

Chapter 31

The nature of consciousness

ADAM ZEMAN^{1*} AND JAN ADRIAAN COEBERGH²

¹*Department of Neurology, Peninsula Medical School, Exeter, UK*

²*Department of Neurology, Ashford St. Peter's Hospital, Chertsey and Department of Neurology, St. George's Hospital, London, UK*

CONCEPTS

Consciousness in context

It is worth asking why the subject has prospered so mightily in recent years. Several interrelated developments have contributed. First, experimental and clinical advances, in cognitive neuroscience and neuropsychology, are revealing ever more exquisite correlations between features of experience and events in the brain. The advent of functional imaging, in particular, is enabling us to see something of what happens in the human brain during experience – and in its absence, for example, during coma. Advances in neurophysiology are allowing us to correlate electric and magnetic activity to experience. The discovery of mirror neurons – cells which are activated by performing actions oneself and by watching others perform the same actions – has fueled the new field of embodied cognition. Second, the realization that unconscious neural processes are ubiquitous in the brain, and often affect our behavior, has helped to throw the topic of conscious (as in willed or volitional) processes into relief. Third, the design of increasingly sophisticated forms of artificial intelligence raises the possibility that we may become able to create conscious systems: what once was science fiction may soon be science fact. The fourth reason for the current fascination with the topic of consciousness is the most profound: the separation of brain and mind, often described as “Cartesian,” in reference to the philosophy of Descartes, is untenable, both intellectually and in clinical practice. Descartes launched modern philosophy and the modern subjective concept of the self, by questioning everything, and finding that the only thing he can be sure of is his own consciousness. Much 20th-century philosophy, from

phenomenology to the existentialism of Sartre and Heidegger that was so influential after World War II, has been dedicated to understanding the relationship between the self and the external world, and solving the dichotomy of mind and matter. But now it seems science can claim to yield new insights into what is perhaps the quintessentially modern question: what is the self? Are we simply our brains, as some modern neuroscientists claim? The topic of consciousness is flourishing, because it touches on the fundamental question of what human beings are.

This central “problem of consciousness,” the mind–brain question in its modern guise, is ancient and persistent. The dichotomy between mind and brain is reflected in the apparent disconnection between work in the two great intellectual domains of relevance to the study of consciousness – the humanities, focusing on the experiences of subjects, and the sciences, highlighting processes in systems (Fig. 31.1). Within medicine, this intellectual divide is mirrored in the historic separation of psychiatry and neurology (White et al., 2012). The hope of contemporary students of consciousness is that progress in solving the central problem of how the brain gives rise to consciousness will build a trustworthy bridge between mind and brain, explaining how experience can be at once real, functional, and rooted in our physical existence (Zeman, 2001). Beyond question, the science will be incomplete until it incorporates a clearer understanding of our subjectivity.

Like the mind–body problem itself, the notion that the brain is the source of consciousness is very ancient, as revealed by this famous and prescient passage from Hippocrates' essay *On the Sacred Disease* (Jones, 1923):

*Correspondence to: Adam Zeman, Professor of Cognitive and Behavioural Neurology, Peninsula Medical School, St Luke's Campus, Magdalen Road, Exeter, EX1 2 LU, UK. Tel: +44-1392-726152 (direct); +44-1392-726151 (secretary), E-mail: adam.zeman@pms.ac.uk

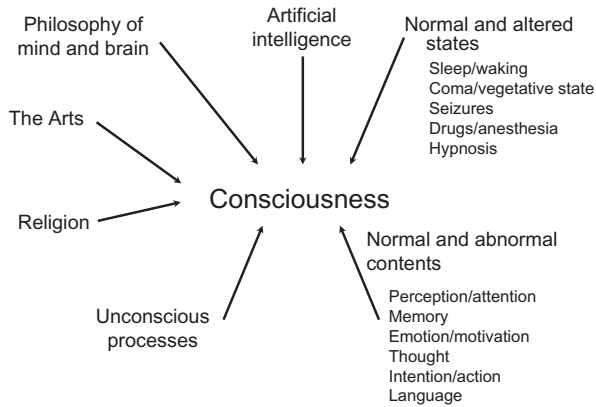


Fig. 31.1. Sources of evidence for the study of consciousness.

Men ought to know that from the brain, and from the brain only, arise our pleasures, joys, laughter and jests, as well as our sorrows, pains, griefs and tears. Through it . . . we think, see, hear, and distinguish the ugly from the beautiful, the bad from the good, the pleasant from the unpleasant . . . sleeplessness, inopportune mistakes, aimless anxieties, absent-mindedness, and acts that are contrary to habit. These things that we suffer all come from the brain.

Yet arguably progress in understanding exactly how experience emerges from the brain has been disappointingly slow. Writing two and a half millennia after Hippocrates, E.O. Wilson (1998) identifies the problem as a central issue for contemporary science:

the master unsolved problem of biology: how the hundred million nerve cells of the brain work together to create consciousness

Granted that science has in fact made great strides in revealing the physical basis of consciousness over the past century, as outlined in the following sections, and yet the “master problem” appears to be unsolved, one has to wonder whether part of the problem here may be conceptual rather than empiric. The philosopher Leibniz (1714) voiced an idea of this kind in his *Monadology*, in a passage that invites us to imagine walking into the midst of an artificial brain:

Perception and that which depend on it are inexplicable by mechanical causes, that is by figures and motions. And supposing there were a machine so constructed as to think, feel and have perception, we could conceive of it as enlarged and yet preserving the same proportions, so that we might enter into it as into a mill. And this granted, we should only find on visiting it, pieces which push against one another, but never anything by which to explain perception.

Leibniz is suggesting here that no mechanistic theory can ever, in principle, provide a really satisfying explanation of consciousness. This view is echoed by some philosophers who stress that the self, the “I” or “you,” is a perspective on the world, rather than part of the world of objects – and therefore by definition not something that can be studied by science, which studies only objects, not subjects. Many people have such intuitions: what is their source?

For better or worse, the concept of consciousness has been shaped by our cultural, religious, and philosophic history. Certainly “consciousness,” as it is generally understood, is far from being a simple scientific variable. Surveys suggest that the predominant notion of consciousness in our western culture is of a private, invisible, immaterial process, inaccessible to the standard observational methods of science (Fig. 31.2). On such an assumption it is indeed hard to see how science could truly fathom the relationship between consciousness and the brain.

However, it may well be that scientific advances, and philosophic analysis, will gradually modify both the scientific and the popular concepts of consciousness. There are strong reasons, discussed below, for doubting that our grasp of the contents and the nature of experience is as firm as we usually take it to be. When we look back from the terminus of the quest for consciousness we may see our point of departure in an entirely new light.

The aims of this introductory chapter are to outline the many meanings of the word consciousness, particularly those relevant to science and medicine; to summarize current knowledge of the neurobiology of consciousness in its two key senses of wakefulness and awareness, and to relate this to the principal pathologies of wakefulness and awareness; to sketch the currently prevailing, overarching, models and theories of consciousness; and finally to return to the philosophic issues just touched on, with a succinct survey of contemporary philosophic views of the relationship between mind and brain.

SENSES OF CONSCIOUSNESS AND SELF-CONSCIOUSNESS

Part of the problem of consciousness is semantic: it is an ambiguous term, with several strands of meaning. This is all the more true of “self-consciousness.” We shall briefly discuss the etymology and principal senses of these words.

The etymology of “consciousness” and “conscience”

The word “consciousness” has its Latin root in *conscio*, formed by the coalescence of *cum*, meaning “with,” and

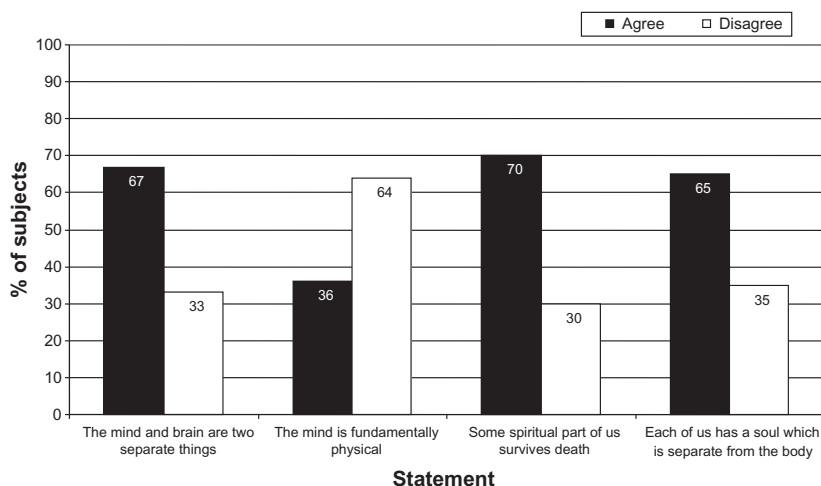


Fig. 31.2. Beliefs about the relationship of mind to brain in a varied group of respondents. (Reproduced from Demertzi et al., 2009.)

scio, meaning “know” (Lewis, 1960). In its original Latin sense, to be conscious of something was to share knowledge of it with someone else, or, metaphorically, to share it with oneself. The knowledge in question was often of something secret or shameful, the source of a bad *conscientia*, a bad conscience. This meaning of *conscientia*, implying knowledge shared, has been referred to as its strong or narrow sense. A weakened, or broad, sense coexisted with it in which *conscientia* meant, simply, knowledge. All three senses – of knowledge shared with another, knowledge shared with oneself, and, simply, knowledge – entered the English language with “conscience,” the first English derivative of *conscientia*. The words “conscious” and “consciousness” first appear early in the 17th century, followed by “self-conscious” and “self-consciousness.”

