LETTER

REPLY TO ADAMO, KEY ET AL., AND SCHILLING AND CRUSE: Crawling around the hard problem of consciousness

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One goal of our paper (1) was to invite constructive empirical debate. We are glad that several authors have taken up this invitation.

Two letters (2, 3) claim that our characterization of subjective experience was too liberal. Adamo (3) misreads us. We do not simply define subjective experience as a type of integrated information processing. Rather, such processing is the mechanism that makes a first-person, phenomenally rich perspective on the world possible.

Schilling and Cruse (2) think we are wrong to set aside access consciousness. They are here and elsewhere (4) committed to the thesis that subjective experience requires access consciousness. This claim is philosophically contentious, even in humans (5), and one that we deny. Broadly speaking, we claim that insects are aware of the world (including the state of the mobile body within the world), and that this awareness feels a certain way to the organism that has it. The stronger thesis, which they endorse, says that awareness is always awareness of one's own mental states. We think that their thesis is less economical, faces harder philosophical challenges, and biases investigation against simple animals. We thus prefer representational models that are "self-interpreting" (6), rather than requiring an extra layer of processing.

Key et al. (7) doubt the vertebrate midbrain supports the capacity for subjective experience. Our case relied on a diverse set of evidence from lesion and anesthesia studies (not just the case of anecephalic infants), although we acknowledged that this localization is far from settled. They also support their claim by reference to work on the supposed absence of pain in fish. That work is itself highly controversial (8), and makes several assumptions about the physiology of pain and cortical contribution to pain that we would deny.

For example, Key (9) emphasizes the role of somatosensory and insular cortex in the human experience of pain. However, lesions of somatosensory cortex disturb only localization of pain (10). More serious insular damage disturbs the motivational force of pain (so-called "pain asymbolia"), but that is only because such damage disturbs the experience of bodily ownership more generally (11). The subjective experiences of any animal, including any experience of pain, will be appropriate to its body and its form of life.

Key et al. (7) also note that cortical damage changes what we are aware of, and that visual cortex damage appears to eliminate conscious vision. One should not confuse the experience of a human with a damaged visual cortex with the experience of an animal that never evolved a cortex in the first place, however. As the Sprague effect (12) illustrates, proper functioning of midbrain visual structures depends on a balance of inhibitory inputs from both the cortex and other midbrain structures.

More generally, in our article, we were careful to distinguish between the contents of subjective experience and the basic capacity to have any experiences at all. Our argument exclusively concerned the latter. More complex animals are capable of more complex experiences. The cortex surely plays an important role in enriching the contents of human experience. It is thus no surprise that damage to (say) the visual cortex would lead to corresponding impoverishments of visual experience.

Adamo (3) proposes that insects have too few neurons in the brain to support subjective experience. We refute this proposition. The insect brain can support the key functions of the vertebrate midbrain, even though far fewer neurons are devoted to a given function in an insect than in vertebrates. For example, we agree with Adamo (3) that insects do not process emotions in the same way vertebrates do; whereas larger vertebrates devote entire nuclei to the processing of "emotional" states, insects support processing of motivational functions with clusters of just a few neurons (13–15). These clusters are specialized circuits that regulate and convey information on vital internal states (arousal, satiation, hunger, and reward) to systems processing sensory information and supporting memory (13–15). As we have argued, this system is sufficient to support a basic subjective experience of the world. This point illustrates the economy of scale of the insect brain, and also demonstrates how the functional organization of the system is a far more important consideration than neuron number, as has been argued elsewhere (16).

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We agree with Schilling and Cruse (2) on the benefits of functional definitions of conscious phenomena. We also agree that a central metric space is not required to support central space foraging. We have not proposed that the only way to navigate or process position and spatial relations is by a "cognitive map". There are many ways to represent spatial relations and functions in the brain, as insect studies have shown (17).

Finally, Schilling and Cruse (2) note that we do not attempt to solve the so-called "hard problem" of consciousness (18). Adamo's response (3) similarly suggests that an explanatory gap remains. We agree. We have presented evidence about the structures that support conscious experience, and the functional properties of those structures that seem to be important. However, we have not tried to explain how the personal feeling of a mental process could arise from a lump of neurons. Our investigation is very much in the spirit of Penfield and Rasmussen, who urged 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" (19).

That said, we think that Schilling and Cruse are fellow travelers in this regard. As they have argued elsewhere (4), the current state of consciousness research resembles the study of "vital forces" in the 18th century. Then too, there seemed like a great gap between the organic and the inorganic. This problem was dissolved, not solved, by the subsequent development of appropriate scientific concepts for understanding life.

We consider our work to be very much in the same vein. The hard problem is hard not because it has no answer, but because we do not yet know what a satisfying answer could look like. It is the job of philosophy to keep alive such questions (20). It is the job of neuroscience to forge ahead regardless, and to do its best to outflank mysteries that cannot presently be tackled head-on.

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