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## Consciousness, Neural Basis of

Consciousness is a puzzling state-dependent property of certain types of complex, adaptive systems. The best example of one type of such system is a healthy and attentive human brain. If the brain is anaesthetized, consciousness ceases. Small lesions in the brain stem and thalamus of patients can lead to a complete loss of consciousness, while destruction of circumscribed parts of the cerebral cortex of patients can eliminate very specific aspects of consciousness, such as the ability to be aware of motion or to recognize objects as faces, without a concomitant loss of vision in general. Given the similarity in brain structure and behavior, biologists commonly assume that at least some animals, in particular nonhuman primates, share certain aspects of consciousness with humans. Brain scientists, in conjunction with cognitive neuroscientists, are exploiting a number of empirical approaches that shed light on the neural basis of consciousness. Since it is not known to what extent artificial systems, such as computers and robots, can become conscious, this entry will exclude these from consideration.

### 1. Some Common Neurobiological Assumptions

By and large, neuroscientists have made a number of working assumptions that, in the fullness of time, need to be justified more fully.

(a) There is something to be explained; that is, the subjective content associated with a conscious sensation—what philosophers refer to as ‘qualia’—does exist and has its physical basis in the brain. To what extent qualia and all other subjective aspects of consciousness can or cannot be explained within a reductionist framework remains highly controversial (Chalmers 1996).

(b) Consciousness is a vague term with many usages. It will, in the fullness of time, be replaced by a vocabulary that more accurately reflects the contribution of different brain processes (for a similar evolution, consider the usage of ‘memory,’ which has

been replaced by an entire hierarchy of more specific concepts). Common to all forms of consciousness is that it feels like something (e.g., to ‘see blue,’ to ‘experience a headache,’ or to ‘reflect upon a memory’); that is, it is usually about something. *Self-consciousness* is but one form of consciousness.

It is possible that all the different aspects of consciousness (smelling, pain, visual awareness, affect, self-consciousness, and so on) employ a basic common mechanism or perhaps a few such mechanisms. If so, then if one can understand the mechanism for one aspect, then one will have gone most of the way towards understanding them all.

(c) Consciousness is a property of the human brain, a highly evolved system. It therefore must have a useful *function* to perform. Crick and Koch (1998) assume that the function of the neuronal correlate of consciousness is to produce the best current interpretation of the environment—in the light of past experiences—and to make it available, for a sufficient time, to the parts of the brain which contemplate, plan, and execute voluntary motor outputs (including language). This needs to be contrasted with *on-line systems* that bypass consciousness but that can generate stereotyped behaviors (see below).

Note that in normally developed individuals, motor output is not necessary for consciousness to occur. This is demonstrated by *lock-in syndrome*, in which patients have lost (nearly) all ability to move yet are clearly conscious.

(d) At least some animal species possess some aspects of consciousness. In particular, this is assumed to be true for nonhuman primates such as the macaque monkey. Consciousness associated with sensory events in humans is likely to be related to sensory consciousness in monkeys for several reasons. First, trained monkeys show similar behavior to that of humans for many low-level perceptual tasks (e.g., detection and discrimination of visual motion or depth: Wandell 1995). Second, the gross neuroanatomies of humans and nonhuman primates are rather similar once the difference in size has been accounted for. Finally, functional magnetic resonance imaging of human cerebral cortex is confirming the existence of a functional organization in sensory cortical areas similar to that discovered by the use of single-cell electrophysiology in the monkey (Tootell et al. 1998). As a corollary, it follows that language is not necessary for consciousness to occur (although it greatly enriches human consciousness).

### 2. Enabling, Modulating, and Specific Factors

It is important to distinguish the general, *enabling* factors in the brain that are needed for any form of consciousness to occur from *modulating* ones that can up- or downregulate the level of arousal, attention, and awareness, and from the *specific* factors responsible for a particular content of consciousness.

An easy example of an enabling factor would be a proper blood supply. Inactivate the heart, and consciousness ceases within a fraction of a minute. This does not imply that the neural correlate of consciousness is in the heart (as Aristotle thought). A neuronal enabling factor for consciousness is the *intralaminar nuclei of the thalamus*. Acute bilateral loss of function in these small structures that are widely and reciprocally connected to the basal ganglia and cerebral cortex leads to immediate coma or profound disruption in arousal and consciousness (Bogen 1995).

Among the neuronal modulating factors are the various activities in nuclei in the brain stem and the midbrain, often collectively referred to as the *reticular activating system*, which control in a widespread and quite specific manner the level of noradrenaline, serotonin, and acetylcholine in the forebrain. Appropriate levels of these neurotransmitters are needed for sleep, arousal, attention, memory, and other functions critical to behavior and consciousness (Baars 1997).