What is meant by “conscious”?

The *Oxford English Dictionary* distinguishes 12 senses of “conscious” and eight of “consciousness.” Consciousness has two key senses in colloquial English that are of relevance to clinical practice – wakefulness and awareness.

CONSCIOUSNESS AS THE WAKING STATE

In everyday neurologic practice consciousness is generally equated with the waking state, and the abilities to perceive, interact, and communicate with the environment and with others in the well-integrated manner that wakefulness normally implies. But while “consciousness” is often equated with wakefulness, it can also be used more broadly to refer to the family of states that collectively describes our overall patterns of behavior. In this sense wakefulness is just one of several possible “states of consciousness,” distinguished from others

such as sleep, coma, and anesthesia. Each of these states admits of degrees or levels: we can be wide or half-awake, lightly or deeply anesthetized. We are normally reasonably confident of our ability to assess and track an individual’s state and level of consciousness, in this first sense, with the help of objective criteria, like those of the Glasgow coma scale (Teasdale and Jennett, 1974) or FOUR score (Wijdicks et al., 2005). Thus we speak of consciousness dwindling, waning, lapsing, and recovering; it may be lost, depressed, and regained. To be conscious in this first sense is essentially to be awake, aroused, alert, or vigilant.

CONSCIOUSNESS AS AWARENESS

While we are conscious in the first sense, we are as a rule conscious of something: our consciousness has content. This is the second sense of consciousness: while conscious in this sense, we undergo experience, and there is “something it feels like” to exist, whereas there is nothing it feels like to be a stone or lost in dreamless sleep. This second sense is often referred to as “awareness,” to underline the distinction between the behavioral features of wakefulness and the experiences that usually, but not always, accompany them. Objective criteria remain helpful in ascertaining the presence of consciousness in this second sense. Anyone who can obey your instructions and tell you the date is presumably aware, and consciousness is not some isolated inner quality separate from the world – rather, it entails a movement towards or relationship with something in the world. Yet it has a much stronger connotation of subjectivity than the first sense: it is notoriously difficult to be sure of what is passing through another person’s mind on the basis of his or her behavior. This second sense is also more problematic philosophically than the first: the technical term “qualia,” which has been used by philosophers

to refer to the subjective texture of experience, is particularly controversial as it suggests that awareness has fundamentally private, unobservable properties (Dennett, 1988). Others refer to the ability of any entity to have subjective perceptual experiences as “sentience.” Eastern religions and animal rights philosophy use the concept of sentience to refer to the capacity for pain and pleasure in nonhumans and equate it with a basic or minimalistic form of consciousness.

Several authors, following William James, the 19th-century American psychologist and philosopher, have tried to characterize the general properties of awareness (James, 1890; Shallice, 1988; Searle, 1992; Crick, 1994; Chalmers, 1996; Greenfield, 1998; Tononi and Edelman, 1998a). There is a consensus about the following: the contents of consciousness are relatively stable for short periods of a few hundred milliseconds, but characteristically changeful over longer ones; they have a narrow focus at a given moment, but over time our awareness can range across the spectrum of our psychologic capacities, allowing us to be aware of sensations, percepts, thoughts, memories, emotions, desires, and intentions (our experience at a given moment often combines elements from several of these psychologic domains); awareness is personal, allowing us a distinctive, limited perspective on the world; it is fundamental to the value we place on our lives: keeping people alive once their capacity for awareness has been permanently extinguished (i.e., by brain death) is regarded by many as a wasted effort (Jennett, 2004).

The relationships between wakefulness, awareness, and their behavioral indices are more complex than they appear at first sight. As a rule, while we are awake we are aware. But the phenomena of wakefulness and awareness do not always run in parallel (Fig. 31.3). The vegetative state, which results from profound damage to the cerebral hemispheres and thalami, with relative preservation of the brainstem, is often characterized as a state of “wakefulness without awareness.” Conversely, when we dream, we are asleep yet aware to some degree. Nor can we always rely on behavioral criteria to diagnose consciousness: patients paralyzed for surgery may be fully aware but completely unable to manifest their awareness; patients “locked in” by a brainstem stroke may appear unconscious until their ability to communicate by movements of their eyes or eyelids is detected and cataplexy can render sufferers temporarily unable to move or communicate.

What is meant by self-conscious?

The term “self-consciousness” is sometimes used in medical contexts as if its meaning were self-evident. This seems doubtful: self-consciousness is a peculiarly complex idea, combining two others—“self” and “conscious”—each

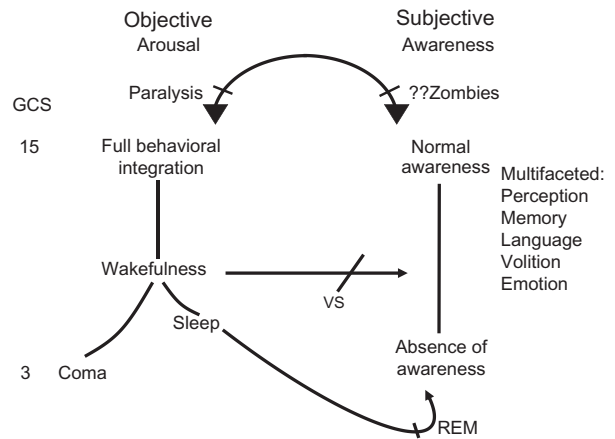


Fig. 31.3. Interrelationships between arousal and awareness. See text for explanation. “Zombies” are theoretic beings discussed by philosophers who display the signs of consciousness, yet lack experience: the plausibility of such beings is controversial. GCS, Glasgow coma scale; VS, vegetative state; REM, rapid eye movement. (Reproduced from Zeman, 2006.)

of which is multifaceted (Berrios and Markova, 2003). We shall try to tease apart its principal strands.

The distinction between self and other is biologically crucial: there are many activities which we need to direct towards other objects in the world – for instance, when we eat something – which it would be disastrous if we directed towards ourselves. Our immune system must continuously distinguish self from other. We should expect to find strategies for drawing this distinction in the simplest organisms. But self-consciousness of a sophisticated kind implies more than an ability to behave differently towards self and other: it requires a representation of self and other. A variety of different kinds of representation fall out of the senses we shall discuss (Fig. 31.4).

SELF-CONSCIOUSNESS AS PRONENESS TO EMBARRASSMENT

This colloquial sense of self-consciousness implies that an individual is aware that the awareness of others is directed on him or her. It is therefore psychologically sophisticated, anticipating the penultimate sense, discussed below. Interestingly, the sense of embarrassment or shame is a higher- or second-order emotion that animals may not share; it implies a concept of self which allows us to realize that, as free and rational agents, we are subject to the judgment of others.

SELF-CONSCIOUSNESS AS SELF-PERCEPTION

This rather minimalistic sense refers to a family of forms of self-consciousness that are probably present in many animals, enabling the organism to perceive stimuli or

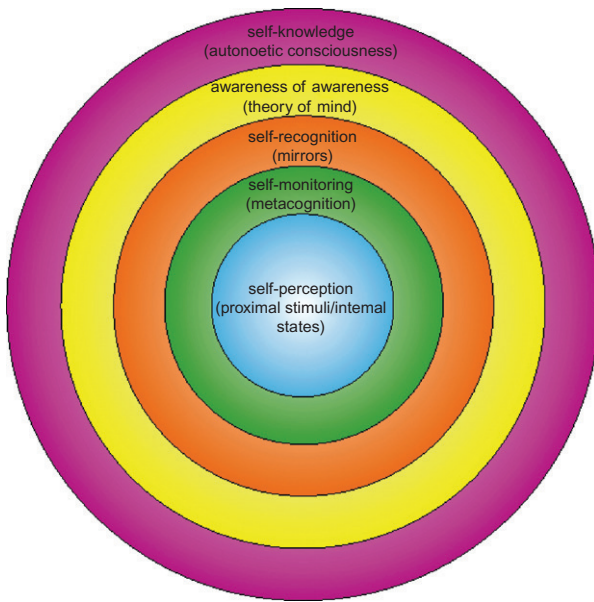


Fig. 31.4. Varieties of self-awareness. See text for explanation.

states that are close at hand or self-generated. These include awareness of stimuli which directly impinge on the body (the ant walking up your arm); of proprioceptive information about bodily position which contributes substantially to our body image; of information about actions which we are performing, giving rise to a sense of agency; of information about bodily state (e.g., hunger, thirst); and of emotions, like fear or affection, which signal the state of our relationship to objects and to people around us.

SELF-CONSCIOUSNESS AS SELF-MONITORING

This form of self-awareness involves the ability to monitor our past and present and predict our future behavior and experience, thus extending self-perception in time, and in depth, by allowing organisms to represent their own experience and actions to themselves. It includes the ability to recall the actions we have recently performed (Beninger et al., 1974) and the ability to predict our chances of success in tasks which challenge memory (Hampton, 2001) or perception (Smith et al., 2003): we undoubtedly possess these metacognitive abilities, and ingenious experiments in comparative psychology (Beninger et al., 1974; Hampton, 2001; Smith et al., 2003) suggest that many other animals have them too. The remaining senses lie closer to what we normally have in mind when we speak of self-awareness.

