropods. *Arthropod Structure & Development*, *31*(1), 77-91.
- Lüersen, K., Faust, U., Gottschling, D.-C., & Döring, F. (2014). Gait-specific adaptation of locomotor activity in response to dietary restriction in *Caenorhabditis elegans*. *Journal of Experimental Biology*, *217*, 2480-2488.



- Ma, X., Hou, X., Edgecombe, G. D., & Strausfeld, N. J. (2012). Complex brain and optic lobes in an early Cambrian arthropod. *Nature*, *490*, 258-261. doi: 10.1038/nature11495
- Mashour, G. A., & Alkire, M. T. (2013). Evolution of consciousness: phylogeny, ontogeny, and emergence from general anesthesia. *Proceedings of the National Academy of Sciences*, *110*(Supplement 2), 10357-10364.
- Masino, T. (1992). Brain-stem control of orienting movements - intrinsic coordinate systems and underlying circuitry. *Brain Behaviour and Evolution*, *40*, 98-111.
- May, P. J. (2006). The mammalian superior colliculus: laminar structure and connections. *Progress in Brain Research*, *151*, 321-378.
- McHaffie, J. G., Stanford, T. R., Stein, B. E., Coizet, V., & Redgrave, P. (2005). Subcortical loops through the basal ganglia. *Trends in Neurosciences*, *28*, 401-407.
- McPeck, R. M., & Keller, E. L. (2004). Deficits in saccade target selection after inactivation of the superior colliculus. *Nature Neuroscience*, *7*, 757-763.
- Menzel, R. (2001). Cognitive architecture of a mini-brain: the honeybee. *Trends in Cognitive Sciences*, *5*(2), 62-71. doi: 10.1016/s1364-6613(00)01601-6
- Merker, B. (2005). The liabilities of mobility: A selection pressure for the transition to consciousness in animal evolution. *Consciousness and Cognition*, *14*, 89-114.
- Merker, B. (2007). Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Sciences*, *30*, 63-81. doi: 10.1017/S0140525X07000891
- Merker, B. (2013). The efference cascade, consciousness, and its self: naturalizing the first person pivot of action control. *Frontiers in Psychology*, *4*, 501.
- Moravec, H. P. (1984). Locomotion, vision and intelligence. In M. Brady & R. Paul (Eds.), *Robotics research 1* (pp. 215-224). Cambridge, MA.: MIT Press.
- Morin, A. (2006). Levels of consciousness and self-awareness: A comparison and integration of various neurocognitive views. *Consciousness and Cognition*, *15*, 358-371.
- Nagel, T. (1974). What is it like to be a bat? *The Philosophical Review*, *83*(4), 435-450.
- Navalpakkam, V., Arbib, M., & Itti, L. (2005). Attention and scene understanding. In L. Itti, G. Rees, & J. K. Tsotsos (Eds.), *Neurobiology of attention* (pp. 197-203). New York: Academic Press.
- Oades, R. D., & Isaacson, R. L. (1978). The development of food search behavior by rats: The effects of hippocampal damage and haloperidol. *Behavioral Biology*, *24*(3), 327-337.
- Parnas, M., Lin, A. C., Huetteroth, W., & Miesenböck, G. (2013). Odor discrimination in *Drosophila*: from neural population codes to behavior. *Neuron*, *79*, 932-944.
- Parvizi, J., & Damasio, A. (2001). Consciousness and the brainstem. *Cognition*, *79*, 135-159.
- Paulk, A. C., Stacey, J. A., Pearson, T. W. J., Taylor, G. J., Moore, R. J. D., Srinivasan, M. V., & van Swinderen, B. (2014). Selective attention in the honeybee optic lobes precedes behavioral choices. *Proceedings of the National Academy of Science of the United States of America*, *111*, 5006-5011.
- Pelizzon, A., & Gagliano, M. (2015). The sentience of plants: animal rights and rights of nature intersecting? *Australian Animal Protection Law Journal*, *11*, 5-14.
- Penfield, W., & Jasper, H. (1954). *Epilepsy and the functional anatomy of the brain*. London: J. & A. Churchill, Ltd.
- Penfield, W., & Rasmussen, T. (1950). *The cerebral cortex of man: a clinical study of localization of function*. New York: Macmillan.

