



Neural networks letter

Minimal neuroanatomy for a conscious brain: Homing in on the networks constituting consciousness

Ezequiel Morsella^{a,b,*}, Stephen C. Krieger^c, John A. Bargh^d^a Department of Psychology, San Francisco State University, United States^b Department of Neurology, University of California, San Francisco, United States^c Department of Neurology, Mount Sinai Medical Center, United States^d Yale University, United States

ARTICLE INFO

Article history:

Received 10 July 2008

Received in revised form 24 July 2009

Accepted 13 August 2009

Keywords:

Neural correlate of consciousness (NCC)

Consciousness

Olfactory system

Awareness

Subjective experience

Sentience

Mind–body problem

ABSTRACT

There is a consensus that consciousness is constituted by only a subset of all neuroanatomical regions and processes, but no agreement exists regarding which particular subset(s) constitutes it. We propose that a consensus will be reached if investigators (a) pool their knowledge regarding the regions whose non-participation does not in principle render the nervous system devoid of consciousness (e.g., the cerebellum, amygdalae, hippocampi, hemispheric commissures, 'pre-cortical' thalamus, and vast regions of the cortex), and (b) focus on the long-overlooked olfactory system. This 'brutally reductionistic' approach may isolate the physical basis of consciousness; even its falsification would help to illuminate this enigma.

© 2009 Elsevier Ltd. All rights reserved.

Remarkable empirical advances have led to the consensus that consciousness¹ is associated with only a subset of all neuroanatomical regions and processes, but no agreement exists regarding which particular subset(s) embodies the physical events (presumably networks) capable of constituting consciousness. At one extreme, researchers propose that consciousness can be constituted at a small scale, by a unique set of cells in particular regions (Koch, 2004); at the other extreme, researchers propose that it requires large-scale synchronization of 'equipotential' elements across the brain (Greenfield, 2000). A consensus will be reached if investigators (a) pool their knowledge regarding the capacious catalog of regions whose non-participation does not render the nervous

system incapable of still exhibiting an identifiable form of consciousness, and (b) focus on the long-overlooked physical basis of olfactory consciousness.

There are numerous neuroanatomical regions that do not render the nervous system incapable of continuing to exhibit an identifiable form of consciousness when they are non-participatory (e.g., extirpated or inactivated). Cataloging such regions prevents researchers from barking up the wrong tree when attempting to isolate the physical basis of consciousness. Through the process of elimination, such a catalog also helps one distill what can be conceptualized as the minimal neuroanatomy for a conscious brain. The following are conservative, a-theoretical conclusions from such a catalog.

Gross anatomy

Although the absence of the spinal cord or cerebellum leads to sensory, motor, and even cognitive deficits, it does not seem to eradicate all forms of consciousness. Similarly, although extirpation of the amygdalae or hippocampi leads to anomalies including deficits in affective processing and episodic memory, respectively, it seems that an identifiable form of consciousness persists without these structures. This is not to imply that these structures are incapable of generating a form of consciousness, but only that, in principle, *a brain can be a conscious brain without them*. With respect to these structures and those listed below,

* Corresponding address: Department of Psychology, San Francisco State University (SFSU), 1600 Holloway Avenue, EP 301, San Francisco, CA 94132-4168, United States.

E-mail address: morsella@sfsu.edu (E. Morsella).

¹ According to the philosopher Thomas Nagel, an organism possesses consciousness (also known as 'awareness' and 'sentience') if there is *something it is like* to be that organism—something it is like, for example, to be human and experience pain or yellow afterimages. At this stage of understanding, we believe it is best to study something as assumption laden as consciousness only in subjects that can self-report. Hence, we focus on the adult human brain, a context in which one can speak about consciousness with certainty.

our approach is valid only if consciousness does not require some hitherto unidentified, large-scale interaction requiring a subset of the regions that are thus ‘conceptually extirpated.’ If the approach is proved to be invalid, then there will be strong evidence that consciousness does require multiple regions (Greenfield, 2000), and much will have been learned regarding its physical nature.

Investigations on ‘split-brain’ patients and split-brain patients experiencing binocular rivalry (O’Shea & Corballis, 2005) suggest that a conscious brain does not require the non-dominant (usually right) cerebral cortex nor the cerebral commissures. Investigations regarding prefrontal lobe syndromes (Gray, 2004) and the psychophysiology of dreaming, which involves prefrontal deactivations (Muzur, Pace-Schott, & Hobson, 2002), suggest that, although the prefrontal lobes are involved in cognitive control, they are not essential for the generation of consciousness, consistent with the view that cognitive control and consciousness are distinct processes (Koch & Tsuchiya, 2007).

Investigators have challenged the prevalent view that the cortex should be construed as *the* organ of consciousness. As noted in Merker (2007), Wilder Penfield concluded from observations of awake patients undergoing brain surgeries involving ablations and direct brain stimulation that, although the cortex may elaborate the contents of consciousness, it is not the *seat* of consciousness. Based on such evidence and clinical observations of anencephaly, Merker (2007) re-introduces this hypothesis in a framework in which consciousness is primarily a phenomenon associated with *mesencephalic* areas. It seems that consciousness can persist even when great quantities of the cortex are absent. The question now is whether an identifiable form of consciousness can exist despite the non-participation of all cortical matter.