SELF-CONSCIOUSNESS AS SELF-RECOGNITION

This alludes to our ability to recognize our own bodies as our own, for example in mirrors (i.e., mirror self-recognition). Gallop (1970) showed that if apes are given

experience with a mirror they will soon realize that they are looking at themselves, while their monkey cousins apparently fail to grasp this fact despite extensive exposure. Recent evidence suggests that a number of other species, ranging from dolphins (Reiss and Marino, 2001) to magpies (Prior et al., 2008) and elephants (Plotnik et al., 2006), can also recognize themselves in mirrors. Human children develop this ability at around 18 months (Parker et al., 1994).

SELF-CONSCIOUSNESS AS AWARENESS OF AWARENESS

Between the ages of 18 months and around 5 years, human children take a further major intellectual stride. They come to appreciate that, as well as being objects, that can be inspected in mirrors, they are also subjects, of experience – they possess, in other words, not only bodies, but also minds (Parker et al., 1994). The awareness of ourselves as subjects of experience opens up a world of new possibilities for understanding our own behavior and the behavior of others in terms of desires and beliefs, and for implanting and manipulating these (Baron-Cohen, 1995; Frith and Frith, 1999). It has been described as the acquisition of a “theory of mind.” Once we realize that others, like ourselves, have a limited, personal perspective on the world we can choose to inform, misinform, and influence them, creating all the Machiavellian complexities of human behavior. The degree to which animals other than humans possess this awareness is debated.

SELF-CONSCIOUSNESS AS SELF-KNOWLEDGE

Finally, we use “self-consciousness” to refer to our self-knowledge in its broadest sense – one’s knowledge of oneself as the hero, or villain, of a personal narrative, conditioned by one’s personal circumstances and cultural background. This capacity to relive our past in a form of mental time travel constitutes the “auto-noetic awareness” that Endel Tulving (1985) has identified as one of the most distinctively human intellectual capacities. Self-depiction is a central focus of art, another distinctively human activity. Atance and O’Neill (2001) extended Tulving’s concept to self-knowledge of our future, terming this episodic future thinking.

THE NEUROBIOLOGY OF CONSCIOUS STATES AND CONTENTS

States of consciousness

THE ELECTRIC CORRELATES OF CONSCIOUS STATES

Nineteenth-century physiologists working across Europe had noted the occurrence of spontaneous electric activity while recording from the brains of experimental animals, but it was not until 1929 that Hans Berger, a psychiatrist

working in Jena, Germany, published his landmark observations, *On the Electroencephalogram of Man*. His foremost achievement was to demonstrate that spontaneous electric activity could be recorded from the human brain with extracranial electrodes, but his underlying purpose was to elucidate the physical basis of consciousness. His first paper closed with a series of questions that were to launch a fertile, continuing program of research: how is the electroencephalogram (EEG) affected by sensory stimulation, by sleep, by drugs that alter mental states, and by intellectual activity?

Recording from the scalp, Berger distinguished two contrasting rhythms of electric activity occurring during wakefulness: alpha, at 8–13 Hz, which characterizes the “passive EEG,” typically recorded from occipital electrodes in wakeful subjects with their eyes closed; and beta rhythm, occurring at frequencies >13 Hz, the “active EEG” which accompanies mental effort and eye opening. It was soon appreciated that slower rhythms (theta waves at 4–7 Hz and “delta” at <3.5 Hz) occurring at higher amplitudes characterize states of reduced arousal in adults (Fig. 31.5). Their cyclic involvement in sleep became apparent in the 1950s, particularly from the work of Kleitman and his collaborators.

In 1955 Aserinsky and Kleitman reported the repeated occurrence of periods of “rapid eye movement sleep” in the course of the night: sleepers woken at these times were likely to report concurrent dreams. Two years later Dement and Kleitman (1957) demonstrated the cyclic structure of sleep on the basis of observations of eye movements, body movements, and EEG appearances in normal sleepers. This work established the distinction between slow-wave sleep (SWS) associated with a high

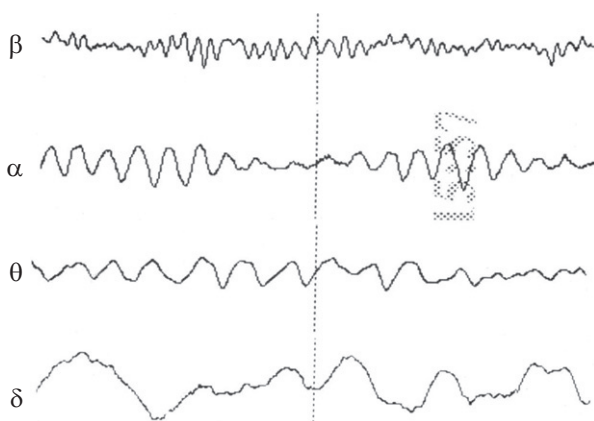


Fig. 31.5. The rhythms of the electroencephalogram. Records from diagnostic encephalograms performed in four different patients, exemplifying beta rhythm (>14 Hz); alpha rhythm (8–13 Hz); theta rhythm (4–7 Hz); delta rhythm (4 Hz). In each case the dotted line bisects a 2-second sample. (Reproduced from Zeman (2001), with permission from Oxford University Press.)

proportion of delta activity in the EEG (20–50% in stage 3 sleep, >50% in stage 4) and rapid eye movement (REM) or paradoxical sleep, during which the features of the EEG resemble those in the waking state, although subjects are paradoxically difficult to arouse. Predictable cycles of descent through light sleep (stage 1 and 2) into SWS, followed by gradual reascent into REM sleep, recur four or five times each night, with decreasing proportions of SWS and increasing proportions of REM sleep as the night proceeds (Fig. 31.6). These observations have helped to define three principal states of consciousness in health, wakefulness, REM sleep, and non-REM/SWS, each of which has a characteristic psychologic, metabolic, physiologic, and pharmacologic profile (Table 31.1). The Upanishads, dating from around 2000 BC, recognized the same three basic states (Jones, 1998b).

While massive synchronization of brain activity has classically been associated with states of reduced consciousness, such as deep sleep and coma, in contrast to the “desynchronized EEG” of wakefulness and REM sleep, there is some evidence that very rapid activity in the gamma range (35–45 Hz), widely synchronized across the brain, occurs in the waking state and REM sleep, but not in SWS (Llinas and Ribary, 1993) (Fig. 31.7). More generally, the very existence of the EEG suggests a tendency to widespread synchronization of brain activity whose functional significance has yet to be fully unraveled.

THE CONTROL OF CONSCIOUS STATES

Anatomy: the reticular activating system

Clinicopathologic studies made at the time of the epidemic of encephalitis lethargica that occurred during and after the First World War suggested to the Viennese pathologist Constantin Von Economo (1931) that structures in the upper brainstem and posterior hypothalamus play a key role in arousal. Frederic Bremer (1929) later confirmed this suggestion experimentally by showing that transection of the cat’s brain at the cervicomedullary junction had no effect on arousal or on the sleep–wake cycle, while transection through the midbrain brought about a state resembling deep sleep.

Bremer hypothesized that this impairment of arousal resulted from interruption of ascending sensory pathways in the midbrain. His student Giuseppe Moruzzi, working with Horace Magoun, later showed that the critical areas were not, in fact, in the sensory pathways but lay rather in the reticular core of the upper brainstem and their thalamic targets (Moruzzi and Magoun, 1949). This region is, at least in part, diffusely organized and polysynaptic, with widespread afferent and efferent connections, well suited to provide the substrate of a nonspecific “alerting system.” Electric stimulation of the region in a drowsy animal activates the EEG and

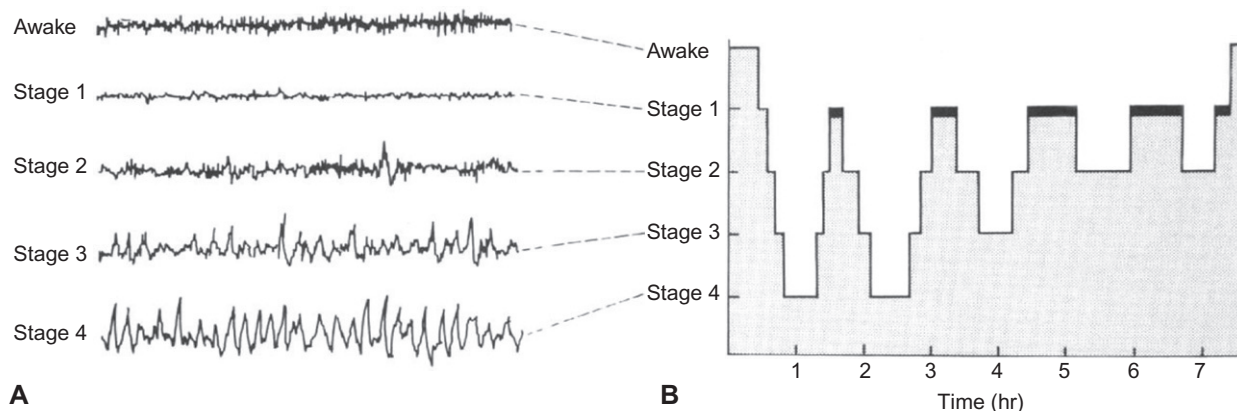


Fig. 31.6. The architecture of sleep. An example of sleep staging over the course of a single night. The sleeper passes from wakefulness to deep sleep and then ascends to rapid eye movement (REM) sleep. Five similar cycles occur in the course of the night. The electroencephalogram (EEG) tracings (A) show the EEG appearances associated with the stages of sleep; the EEG in REM resembles the “awake” trace. (Reproduced from [Kandel et al. \(2000\)](#), with permission from McGraw Hill Medical.)

alerts the animal. These observations gave rise to the concept of the ascending reticular activating system (ARAS). While the central insight, that structures in the brainstem regulate our states of consciousness, still holds true, a much more complex picture has emerged since the pioneering work of Moruzzi and Magoun. The ARAS is no longer regarded as a monolithic unit, nor as a system restricted to the classically defined reticular regions of the brainstem. Indeed, activating structures are not confined to the brainstem at all, and their influence descends to the spinal cord as well as ascending to the cerebral hemispheres.