- Perry, C. J., & Barron, A. B. (2013). Neural mechanisms of reward in insects. *Annual Review of Entomology*, 58, 543-562.
- Petie, R., Garm, A., & Nilsson, D.-E. (2011). Visual control of steering in the box jellyfish *Tripedalia cystophora*. *Journal of Experimental Biology*, 214, 2809-2815.
- Pfeiffer, K. J., & Crailsheim, K. (1998). Drifting of honeybees. *Insectes Sociaux*, 45, 151-167.
- Pfeiffer, K., & Homberg, U. (2014). Organization and functional roles of the central complex in the insect brain. *Annual Review of Entomology*, 59, 165-184.
- Philippi, C. L., Feinstein, J. S., Khalsa, S. S., Damasio, A., Tranel, D., Landini, G., Williford, K., & Rudrauf, D. (2012). Preserved self-awareness following extensive bilateral brain damage to the insula, anterior cingulate, and medial prefrontal cortices. *PLoS ONE*, 7(8), e3841.
- Plath, J. A., & Barron, A. B. (2015). Current progress in understanding the functions of the insect central complex. *Current Opinion in Insect Science*, 12, 11-18.
- Redgrave, P., Prescott, T. J., & Gurney, K. N. (1999). The basal ganglia: a vertebrate solution to the selection problem?. *Neuroscience*, 89, 1009-1023.
- Rosenthal, D. M. (2005). *Consciousness and mind*. New York: Oxford University Press.
- Rosner, R., & Homberg, U. (2013). Widespread sensitivity to looming stimuli and small moving objects in the central complex of an insect brain. *Journal of Neuroscience*, 33, 8122-8133.
- Sareen, P., Wolf, R., & Heisenberg, M. (2011). Attracting the attention of a fly. *Proceedings of the National Academy of Science of the United States of America*, 108(17), 7230-7235.
- Schiff, N. D. (2010). Recovery of consciousness after brain injury: a mesocircuit hypothesis. *Trends in Neurosciences*, 33(1), 1-9.
- Schwaerzel, M., Monastirioti, M., Scholz, H., Friggi-Grelin, F., Birman, S., & Heisenberg, M. (2003). Dopamine and octopamine differentiate between aversive and appetitive olfactory memories in *Drosophila*. *Journal of Neuroscience*, 23, 10495-10502.
- Seeley, T. D. (1995). *The wisdom of the hive*. Cambridge: Harvard University Press.
- Seelig, J. D., & Jayaraman, V. (2013). Feature detection and orientation tuning in the *Drosophila* central complex. *Nature*, 503, 262-266.
- Seelig, J. D., & Jayaraman, V. (2015). Neural dynamics for landmark orientation and angular path integration. *Nature*, 521, 186-191.
- Shu, D.-G., Conway Morris, S., Han, J., Zhang, Z.-F., Yasui, K., Janvier, P., Chen, L., Zhang, X.-L., Liu, J.-N., Li, Y., & Liu, H.-Q. (2003). Head and back bone of the Early Cambrian vertebrate *Haikouichthys*. *Nature*, 421, 526-529. doi: 10.1038/nature01264
- Skorupski, P., & Chittka, L. (2006). Animal cognition: an insect's sense of time? *Current Biology*, 16(19), R851-R853.
- Søvik, E., Perry, C. J., & Barron, A. B. (2015). Insect reward systems: comparing flies and bees. In A. Zayed & C. Kent (Eds.), *Genomics, physiology and behaviour of social insects* (Vol. 48, pp. 189-226). London: Academic Press
- Sparks, D. L. (1988). Neuronal cartography: Sensory and motor maps in the superior colliculus. *Brain, Behavior and Evolution*, 31, 49-56.
- Sprague, J. M. (1966). Interaction of cortex and superior colliculus in mediation of visually guided behavior in the cat. *Science*, 153(3743), 1544-1547.
- Stephenson-Jones, M., Samuelsson, E., Ericsson, J., Robertson, B., & Grillner, S. (2011). Evolutionary conservation of the basal ganglia as a common vertebrate mechanism for action selection. *Current Biology*, 21, 1081-1091.
- Strausfeld, N. J. (1976). *Atlas of an insect brain*. Berlin: Springer-Verlag.