The case for olfaction

To understand the neural basis of consciousness, researchers have followed Sir Francis Crick’s recommendation and focused on the visual system, but this dominant, neuroanatomically vast, and far from primitive modality may not be the easiest arena for our reductionistic approach. Olfaction is better suited for such purposes. For example, it is tempting to hypothesize that a conscious brain requires thalamocortical interaction between thalamic ‘relay’ neurons and the cortex, but this is inconsistent with the fact that we consciously experience aspects of olfaction even though olfactory afferents bypass the thalamus and directly target regions of the ipsilateral cortex. This is not to imply that the *relay thalamus* is unnecessary for other forms of consciousness (e.g., visual or auditory) or that a conscious brain experiencing only olfaction does not require the thalamus: in post-cortical stages of processing, the thalamus receives inputs from cortical regions involved in olfaction.

The neural correlates of conscious olfactory perceptions, imagery, and hallucinations, as revealed by direct stimulation of the brain, neuroimaging, and lesions, suggest that olfactory consciousness does not require the olfactory bulb (Mizobuchi et al., 1999). It seems that patients can still experience explicit, olfactory memories following bilateral olfactory bulbectomies, though definitive evidence is wanting. It seems that the minimal neuroanatomy for consciousness does not require the relay thalamus nor at least one structure (the olfactory bulb) proposed to serve a function similar to that of the relay thalamus (Kay & Sherman, 2007).

In addition to its relatively simple, neuroanatomically accessible, and phylogenetically primitive structure, olfaction is well suited for consciousness research because of its phenomenological characteristics: unlike most other modalities, it regularly yields no subjective experience of any kind when the system is understimulated, as during sensory habituation or when odorants are subliminal (as in *blind-smell*; Bensafi et al., 2004). This ‘experien-

tial nothingness’ (an informative baseline condition for consciousness research) is more akin to the phenomenology of the blind spot than to that which is experienced when visual stimulation is absent (darkness).

A critical question is whether the olfactory system can generate some form of consciousness (a ‘microconsciousness’, as in Semir Zeki’s work; Koch, 2004) by itself or whether olfactory consciousness requires interactions with non-olfactory regions of the minimal brain proposed above. Perhaps one becomes conscious of olfactory percepts only when they ‘cross-talk’ with other systems or when they influence processes that are motor (Bensafi et al., 2004) or semantic–linguistic (Herz, 2003). According to Buck (2000), conscious aspects of odor discrimination depend primarily on the activities of the frontal and orbitofrontal cortices; according to Barr and Kierman (1993), olfactory consciousness depends on the pyriform cortex. These proposals appear inconsistent with subcortical accounts of consciousness (Merker, 2007). Research on phantasias and explicit versus implicit olfactory processing may resolve this discrepancy. Hence, it is critical to identify the minimal region(s) whose stimulation is sufficient to induce olfactory hallucinations.

Therefore, the minimal neuroanatomy for a conscious brain need not in principle include the spinal cord, cerebellum, amygdalae, hippocampi, pre-cortical relay thalamus, hemispheric commissures, non-dominant cortical hemisphere, nor many portions of the dominant hemisphere. Hypothetically, consciousness can be instantiated in a minimal nervous system without these regions and their associated processes. This hypothesis can be falsified if the remaining areas alone are insufficient to constitute consciousness, perhaps because the physical basis of consciousness lies outside these regions, or consciousness requires a larger-scale network (Greenfield, 2000). Such a falsification would advance research on consciousness. Through multidisciplinary research, the subset(s) of regions constituting consciousness may be further isolated by eliminating regions of this minimal brain.

Acknowledgment

We acknowledge the assistance of Donald Leopold.

References

- Barr, M. L., & Kierman, J. A. (1993). *The human nervous system. An anatomical viewpoint* (6th ed.). Philadelphia: Lippincott.
- Bensafi, M., Zelano, C. M., Johnson, B. N., Mainland, J. D., Khan, R., & Sobel, N. (2004). Olfaction: From sniff to percept. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences III* (pp. 259–280). Cambridge, MA: MIT Press.
- Buck, L. B. (2000). Smell and taste: The chemical senses. In E. R. Kandel, J. H. Schwartz, & T. M. Jessell (Eds.), *Principles of neural science* (fourth edition) (pp. 625–647). New York: McGraw-Hill.
- Gray, J. A. (2004). *Consciousness: Creeping up on the hard problem*. New York: Oxford University Press.
- Greenfield, S. A. (2000). *The private life of the brain*. New York: Wiley.
- Herz, R. S. (2003). The effect of verbal context on olfactory perception. *Journal of Experimental Psychology: General*, 132, 595–606.
- Kay, L. M., & Sherman, S. M. (2007). An argument for an olfactory thalamus. *Trends in Neurosciences*, 30, 47–53.
- Koch, C. (2004). *The quest for consciousness: A neurobiological approach*. Colorado: Roberts and Company.
- Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences*, 11, 16–22.
- Merker, C. (2007). Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Sciences*, 30, 63–134.
- Mizobuchi, M., Ito, N., Tanaka, C., Sako, K., Sumi, Y., & Sasaki, T. (1999). Unidirectional olfactory hallucination associated with ipsilateral unruptured intracranial aneurysm. *Epilepsia*, 40, 516–519.
- Muzur, A., Pace-Schott, E. F., & Hobson, J. A. (2002). The prefrontal cortex in sleep. *Trends in Cognitive Sciences*, 6, 475–481.
- O’Shea, R. P., & Corballis, P. M. (2005). Visual grouping on binocular rivalry in a split-brain observer. *Vision Research*, 45, 247–261.