Rather than revealing any single “place where consciousness dwells,” the exploration of these structures has identified a series of somewhat specialized nodes in a complex network controlling aspects of arousal ([Fig. 31.8](#)). It would be surprising if functions as fundamental as the maintenance of wakefulness or the control of the sleep–wake cycle depended exclusively and unalterably on any single region of the brain. Experimental work in animals and clinical observations in humans suggest that the following structures play key roles in the maintenance and modulation of wakefulness: cholinergic nuclei in the upper brainstem and basal forebrain; noradrenergic nuclei, in particular the locus coeruleus in the upper brainstem; histaminergic and hypocretinergic projections from the hypothalamus; and dopaminergic and serotonergic projections arising from the brainstem ([Robbins and Everitt, 1995](#); [Hobson and Pace-Schott, 2002](#); [Pace-Schott and Hobson, 2002](#)). Part of the influence exerted by these pathways is mediated by the thalamus, especially its intralaminar nuclei ([Jones, 1998b](#)), which makes a major contribution to the maintenance of cerebral arousal as well as providing a critical synaptic relay in corticospinal and corticocortical pathways. The roles of the brain regions involved in

arousal are not, of course, confined to the maintenance of wakefulness or vigilance: they are of profound importance to a range of interrelated functions, including mood, motivation, attention, learning, memory, movement, and autonomic function.

Some specific contributions made by these regions and related structures to the regulation of conscious states have been defined. For example, the suprachiasmatic nucleus of the hypothalamus is the main time-keeper of consciousness. It normally entrains the sleep–wake cycle to the alternation of night and day under the influence of the direct retinohypothalamic projection ([Kilduff and Kushida, 1999](#)). The molecular mechanisms of the circadian rhythm are controlled by a series of “clock genes” ([Pace-Schott and Hobson, 2002](#)). Transection experiments by [Jouvet \(1979\)](#) and subsequent work have established the key importance of cholinergic nuclei at the pontomesencephalic junction, the laterodorsal tegmental and pedunculopontine nuclei, in orchestrating the phenomenon of REM sleep ([McCarley, 1999](#)). During SWS, there is a marked reduction in the activity of the cholinergic, noradrenergic, and histaminergic nuclei that maintain wakefulness, coordinated at least in part by activation of the ventrolateral preoptic nucleus of the anterior hypothalamus ([Shneerson, 2005](#)): mutually inhibitory interactions between the histaminergic tuberomammillary nucleus and ventrolateral preoptic nucleus are thought to play a particularly important role in controlling oscillations between wakefulness and sleep.

Physiology: patterns of neuronal discharge and brain metabolism

It should in principle be possible to explain the features of the three major states of consciousness in terms of the

Table 31.1

Features of three principal states of consciousness in health

	Wakefulness	NREM sleep	REM sleep
Psychologic functioning			
Orientation	Intact	Reduced	Delusional
Memory	Intact	Reduced	Dream recall; impaired after delay
Thought	Logical, progressive	Reduced, perseverative	Illogical
Insight	Intact	Reduced	Impaired
Perception	External, vivid	Dull or absent	Internal, vivid
Emotion	Reactive	Dull or absent	Strong, basic
Cerebral metabolism			
Global	~7 mg glucose/100 g/min	Up to 40% reduced	~Wakefulness
Regional	Varies with task; cf. Gusnard et al. (2001) for “functional resting state” or default mode network (Raichle et al., 2001)	Most marked reduction in upper brainstem, cerebellum, thalami, basal glia, basal forebrain, prefrontal cortex, anterior cingulate, precuneus	Cf. waking, reduction in DLPF, inferior parietal cortex, precuneus; cf. slow-wave sleep activation of thalami, paralimbic regions, temporo-occipital cortex
Physiology			
EEG	Alpha, beta dominate	I: low-voltage, mixed-frequency II: sleep spindles, k complexes III, IV: theta, delta dominate	~Wakefulness
Eye movements	Interactive	I: rolling eye movements II, III, IV: absent	REM
Muscle tone	High, variable	Reduced	Atonic
Autonomic function	Reactive	Reduced cardiac rate/output, respiration rate/ventilation, blood pressure	Autonomic arousal and lability, irregular breathing, reduced ventilation
Pharmacology	High but variable, globally reduced. Activation activity in ntr systems modulating arousal (see text)	Globally reduced activation	Cholinergic dominance

NREM, nonrapid eye movement; REM, rapid eye movement; DLPF, dorsolateral prefrontal cortex; EEG, electroencephalogram; ntr, neurotransmitter. For estimate of basal glucose metabolism, see [Laureys et al. \(2001\)](#); for functional resting state see [Gusnard et al. \(2001\)](#).

characteristics of relevant neuronal types and the networks into which they are organized, and of the resulting neuronal and regional firing patterns. The contrast seen in patterns of neuronal discharge during sleep and wakefulness within the thalamus illustrates this avenue of research.

In the waking state thalamocortical projection neurons are tonically depolarized by cholinergic, noradrenergic, and histaminergic inputs from the brainstem and hypothalamus, which block a hyperpolarizing potassium conductance ([Steriade et al., 1993](#); [McCarley, 1999](#); [Steriade, 1999](#)). This induces a “spike” mode of response in thalamocortical cells, permitting faithful onward transmission of afferent signals to the thalamus. The reduction of this depolarizing input in sleep induces a contrasting “burst” mode of response, dependent upon

a low-threshold calcium conductance, which predisposes these cells to repetitive discharge while hyperpolarized ([Fig. 31.9](#)). The simultaneous disinhibition of the reticular nucleus of the thalamus in early sleep, following reduction of inhibitory cholinergic input from the brainstem, allows it to exert a synchronized GABAergic inhibition of thalamocortical cells, that ultimately gives rise to the distinctive spindles abounding in the EEG of stage 2 sleep. Further hyperpolarization of thalamocortical cells, as sleep deepens, allows them to participate in slow-wave oscillations, to which the individual and network properties of thalamocortical cells, corticothalamic cells, and neurons of the reticular nucleus all contribute. Reduction of direct nonspecific excitatory inputs to the cortex, as well as effects occurring primarily at the level of the thalamus, are conducive to the generation of these

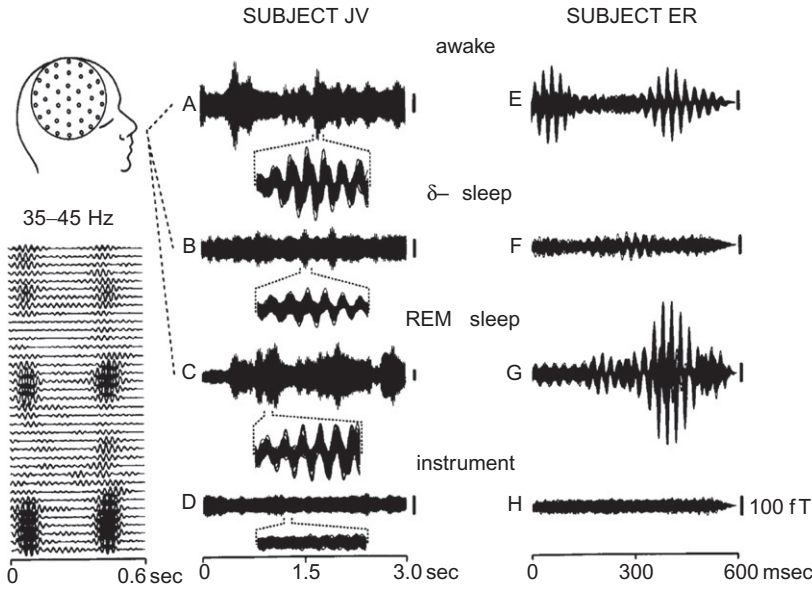


Fig. 31.7. Recordings of rapid (gamma) oscillations in wakefulness, delta or slow-wave sleep and rapid eye movement (REM) sleep made using magnetoencephalography. The diagram at top left indicates distribution of sensors over the head; recordings from these sensors, filtered to pass signals at 35–45 Hz, are shown below. The figures at right show superimpositions of these oscillations in two subjects during wakefulness, slow-wave sleep, and REM sleep. Note the differing time bases of the two recordings. The amplitude of synchronized gamma oscillations is markedly diminished in slow-wave sleep in comparison to wakefulness and REM sleep (with acknowledgment to [Linas and Ribary \(1993\)](#)). Copyright (1993) National Academy of Sciences, U.S.A).