- Strausfeld, N. J. (2012). *Arthropod brains: Evolution, functional elegance, and historical significance*. Cambridge, MA: Belknap Press.
- Strausfeld, N. J., & Hirth, J. (2013). Deep homology of arthropod central complex and vertebrate basal ganglia. *Science*, *340*, 157-161.
- Strawson, G. (2006). Realistic monism: Why physicalism entails panpsychism. *Journal of Consciousness Studies*, *13*(10/11), 3-31.
- Strube-Bloss, M. F., Nawrot, M. P., & Menzel, R. (2011). Mushroom body output neurons encode odor-reward associations. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *31*(8), 3129-3140. doi: 10.1523/jneurosci.2583-10.201
- Swanson, L. W. (2000). Cerebral hemisphere regulation of motivated behavior. *Brain Research*, *886*, 113-164.
- Tononi, G. (2004). An information integration theory of consciousness. *BMC Neuroscience*, *5*(42).
- Tononi, G. (2008). Consciousness as integrated information: a provisional manifesto. *The Biological Bulletin*, *215*(3), 216-242.
- Tononi, G., & Koch, C. (2015). Consciousness: here, there and everywhere? *Philosophical Transactions of the Royal Society B*, *370*(1668). doi:10.1098/rstb.2014.0167
- Trestman, M. (2013). The Cambrian explosion and the origins of embodied cognition. *Biological Theory*, *8*, 80-92.
- Van Opstal, A. J., Hepp, K., Suzuki, Y., & Henn, V. (1995). Influence of eye position on activity in monkey superior colliculus. *Journal of Neurophysiology*, *74*, 1539-1610.
- Van Swinderen, B. (2005). The remote roots of consciousness in fruit-fly selective attention? *BioEssays*, *27*, 321-330.
- Van Swinderen, B., & Greenspan, R. J. (2003). Saliency modulates 20-30 Hz brain activity in *Drosophila*. *Nature Neuroscience*, *6*, 579-586.
- Von Holst, E., & Mittelstaedt, H. (1950). Das reafferenzprinzip (wechselwirkungen zwischen zentralnervensystem und peripherie). *Naturwissenschaften*, *37*, 464-476.
- Webb, B. (2004). Neural mechanisms for prediction: do insects have forward models? *Trends in Neurosciences*, *27*, 278-282.
- Webb, B. (2006). Transformation, encoding and representation. *Current Biology*, *16*(6), R18.
- Wehner, R. (2013). Life as a cataglyphologist – and beyond. *Annual Review of Entomology*, *58*, 1-18.
- Weir, P. T., Schnell, B., & Dickinson, M. H. (2014). Central complex neurons exhibit behaviorally gated responses to visual motion in *Drosophila*. *Journal of Neurophysiology*, *111*, 62-71.
- Wimsatt, W. C. (2007). *Re-engineering philosophy for limited beings: piecewise approximations to reality*. Cambridge: Harvard University Press.
- Zenon, A., & Krauzlis, R. J. (2012). Attention deficits without cortical neuronal deficits. *Nature*, *489*, 434-437.
- Zompa, I. C., & Dubuc, R. (1996). A mesencephalic relay for visual inputs to reticulospinal neurones in lampreys. *Brain Research*, *718*, 221-227.
- Zompa, I. C., & Dubuc, R. (1998). Electrophysiological and neuropharmacological study of tectoreticular pathways in lampreys. *Brain Research*, *804*, 238-252.



