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Insects have the capacity for subjective experience

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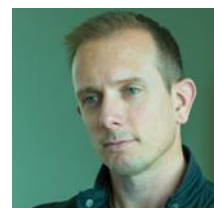
Abstract: To what degree are non-human animals conscious? We propose that the most meaningful way to approach this question is from the perspective of functional neurobiology. Here we focus on subjective experience, which is a basic awareness of the world without further reflection on that awareness. 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



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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).

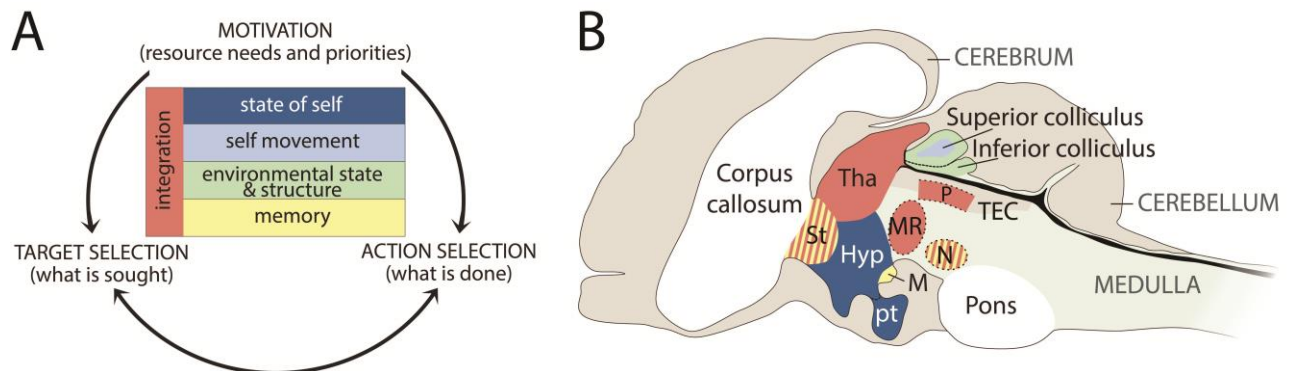


Figure 1: The vertebrate behavioral core control system. Following Merker (2007), autonomous animal decision making can be considered to involve three related domains: motivation, target selection, and action selection (A). These domains can be resolved and decisions can be made by an integrated neural 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).

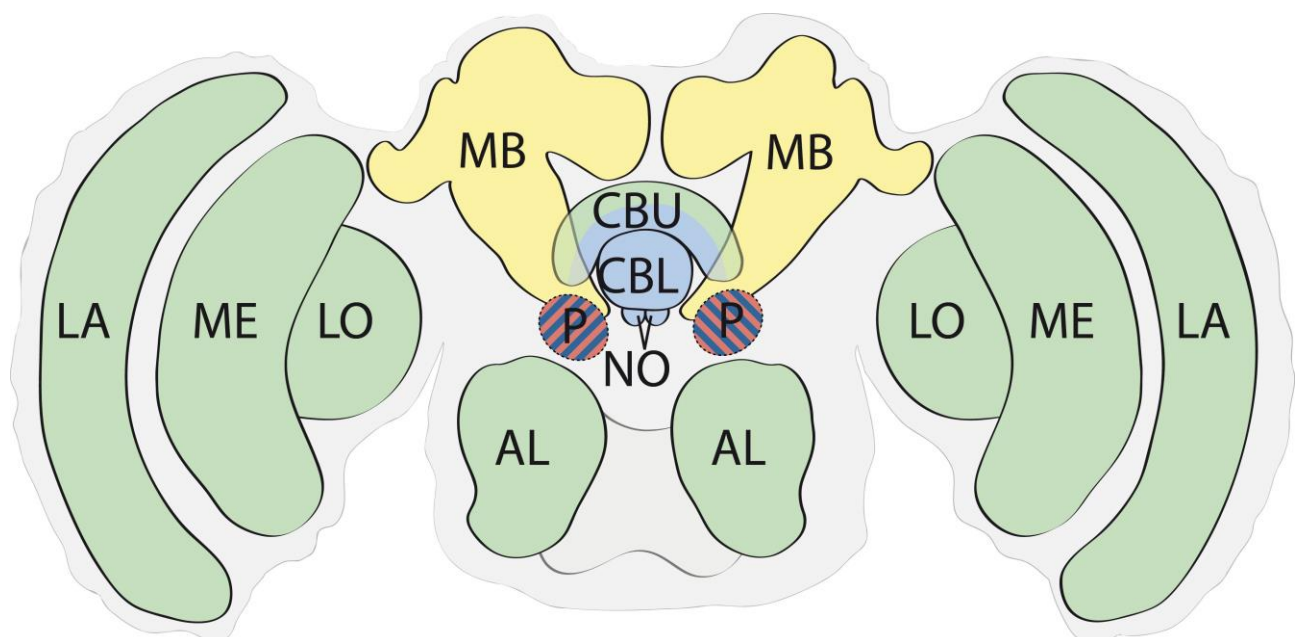


Figure 2: Basic functional anatomy of the insect brain (not to scale). The structures of the insect brain are functionally analogous to those functions of the vertebrate midbrain described in **Figure 1**. (Regions are colored to highlight the functional analogy with **Figure 1A**.) Sensory lobes, of 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.

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