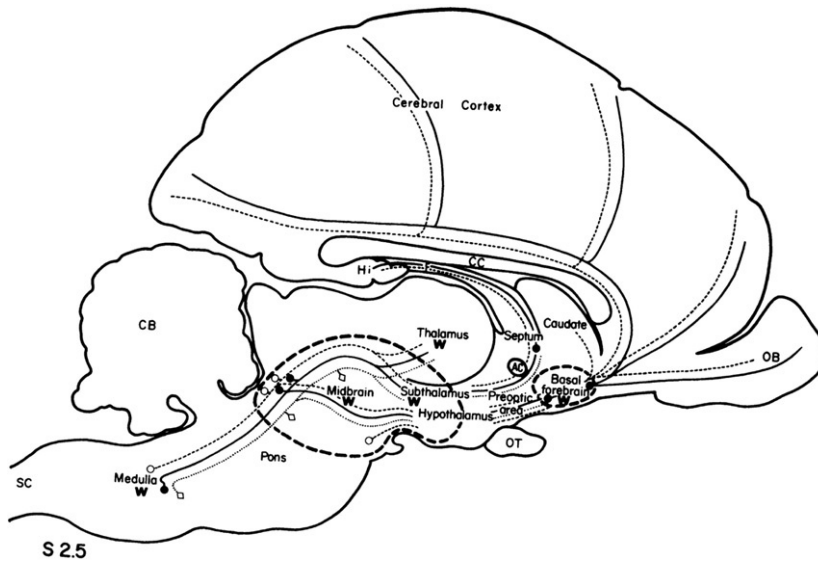


Fig. 31.8. A sagittal drawing of a cat brain indicating the structures implicated in generating and maintaining the waking state. Areas marked with a W are those from which electric stimulation elicits, and where cells are maximally active during wakefulness. Areas encircled by dashed lines in bold are those where selective lesions most commonly cause coma. These regions contain glutamatergic neurons of the reticular formation (open diamonds), noradrenergic and other catecholaminergic neurons (open circles) and cholinergic neurons (filled circles). Projections from the thalamus are not shown. AC, anterior commissure; CB, cerebellum; CC, corpus callosum; Hi, hippocampus; OB, olfactory bulb; OT, optic tract; S, sagittal; SC, spinal cord. (Reproduced from [Jones, 1998a.](#))

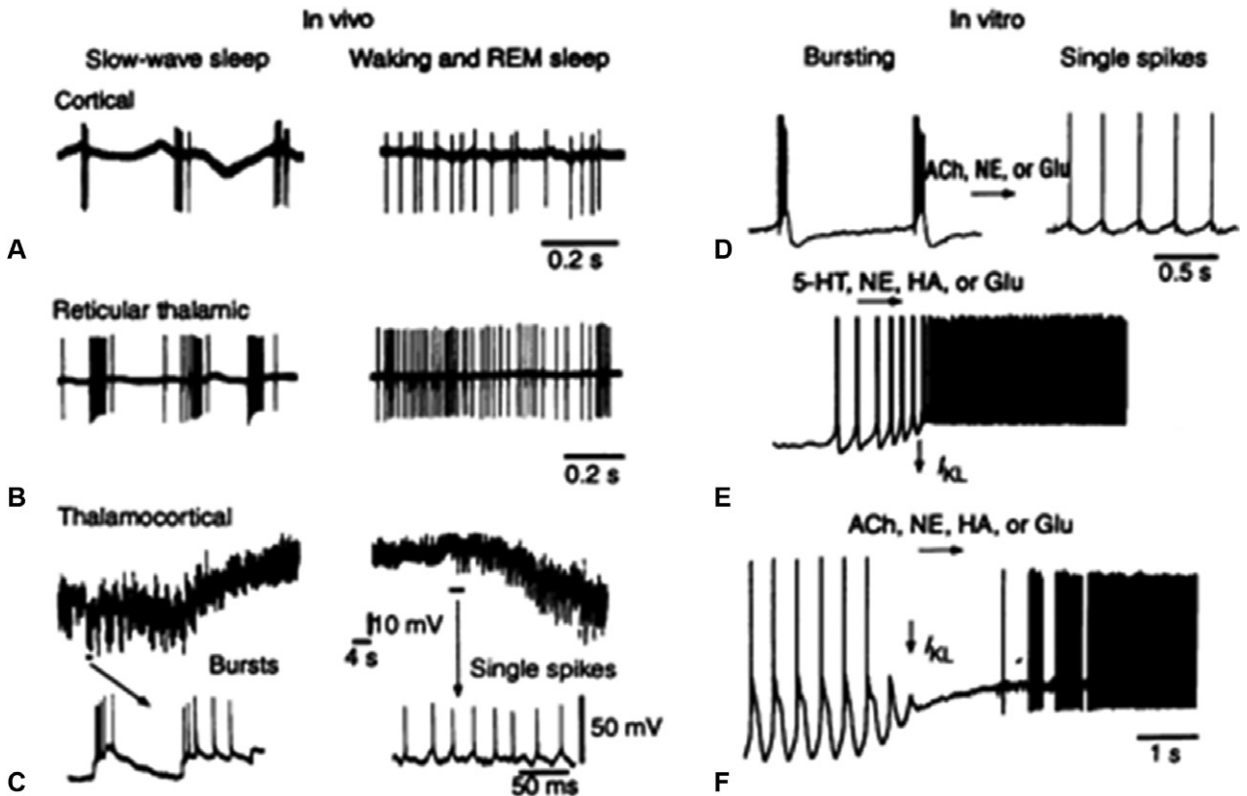


Fig. 31.9. State-dependent activity in thalamic and cortical neurons. Neurons from the cerebral cortex of chronically implanted, behaving cats, in the cerebral cortex (A), reticular thalamic nucleus (B) and thalamic relay nuclei (C) change their activity from rhythmic spike bursts during natural slow-wave sleep to firing of single spikes during waking and rapid eye movement sleep. Similar changes can be demonstrated *in vitro* in response to neurotransmitters involved in modulating sleep and wakefulness. (D) Cortical cell; (E) reticular thalamic nucleus cell; (F) thalamic relay cell. Depolarization results from the reduction of specialized conductances, including I_{kL} , a potassium conductance. ACh, acetylcholine; Glu, glutamate; HA, histamine; 5-HT, serotonin; NE, norepinephrine. (Reproduced from Steriade et al., 1993; with permission; copyright 1993, The American Association for the Advancement of Science, U.S.A.)

rhythms. Thus the distinction at an electrophysiologic level between spike and burst modes of response in thalamocortical neurons corresponds with the behavioral distinction between the responsiveness of the waking state and the inaccessibility of sleep and underlies the global shift between the high-frequency EEG of wakefulness and the low-frequency EEG of sleep.

Functional imaging studies have made it possible to explore the anatomy and physiology of sleep and arousal in the healthy human brain. Global cerebral glucose metabolism falls in SWS by *circa* 20%, rising back to, or even above, waking levels in REM (Heiss et al., 1985; Buchsbaum et al., 1989). During SWS regional blood flow declines, in proportion to the amount of slow-wave activity in the EEG, in the rostral brainstem, thalamus, prefrontal and cingulate cortex (Hofle et al., 1997; Macquet et al., 1997). In REM sleep regional blood flow increases in the rostral brainstem, thalamus, and limbic regions, in keeping with the electric and subjective

features of dreaming sleep, but declines in prefrontal and posterior cingulate cortex and in some regions of parietal cortex (Macquet et al., 1996). Massimini and colleagues (2005, 2009) have used transcranial magnetic stimulation to probe the brain in sleep and wakefulness. This work has vividly demonstrated the contrast between the “open” character of the waking brain in which a magnetic pulse evokes widespread, extended activity while in the sleeping brain the evoked activity is relatively restricted and short-lived.

Variations in the level of arousal during wakefulness also appear to correlate with levels of activity in the structures of midbrain and thalamus that regulate conscious states. The midbrain tegmentum and intralaminar nuclei of the thalamus activate in the transition from a resting state to the performance of visual and somatosensory reaction time tasks (Kinomura et al., 1996). Paus and colleagues (1997) described a decrease in midbrain and thalamic activation during a tedious 1-hour

auditory detection task associated with declining performance and increasing slow-wave activity on EEG. Sleep deprivation affects cognition widely (for review, see [Kilgore, 2010](#)) and is associated with decreased cerebral blood flow in the same regions that recover last after awakening (sleep inertia), namely the prefrontal cortex and ventromedial caudate nucleus ([Balkin et al., 2002](#)).

Finally, as discussed further below, there is evidence that the loss of consciousness induced by some anesthetics is associated with selective depression of thalamic function, linking the mechanisms of anesthesia and sleep ([Fiset et al., 1999](#); [Alkire, 2000](#)). The “network inhibition hypothesis” suggests that the loss of consciousness that occurs in complex partial seizures results from a depressant effect of epileptic activity on the subcortical activating system, leading to bilateral cortical inhibition. In absence seizures abnormally synchronized corticothalamic activity in the association (especially frontal) cortex leads to impairment of consciousness ([Blumenfeld and Taylor, 2003](#); [Blumenfeld, 2012](#)).

Pharmacology: modulation of sleep and wakefulness

As we have seen, the pharmacologic dissection of the reticular activating system has revealed the presence of several chemically distinct but interactive subsystems: cholinergic, noradrenergic, dopaminergic, serotonergic, histaminergic and, recently, hypocretineric. The actions of each of these transmitters are complex, depending on the site of release and the nature of the receptor targeted. Nonetheless it is clear that the firing of cells in the nuclei synthesizing these transmitters is often state-dependent, varying with conscious state ([Sutcliffe and de Lecea, 2002](#)) (Fig. 31.10).