THE HUMANE SOCIETY  
OF THE UNITED STATES

Institute for Science and Policy

# ANIMAL STUDIES REPOSITORY

[Home](#) | [About](#) | [FAQ](#) | [My Account](#)

[Journal Home](#)  
[About This Journal](#)  
[Aims & Scope](#)  
[Editorial Board](#)  
[Policies](#)  
[Ethical Guidelines](#)  
[Author Guidelines](#)

[Submit Article](#)

[Receive Email Notices or RSS](#)

Select an issue:  
[All Issues](#)

## Search

Enter search terms:

[in this journal](#)

[Advanced Search](#)

ISSN: 2377-7478

## Links

[Center for Animal Thinking and Emotion \(CATE\) ListServ](#)

[Home](#) > [ASent](#)

## [Animal Sentience: An Interdisciplinary Journal on Animal Feeling](#)

### About This Journal

*Animal Sentience [ASent]* is the first journal to focus on the capacity of nonhuman animals to feel. Feeling can be any sensation, such as seeing, hearing, touching, tasting, smelling, moving, wanting, pain, pleasure, emotion, mood, anticipation or intention. We distinguish *sentience* (the capacity to feel) from *sapience* (the capacity to think), but it also feels like something to think. Hence, we welcome submissions concerning animal consciousness and cognition.

*ASent* is a peer-reviewed, interdisciplinary and open-access journal. We encourage empirical studies, theoretical modeling, peer commentaries and integrative review/syntheses from any academic discipline within the sciences, humanities, or any other field that bears on animal sentience.

*ASent* is a publication of the Humane Society Institute for Science and Policy (HSISP). Based in Washington DC, HSISP's mandate is to advance the application of scientific and technical analysis and expertise to animal welfare issues and policy questions worldwide. The HSISP is an affiliate of The Humane Society of the United States, the world's largest animal protection organization.

Authors' opinions do not necessarily reflect those of the publisher or editors.



[Home](#) | [About](#) | [FAQ](#) | [My Account](#) | [Accessibility Statement](#)

THE HUMANE SOCIETY  
OF THE UNITED STATES

Institute for Science and Policy

## ANIMAL STUDIES REPOSITORY

[Home](#) [About](#) [FAQ](#) [My Account](#)[Journal Home](#)  
[About This Journal](#)  
[Aims & Scope](#)  
[Editorial Board](#)  
[Policies](#)  
[Ethical Guidelines](#)  
[Author Guidelines](#)[Submit Article](#)[Receive Email Notices or RSS](#)Select an issue:  
[All Issues](#)**Search**

Enter search terms:

[in this journal](#)[Advanced Search](#)

ISSN: 2377-7478

**Links**[Center for Animal Thinking and Emotion \(CATE\) ListServ](#)[Home > ASent](#)[Animal Sentience: An Interdisciplinary Journal on Animal Feeling](#)**Policies****Contents**

- [Philosophy](#)
- [Who Can Submit?](#)
- [General Submission Rules](#)
- [Formatting Requirements](#)
- [Creative Commons License](#)

**Philosophy**

For more information, please see the *ASent* [Aims and Scope](#) page.

**Who Can Submit?**

Authors in any field may submit an original article to be considered for publication, provided that they own the copyright to the work or are authorized by the copyright owner to submit the material. (In general, authors own the copyright to their own original work except when they have agreed to transfer copyright to their employer.)

**General Submission Rules**

All submissions are eligible for consideration including updates of already published articles now soliciting Open Peer Commentary. Questions or concerns about the submission terms should be [directed to the editors](#).

**Rationale for Soliciting Commentary and Potential Commentator List**

All submissions should be accompanied by a cover letter including (1) a rationale for soliciting open peer commentary and (2) a list of potential commentators, across disciplines, along with their emails and website URLs

**Formatting Requirements**

Drafts submitted to *ASent* should be digital and formatted along the lines of the latest edition of the [Publication Manual of the American Psychological Association \(APA\)](#). Once refereed, revised and accepted, the final draft will be formatted according to the [Final Manuscript Preparation Guidelines](#). Although bepress can provide limited technical support, it is the author's responsibility to provide an electronic version of the article in XML, Word docx, or RTF formats, which can also be converted to a high-quality PDF (Adobe's Portable Document Format) and HTML at a later date.

**Creative Commons License**

All papers accepted for publication in *ASent* are published under a [CC-BY-NC license](#). Anyone may access and re-use an article for non-commercial purposes as long as the author is credited. Authors may make the license more liberal ([CC-BY](#)) or more restrictive ([CC-BY-NC-ND](#)) at their own discretion.