Yet any particular content of consciousness is unlikely to arise from these structures, since they appear to lack the specificity necessary to mediate a sharp pain in the right molar, the percept of the deep, blue California sky, the bouquet associated with a rich Bordeaux, or a haunting musical melody. These must be caused by specific neural activity in cortex, thalamus, basal ganglia, and associated neuronal structures. The question motivating much of the current research into the neuronal basis of consciousness is the notion of the *minimal* neural activity that is *sufficient* to cause a specific conscious percept or memory (see below).

For instance, when a subject consciously perceives a face, the retinal ganglion cells whose axons make up the optic nerve that carries the visual information to the brain proper are firing in response to the visual stimulus. Yet it is unlikely that this retinal activity directly correlates with visual perception. While such activity is evidently necessary for seeing a physical stimulus in the world, retinal neurons by themselves do not give rise to consciousness.

Given the comparative ease with which the brains of animals can be probed and manipulated, it seems opportune at this point in time to concentrate on the neural basis of sensory consciousness. Because primates are highly visual animals and much is known about the neuroanatomy, psychology, and computational principles underlying visual perception, vision has proven to be the most popular model system in the brain sciences.

### 3. *Information Processing in the Brain that Bypasses Consciousness*

Cognitive and clinical research demonstrates that much complex information processing can occur

without involving consciousness. This includes visual, auditory, and linguistic priming, implicit memory, the implicit recognition of complex sequences, automatic behaviors such as driving a car or riding a bicycle, and so on (Velmans 1991), and the dissociations found in patients with lesions in cerebral cortex (e.g., such as residual visual functions in the professed absence of any visual awareness known as *clinical blindsight* in patients with lesions in primary visual cortex: Weiskrantz 1997).

The cognitive scientist Jackendoff (1987) argues at length against the notion that consciousness and thoughts are inseparable and that introspection can reveal the contents of the mind. According to Jackendoff, what is conscious about thoughts are sensory aspects, such as visual images, sounds, or silent speech. Both the process of thought and its content are not directly accessible to consciousness. Indeed, one tradition in psychology and psychoanalysis—going back to Sigmund Freud—hypothesizes that higher-level decision making and creativity are not accessible at a conscious level, although they influence behavior.

Within the visual modality, Milner and Goodale (1995) have made a masterful case for the existence of so-called *on-line systems* that bypass consciousness. Their function is to mediate relative stereotype visuomotor behaviors, such as eye and arm movements, reaching, grasping, posture adjustments, and so on, in a very rapid, reflex-like manner. On-line systems work in egocentric coordinate systems, and lack certain types of perceptual illusions (e.g., size illusion) as well as possessing no direct access to working memory. This contrasts well with the function of consciousness alluded to above, namely to synthesize information from many different sources and use it to plan behavioral patterns over time. Milner and Goodale argue that on-line systems are associated with the *dorsal stream* of visual information in the cerebral cortex, originating in the primary visual cortex (V1) and terminating in the posterior parietal cortex.

### 4. *The Neuronal Correlate of Consciousness (NCC)*

The problem of consciousness can be broken down into several separate questions. Most, if not all of these, can then be subjected to scientific inquiry.

The major question that neuroscience must ultimately answer can be bluntly stated as follows: it is probable that at any moment some active neuronal processes in our head correlate with consciousness, while others do not; *what is the difference between them?* The specific processes that correlate with the current content of consciousness are referred to as the *neuronal correlate of consciousness*, or as the NCC. Whenever some information is represented in the

NCC it is represented in consciousness. The NCC is the minimal (minimal, since it is known that the entire brain is sufficient to give rise to consciousness) set of neurons, most likely distributed throughout certain cortical and subcortical areas, whose firing directly correlates with the perception of the subject at the time. Conversely, stimulating these neurons in the right manner with some yet unheard of technology should give rise to the same perception as before. Discovering the NCC and its properties will mark a major milestone in any scientific theory of consciousness.

What is the character of the NCC? Most popular has been the belief that consciousness arises as an emergent property of a very large collection of interacting neurons (for instance, Libet 1993) possibly in connection with exceeding some level of complexity (Edelman and Tononi 2000). In this view, it would be foolish to locate consciousness at the level of individual neurons. An alternative hypothesis is that there are special sets of 'consciousness' neurons distributed throughout cortex and associated systems. Such neurons represent the ultimate neuronal correlate of consciousness, in the sense that the relevant activity of an appropriate subset of them is both necessary and sufficient to give rise to an appropriate conscious experience or percept (Crick and Koch 1998). Generating the appropriate activity in these neurons, for instance by suitable electrical stimulation, would give rise to the specific percept.