Evidence that REM sleep is dependent upon activity in cholinergic nuclei, while noradrenergic and serotonergic nuclei are least active in this phase of sleep, has given rise to a “reciprocal interaction” model of sleep architecture ([Pace-Schott and Hobson, 2002](#)). This proposes that the regular interaction of SWS and REM sleep over the

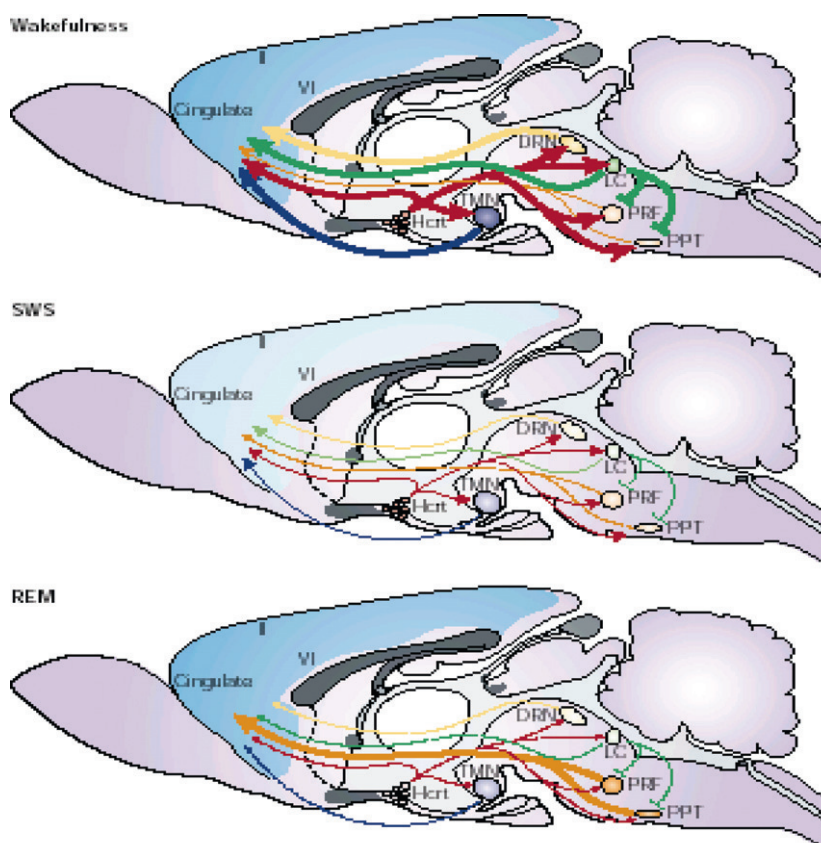


Fig. 31.10. State-dependent changes in the activating system. During wakefulness, hypocretin (Hcrt) activity excites noradrenergic (green), histaminergic (deep blue), and serotonergic (yellow) neurons, which give rise to enhanced cortical activity and arousal. Slow-wave sleep (SWS) is characterized by synchronous intrinsic cortical activity, and most subcortical afferents show reduced activity. During rapid eye movement (REM) sleep, low hypocretin activity results in the disinhibition of rapid eye movement (REM)-on-cholinergic neurons (orange). DRN, dorsal raphe nucleus; LC, locus coeruleus; PPT, pedunculo-pontine tegmental nucleus; PRF, pontine reticular formation; TMN, tuberomammillary nucleus. (Reproduced from [Sutcliffe and de Lecea, 2002](#).)

course of the night is regulated by the waxing and waning of mutually inhibitory activity in these nuclei.

The pharmacologic basis of “sleep debt,” the increasing pressure to sleep as the period of wakefulness extends, remains a confusing area. A number of potential hypnogens, sleep-promoting substances, including peptidergic and other neurotransmitters, have been identified (Zoltoski et al., 1999; Shneerson, 2005). A gradual increase in extracellular adenosine levels during wakefulness appears to be one critical factor, leading to inhibition of activating cholinergic nuclei in the upper brainstem and basal forebrain (McCarley, 1999).

Further work on the pharmacology of wakefulness is likely to demonstrate distinctive roles for the neurotransmitters of the activating system in modulating different aspects of arousal. “Wakefulness,” after all, is shorthand for a set of associated neural, behavioral, and psychologic functions that are, to some extent, independently controlled, as evidenced by a number of the disorders of consciousness discussed below. In work in animals exploring the idea that the neurotransmitters linked with arousal make distinctive contributions, Robbins and Everitt (1995) have found, using a consistent set of behavioral tests, that selective damage to the noradrenergic system impairs selective attention, damage to the cholinergic system impairs baseline accuracy, damage to the dopaminergic system lengthens response latency and reduces probability of response, and damage to the serotonergic system leads to impulsive responding.

Awareness: the “contents of consciousness”

DO WE KNOW WHAT WE EXPERIENCE?

Many questions remain to be answered about the neurobiology of sleep and wakefulness but the phenomena under study are relatively unambiguous, objective, and quantifiable. The same cannot be said of awareness, experience, or “the contents of consciousness,” three terms often used interchangeably for the second principal sense of consciousness picked out in the section on consciousness in context, above. There is major controversy about both the ultimate nature and the detailed content of awareness. This is an appropriate moment to flag up the somewhat more empiric debate about its content.

We all tend to consider ourselves experts on the features of our experience: after all, how could we be mistaken about them? However, there is plenty of evidence that we are sometimes misled by introspection and that our experience is not always as we take it to be. How so? This may be a realm in which observation is more than usually theory-laden. As we have seen, our intuitive theories of consciousness owe as much to religion and

philosophy as science: theoretic expectations about the features of our experience may distort our informal observations (Demertzi et al., 2009). For example, systematic research requiring subjects to give instantaneous reports of their current experience, at the moment that a random buzzer sounds, reveals a surprising preponderance of “inner thought” (Hurlburt, 2000; Hurlburt and Heavey, 2001); research on change in our visual surroundings indicates that we fail to notice many large-scale alterations in a scene that most of us would expect to recognize readily, a phenomenon described as “change blindness” (O’Regan and Noe, 2001) and, similarly, an inability to detect a change between two voices as “change deafness” (Vitevitch, 2003); related work on visual attention reveals that salient stimuli go unnoticed when visual attention is highly focused, to the subsequent astonishment of the experimental subject, the phenomenon of “inattention blindness” (Mack and Rock, 2000).

Work along these lines suggests that our knowledge of our own experience is not incorrigible: on the contrary, it is often mistaken. This prompts the thought that other beliefs about experience that are often strongly held – for example, that it is essentially private and somehow ineffable – are also open to question or redefinition (Kevin et al., 2005; O’Regan et al., 2005). These beliefs are relevant to science, as the questions we frame for neuroscience about awareness will of course depend on what we take our experience to be. Despite these reservations, there is a measure of agreement about at least some of the features of our experience, and there has been spectacular progress in the definition of their correlates in the brain.

EXQUISITE CORRELATIONS

Visual awareness

Although it has not, as a rule, been explicitly directed at the question of consciousness, the path-breaking work of the past century on the neurology of perception, language, memory, emotion, and action has transformed our understanding of the neural basis of awareness. The study of vision has attracted particularly intense attention as a test case for students of consciousness. We shall briefly summarize the key findings.

These landmark discoveries include the definition of the retinotopic map in striate cortex (Holmes and Lister, 1916); the discovery of orientation-specific cell columns in visual cortex by Hubel and Wiesel (1977); the realization that 30–40 functionally and anatomically distinct visual areas surround area V1 (Cowey, 1994); the evidence that “parallel” though interconnected streams of visual information flow through these areas, subserving the perception of form, color, depth, and motion (Livingstone and Hubel, 1988); the broad distinction

between an occipitotemporal stream concerned with object identification (“what” pathway) and an occipitoparietal stream concerned with visually guided action (“where” pathway) (Milner and Goodale, 1995); the discovery of specific visual association areas such as the region of fusiform cortex that is highly responsive to faces (fusiform face area, FFA), and the region of parahippocampal cortex that is highly responsive to the visual appearance of locations (parahippocampal place area, PPA) (Kanwisher, 2001). The demonstrations that illusory and implied movement in stationary visual stimuli activates area V5, the visual area most selective for moving stimuli, are elegant extensions of this broad line of work, elucidating the neural basis of visual experience (Zeki et al., 1993). The role of top-down feedback on visual perception is being explored by using transcranial magnetic stimulation and this does seem to influence perception at early stages of visual encoding (Ro et al., 2003).

Changing experience without altering stimuli

Inferences about the generation of visual awareness, drawn from work of this kind, are open to the potential objection that the mere activation of a cortical visual area by an appropriate stimulus does not show that it mediates the conscious experience of vision. Correlation does not imply cause, and, after all, much of the work on cortical visual responses in animals has been performed under anesthesia. Several authors have argued, for example, that area V1 does not contribute directly to visual awareness (Crick and Koch, 1995; Rees et al., 2000; Koch and Tsuchiya, 2012). This objection can be met, at least in part, by using paradigms in which visual awareness changes while external stimulation is held constant. Changes in neuronal activity detected under these circumstances are likely, although not guaranteed, to be linked closely to visual awareness itself. Several lines of research, discussed below, have adopted this strategy, examining the neural basis of imagery, illusions, hallucinations, attentional shifts, and binocular rivalry. Related research has used functional magnetic resonance imaging to compare brain regions activated by a fast sensory categorization paradigm to those engaged during self-reflective emotional introspection, using similar sensory stimuli. Areas engaged by introspection were actually inhibited during fast categorization. Self-awareness was correlated to the amount of introspection. This study demonstrated the complex relationship between sensory perception and the forms of awareness which can be associated with it (Goldberg et al., 2006).