Any one subtype of NCC neurons would, most likely, be characterized by a unique combination of molecular, biophysical, pharmacological, and anatomical traits. It is possible, of course, that all cortical neurons may be capable of participating in the representation of one percept or another, though not necessarily doing so for all percepts. The secret of consciousness would then be the type of activity of a temporary subset of them, consisting of all those cortical neurons which represent that particular percept at that moment. How activity of neurons across a multitude of brain areas that encode all of the different aspects associated with an object (e.g., the color of the face, its facial expression, its gender and identity, the sound issuing from its mouth) is combined into a single percept remains puzzling and is known as the *binding problem*.

What, if anything, can we infer about the location of neurons whose activity correlates with consciousness? In the case of visual consciousness, it was surmised that these neurons must have access to visual information, and project to the planning stages of the brain; that is, to premotor and frontal areas (Fuster 1997). Since no neurons in the primary visual cortex of the macaque monkey project to any area forward of the central sulcus, Crick and Koch (1998) propose that neurons in V1 do not give rise to consciousness (although V1 is necessary for most forms of vision, just as the retina is). Ongoing electrophysiological, psy-

chophysical, and imaging research in monkeys and humans is evaluating this prediction.

While the set of neurons that can express any one particular conscious percept might constitute a relative small fraction of all neurons in any one area, many more neurons might be necessary to support the firing activity leading up to the NCC. This might resolve the apparent paradox between clinical lesioning data suggesting that small and discrete lesions in cortex can lead to very specific deficits (such as the inability to see colors or to recognize faces in the absence of other visual losses) and the functional imaging data that any one visual stimulus can activate large swaths of cortex.

Conceptually, several other questions need to be answered about the NCC. What type of activity corresponds to the NCC (it has been proposed as long ago as the early part of the twentieth century that spiking activity synchronized across a population of neurons is a necessary condition for consciousness to occur)? What causes the NCC to occur? And, finally, what effect does the NCC have on postsynaptic structures, including motor output.

### 5. Experimental Approaches

A promising experimental approach to locate the NCC is the use of *bistable percepts* in which a constant retinal stimulus gives rise to two percepts alternating in time, as in a Necker cube (Logothetis 1998). One version of this is *binocular rivalry*, in which a small image, say of a horizontal grating, is presented to the left eye and another image, say a vertical grating, is shown to the corresponding location in the right eye. In spite of the constant visual stimulus, observers 'see' the horizontal grating alternate every few seconds with the vertical one (Blake 1989). The brain does not allow for the simultaneous perception of both images.

It is possible, although difficult, to train a macaque monkey to report whether it is currently seeing the left or the right image. The distribution of the switching times and the way in which changing the contrast in one eye affects this leave little doubt that monkeys and humans experience the same basic phenomenon. In a series of elegant experiments, Logothetis and colleagues (Logothetis 1998) recorded from a variety of visual cortical areas in the awake macaque monkey while the animal performed a binocular rivalry task. In primary visual cortex, only a small fraction of cells modulate their response as a function of the percept of the monkey, while 20–40 percent of neurons in higher visual areas in cortex do so. The majority of cells increased their firing rate in response to one or the other retinal stimulus with little regard to what the animal perceived at the time. In contrast, in a high-level cortical area such as the inferior temporal (IT) cortex, almost all neurons responded only to the

perceptual dominant stimulus (in other words, a 'face' cell only fired when the animal indicated by its performance that it saw the face and not the pattern presented to the other eye). This makes it likely that the NCC involves activity in neurons in the inferior temporal lobe. Lesions in the homologue area in the human brain are known to cause very specific deficits in conscious face or object recognition. However, it is possible that specific interactions between IT cells and neurons in parts of the prefrontal cortex are necessary in order for the NCC to be generated.

Functional brain imaging in humans undergoing binocular rivalry has revealed that areas in the right prefrontal cortex are active during the perceptual switch from one percept to the other (Lumer et al. 1998).

A number of alternate experimental paradigms are being investigated using electrophysiological recordings of individual neurons in behaving animals and human patients, combined with functional brain imaging. Common to these is the manipulation of the complex and changing relationship between physical stimulus and the conscious percept. For instance, when an image is briefly flashed onto the screen and is immediately followed by presentation of a second image, the first image often remains invisible (it is said to be *masked*). Yet neurons can still respond in a selective manner to the first stimulus that is not consciously registered. Under other conditions, subjects will respond to a target although it is physically not present. The NCC in the appropriate sensory area should mirror the perceptual report under these dissociated conditions. Perceptual report can be influenced by delivering current pulses to the cerebral cortex in the absence of any physical stimulus or in the presence of an ambiguous stimulus, as explored in the context of elective surgery for epileptic patients (Penfield and Perot 1963) or in animal studies (Parker and Newsome 1998). Visual illusions constitute another rich source of experiments that can provide information concerning the neurons underlying these illusory percepts. A classical example is the *motion after effect*, in which a subject stares at a constantly moving stimulus (such as a waterfall) for a fraction of a minute or longer. Immediately after this conditioning period, a stationary stimulus will appear to move in the opposite direction. Because of the conscious experience of motion, one would expect the subject's cortical motion areas to be activated in the absence of any moving stimulus. Another approach, suitable for the establishment of a rodent model to study the NCC, relies on the differential involvement of consciousness that appears necessary to establish associative trace conditioning, but not for associative delay conditioning (Clark and Squire 1998). That is, subjects need to be aware of the temporal relationship between conditioning stimulus (CS) and unconditioned stimulus (US) if there is a delay between the end of the CS and the onset of the US, while this is not the case if the time

course of the two overlap. Finally, understanding the specific actions of the different classes of anesthetic agents on cortical, thalamic, and basal ganglia neural networks will aid both the development of systems-level theories of anesthesia and the search for the NCC. Future techniques, most likely based on the molecular identification and manipulation of discrete and identifiable subpopulations of cortical and thalamic cells in appropriate animals, will greatly help in this endeavor.

Identifying the type of activity and the type of neurons that give rise to specific conscious percept in animals and humans would only be the first, albeit critical, step in understanding consciousness. One also needs to know where these cells project to, their postsynaptic action, how they develop in early childhood, what happens to them in mental diseases known to affect consciousness in patients, such as schizophrenia or autism, and so on. And, of course, a final theory of consciousness would have to explain the central mystery: why a physical system with a particular architecture gives rise to feelings and qualia (Chalmers 1995).

*See also:* Consciousness and Sensation: Philosophical Aspects; Consciousness, Cognitive Psychology of; Free Will and Action; Mind–Body Dualism

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C. Koch and F. Crick

## Conscription, Policy of

Conscription is the compulsory enlistment of people into military service. In modern democratic states, conscription is governed by a set of rules regulating eligibility, length of service, pay, and benefits. Conscription may involve universal military service, but it need not. The terms 'to conscript' and 'to draft' have become virtually synonymous.

### 1. Scholarship on Conscription

Conscription is one of the most important policies available to states. The very essence of the state, at least according to Max Weber, is its power to monopolize coercive power within a given territory, and this power depends on the state's control of an army, which in turn depends on the ability of government to recruit soldiers. Nonetheless, scholars concerned with developing a more adequate theory of the state have given relatively scant attention to military obligations and the institutions that enforce these obligations. Military service is demonstrably as important an aspect of the state–citizen relationship as any that exists. A government's decision to conscript and its policy implementing conscription have significant political and social implications for state building and for citizenship.

There has not, of course, been total neglect. Anthony Giddens, Michael Mann, Pierre Birnbaum, and other political sociologists have, on occasion, addressed the significance of military service and, more specifically, conscription for state building. Specialists in international relations and international

political economy have certainly considered the importance of national defense and military power, but the state theorists among them have, on the whole, focused on civil vs. military domestic power, international cooperation, and trade. Military theorists and historians, including such luminaries as Thucydides, Niccolò Machiavelli, Carl von Clausewitz, and John Mahon and a host of more contemporary scholars, have discussed the political and social importance of military format as well as the role of nationalism and voluntary compliance in increasing acquiescence with conscription. However, to the extent there has been any systematic attention to the link between conscription and state building or citizenship, it has generally come from historically oriented political scientists, sociologists, and economists.

In addition to the investigations of conscription in state theory, there are two additional traditions of conscription scholarship. One focuses on contemporary policy issues: what role conscription should play in the recruitment of modern armies. The other deals with conscription data as a source of information about the population over time.

### 2. Conscription and State Theory

There are at least three strands to this literature. The first emphasizes the relationship between war, nation building, and state making. Here the major issues are the development of state capacity and the form of governance. The second emphasizes the relationship between conscription and citizenship. It, too, is a literature focused on the changing nature of the state, but the focus is on transformation of subjects into citizens. The third stresses the bases for and history of objection to conscription.

#### 2.1 Nation and State Building

Otto Hintze (1994 [1906]), Samuel Finer (1975), Charles Tilly (1990), and Brian Downing (1991) capture the important role that military activity and institutions generally play in forging the infrastructure of governments. To wage war requires economic resources, including the ability to tax subjects for money and men. The way in which war is waged also has consequences for the form and power of the state. Joseph Schumpeter's (1954 [1918]) initial insight, while obvious, remains important: war permits increased government expenditure, which is sustained in peacetime, and increased government expenditure implies increased taxation. Moreover, the emergence of constitutional democracies or authoritarian regimes can be affected by the processes of extracting resources during wartime.

Conscription played a crucial role historically in the development of state capacity, particularly since the French and American revolutions. Throughout the