We can summon up images “in the mind’s eye” and interrogate them much as we do a real visual scene.

Psychologic studies indicating that mental images are processed in similar ways to percepts of items in the real world (Shepard, 1978; Kosslyn and Shin, 1994) have recently been complemented by a series of functional imaging studies, showing that the neural correlates of mental imagery overlap substantially with the correlates of perception (Kosslyn et al., 1995; Cohen et al., 1996; Ishai et al., 2000; Kanwisher, 2000; Ishai, 2010). Like mental images, visual hallucinations are visual percepts that occur in the absence of a corresponding external stimulus, but, unlike images, hallucinations are perceived as if they occurred in the external world. Functional imaging studies in both visual and auditory domains reveal that hallucinations are accompanied by activity in cortical areas associated with the normal perceptual processing of the hallucinated items (Ffytche et al., 1998; Griffiths, 2000; Allen et al., 2008).

Attention is the sentry at the gate of consciousness: “my experience is what I agree to attend to” (James, 1890). The essence of attention is selection: whether we are displaying preparatory attention as we await an anticipated event, switching our attention between the senses or between several targets presented to a single sense, or sustaining our attention on a task, we are excluding a range of rival stimuli from the focus of our interest. Changes in the neural representation of items as they move in and out of the focus of attention should shed light on the neural accompaniments of consciousness. These changes have been termed the “neural expression” of attention (LaBerge, 1995).

Single-cell recordings from monkeys trained to shift visual attention without moving their eyes indicate that firing rates are increased in cells responding to attended stimuli, and reduced in cells responding to unattended stimuli in extrastriate visual areas, for example, areas V4 and V5 (Moran and Desimone, 1985; Treue and Maunsell, 1996). Recent functional imaging studies suggest that the neural expression of attention in humans also involves focal enhancement and inhibition of neural activity; for example, switches of attention between faces and places presented simultaneously are associated with detectable modulations of activity in the fusiform and parahippocampal regions mentioned above (Kanwisher, 2000). Synchronization of activity allowing “communication through coherence” may provide a further important mechanism by which attended stimuli are processed preferentially (Landau and Fries, 2012).

Multistable or ambiguous visual stimuli, like the Necker cube, which appears to reverse in depth repeatedly during protracted viewing, are open to alternative visual readings. Similarly, if different visual stimuli are presented to the two eyes, most viewers see each of the two images alternately rather than experiencing

a fusion of the two. This paradigm, binocular rivalry, has been applied both to animals and humans in studies of the neural correlates of the alternating percept. Logothetis, working with monkeys, has reported that, while many neurons in visual areas respond to both stimuli throughout their presentation, regardless of the current conscious percept, a subset of extrastriate neurons recorded in V4 and V5 raise or lower their firing rate markedly as the stimulus to which they respond gains or loses perceptual predominance (Logothetis and Schall, 1989; Leopold and Logothetis, 1996). Work by Engel and colleagues (1999) suggests that cells responding to the currently perceived member of a pair of rivalrous stimuli synchronize their discharges during the period of perceptual dominance to a greater degree than during periods of suppression.

Further down the processing stream, in experiments with human subjects, the modulation of neuronal activity in the FFA and PPA, as simultaneously presented faces and places alternate in awareness, is of similar size to the modulation seen when faces and places are alternately presented (Kanwisher, 2000). Thus, by this stage of processing in the human brain, activity correlates with the contents of awareness rather than with the raw features of the impinging stimuli. Using magnetoencephalography, Tononi and Edelman (1998a) have reported that, as conscious perception shifts between two gratings of different orientations, flickering at different frequencies, so the power of electromagnetic activity at the corresponding frequency waxes and wanes by 30–60% over wide regions of cortex. Lumer and colleagues (1998) have found that the moments of transition between multistable percepts are associated with right frontoparietal activation, suggesting that the neural control of these transitions shares common ground with the direction of spatial attention.

These experiments, investigating imagery, hallucinations, attention, and binocular rivalry, are beginning to capture the neural correlates of visual experience. The precise definition of the “neural correlate of consciousness” (NCC) in humans remains a goal for the future, and will probably require more sophisticated methods than those currently available, allowing the detailed measurement of disparate neuronal activity over short time scales in the human brain. Nevertheless, these results help to bolster the neuroscientist’s long-held article of faith: that distinction drawn in experience will be reflected in distinctive patterns of neural activity.

INTERNAL AND EXTERNAL AWARENESS, THE “RESTING STATE” AND THE “DEFAULT NETWORK”

Much of 20th-century neuroscience treated the brain as a stimulus-driven system. Clearly one of the brain’s key

roles is indeed to respond appropriately to impinging stimuli, but an exclusive emphasis on this kind of brain work risks losing sight of the brain’s inherent dynamism and autonomy. These are suggested by the simple observation that, while the brain is responsible for around 20% of the body’s energy expenditure at rest, its energy consumption is only marginally affected by stimulation. Brains, like their owners, are spontaneously active. Two lines of recent work have converged on the discovery of a “default mode” of brain functioning which is conspicuous when subjects rest between experimental tasks. The first of these sprang from the realization that a consistent network of brain regions is deactivated by a wide range of cognitive tasks: these regions, conversely, are particularly active in the “resting brain” (Raichle, 2010). The second line of work flows from the discovery that most, if not all, of the brain’s functional networks can be identified in the resting brain using techniques which hunt for correlations between activity in multiple cortical regions: approaches of this kind can identify networks involved, for example, in motor control, vision, audition, and attention (Smith et al., 2009). The “default network,” the “resting state network” par excellence, emerges strongly from analyses of this kind. The key nodes of the default network are cortical midline regions – posterior-cingulate/precuneus, anterior cingulate/mesiofrontal cortices – with additional contributions from inferior parietal and lateral temporal regions, the medial temporal lobes, and parts of the cerebellum (Buckner et al., 2008) (Fig. 31.11). Its functions remain a topic of debate, but the areas just listed contribute substantially to the neural processes linked to “self-processing,” and are thought to be involved specifically in theory of mind, recollection of the past, imagination of the future, moral thinking, and semantic processing more generally (Buckner et al., 2008; Binder et al., 2009).

The regions of the default network appear to be engaged particularly, though not exclusively, by endogenous or internally generated thoughts. A complementary set of regions comprises an “external” network, directed to events in the external world. There is some evidence that activity in these two sets of regions is anticorrelated, with a slow oscillation in their relative levels of activity in the resting brain which has a measurable influence on the threshold for detecting sensory events (lower when the external network is more active) (Buckner et al., 2008). Collectively, these internal and external networks of higher-order cortical regions, lying mainly on the medial and lateral surfaces of the hemispheres respectively, coincide broadly with the areas identified as the neural instantiation of the putative “global workspace” of consciousness, discussed further below (see section on anatomy and physiology: the “where” and “how” of consciousness?) (Boly et al., 2008).

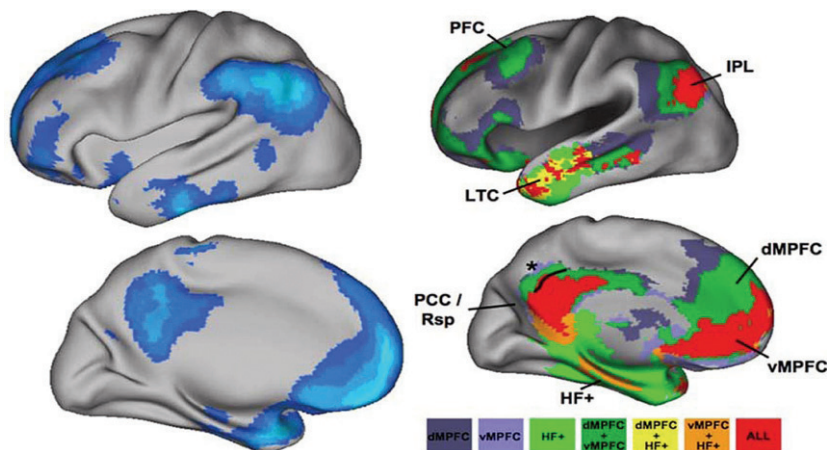


Fig. 31.11. The default network: both images show side (above) views and medial (inner, below) views of the left hemisphere. The left-hand panel shows regions that are more active at rest than during (most) active tasks. The right-hand panel shows regions within the default network mapped using functional connectivity analysis. The areas of maximum overlap correspond to the regions most active at rest in the left panel. PFC, prefrontal cortex; IPL, inferior parietal lobule; LTC, lateral temporal cortex; PCC/Rsp, posterior cingulate cortex/retrosplenial cortex; HF, hippocampal formation; dMPFC, dorsomedial prefrontal cortex; vMPFC, ventromedial prefrontal cortex. (Reproduced from Buckner et al., 2008.)

UNCONSCIOUS PROCESSES

The concept of unconscious processes

The idea that much of the activity occurring in the brain never gives rise to awareness is supported by a host of observations made in both health and disease, including the study of habitual and automatic behavior, procedural memory, and unconscious perception (for a wide-ranging survey of concepts of the unconscious, see Claxton, 2005; Dehaene et al., 2006). The existence of unconscious neural processes provides an opportunity to approach the neurology of consciousness using a method of contrast or subtraction, focusing on the differences between processes that are and that are not linked to consciousness.

The major methodologic problem for students of unconscious processes is how to determine the presence or absence of awareness. Much of the neuropsychologic work in this area relies on verbal report (Barbur et al., 1993) or the use of a “commentary key” (Weiskrantz, 1997) to indicate the degree of awareness. But verbal reports and presses on commentary keys may not provide exhaustive measures of the information available to consciousness. Indeed, there are no conclusive reasons for holding that consciousness should always be reportable, even in principle (Zeman, 2009). On the other hand, if every successful discrimination is taken to provide evidence of conscious perception, the possibility of unconscious perception is ruled out by definition (Kihlstrom et al., 1992). The lack of any “exhaustive measure that exclusively indexes relevant conscious perceptual experiences” is therefore a significant problem,

though not necessarily an insuperable one (Merikle and Reingold, 1992). Psychologists have suggested a range of solutions to the dilemma (Jacoby et al., 1992; Merikle and Reingold, 1992).

The terminology of unconscious processes is confusing. Besides the variety of cognate options – subconscious, preconscious, nonconscious – a number of technical terms have been used in related senses. “Implicit” or “subliminal” – neural or cognitive – processes are those occurring in the absence of any conscious experience of the information concerned, by contrast to “explicit” – or “suprathreshold” processes. A key distinction is whether nonconscious stimuli are subliminal (too weak to enter conscious experience) or preconscious (potentially conscious but currently unattended) (Fig. 31.12). “Direct” tasks are those that involve instructions referring directly to the dimension of interest to the experimenter: a direct test of memory might ask for the contents of a word list, whereas an indirect task might examine whether prior exposure to the list increased the ease with which they are later identified on a brief presentation. Note that a direct task may tap an implicit process – if, for example, we are asked to guess at the location of a stimulus that we have not consciously perceived – and an indirect task may tap an explicit process, if I recognize the items from the word list on their brief presentation.

Changing behavior without altering experience

It is no surprise that stimuli impinging on the nervous system can have neural effects in the absence of any

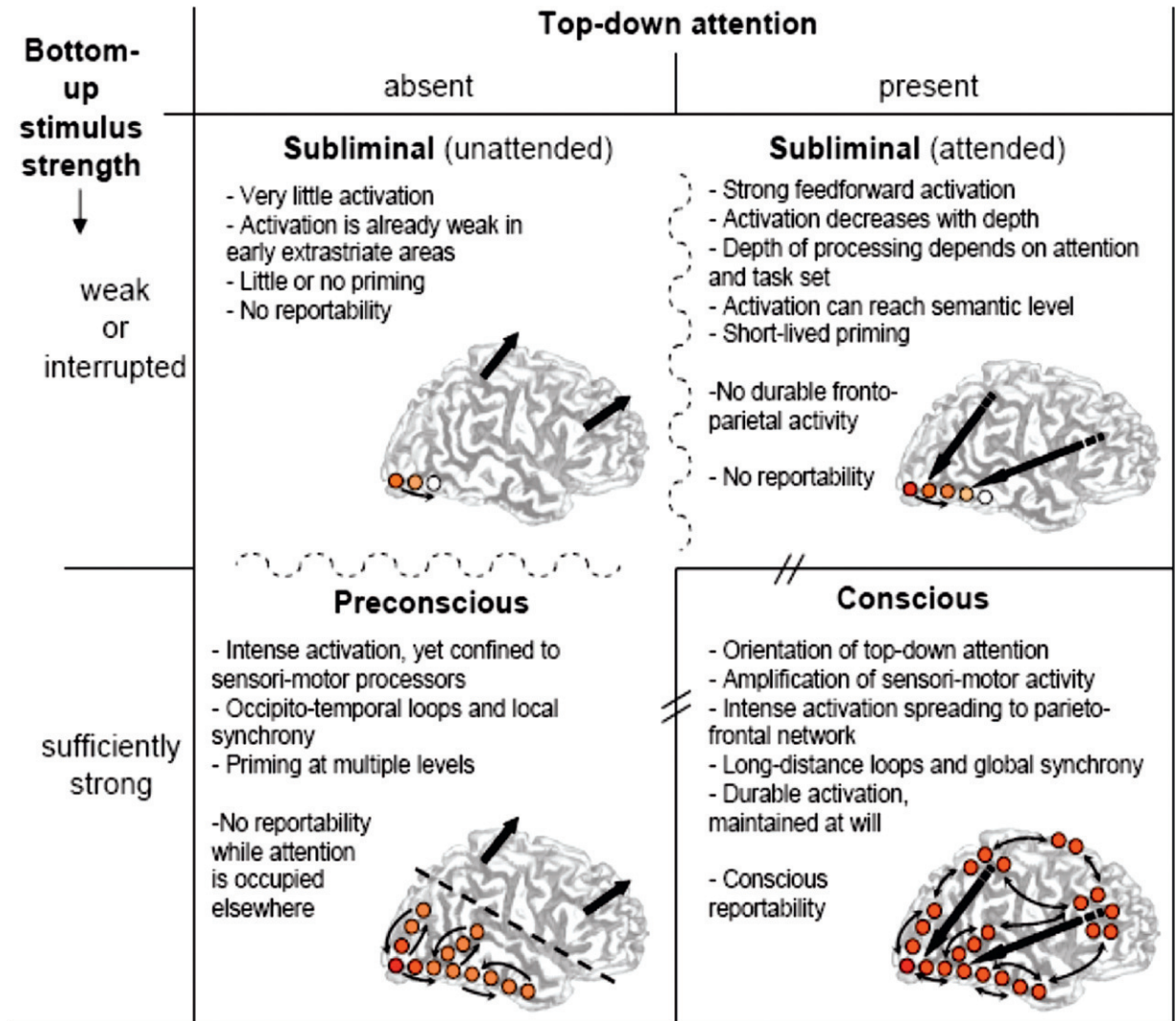


Fig. 31.12. Subliminal, preconscious, and conscious processes as conceived by the global neuronal workspace theory. (Reproduced from Dehaene et al., 2006.)

discernible effect on our awareness or behavior. There is greater theoretic interest in events that “influence our experience, thought and behaviour even though they are not consciously perceived” (Kihlstrom et al., 1992). Examples include the effects of unperceived stimuli on judgments made by normal subjects in direct and indirect tasks (unperceived because, for example, they are too weak, too brief, or masked by preceding or succeeding stimuli); their effects in normal controls subjected to procedures like anesthesia or hypnosis; and their effects in subjects with neuropsychologic syndromes such as blindsight, neglect, and, possibly, hysteria (now more commonly referred to as “functional disorder” in neurology or “dissociative disorder” in psychiatry).

A 19th-century experiment by Pierce and Jastrow illustrates the effect of stimuli too subtle to allow

confident verbal report on judgment in a direct test. Subjects were required to judge or guess which of two similar pressures was the greater. At the same time they indicated their degree of confidence in their judgment. Even when the confidence rating had fallen to zero, their guesses proved correct significantly more often than chance would have allowed (Kihlstrom et al., 1992). In a modern reworking of the theme, a study of the functional imaging correlates of the perception of low-concentration odors demonstrated above-chance detection in the absence of reported awareness, associated with brain activation in the anterior medial thalamus and inferior frontal gyrus (Sobel et al., 1999). “Mere exposure” effects illustrate the effects of unperceived stimuli in an indirect test (Zajonc, 1980). Abstract stimuli presented extremely briefly, for 1 ms, tend to be chosen

in a subsequent task in which subjects are asked to state which of two stimuli they prefer, even though they are not recognized as familiar. In a study directed to the neural correlates of unperceived stimuli rather than to their behavioral effects, it was found that, in a task requiring subjects to classify numbers as larger or smaller than 5 by pressing a button with the left or right hand, presentation of masked, unreported, numeric primes sets in train a stream of perceptual, cognitive, and motor processes in precisely the areas that are also engaged by the perceived stimulus (Dehaene et al., 1998). The occurrence of implicit perception under anesthesia has been supported by a number of studies. Schwender and colleagues (1994), for example, showed that, in the absence of any explicit recall of events during cardiac surgery, some patients associated key words with material that had been read aloud during the operation; these patients were distinguished by the relatively normal latencies of their mid-latency auditory evoked potentials under anesthesia.

In neuropsychology, the most widely quoted example of unconscious perception is undoubtedly blindsight (Stoerig and Cowey, 1997; Weiskrantz, 1998). This paradoxical term, coined in 1974 (Sanders et al., 1974), describes a range of visually based abilities that can be demonstrated in the absence of visual awareness following damage to striate cortex in some, but not all, subjects. The possibility that abilities of this kind might exist was suspected on the basis of the relatively good recovery of visual function in monkeys after experimental ablation of striate cortex. An experiment by Poppel and colleagues (1973), in which war veterans with scotomata due to gunshot wounds were encouraged to look in the direction of “unseen” stimuli, suggested that similar abilities might be found in humans. This was confirmed when DB, a patient in whom the right calcarine cortex had been excised as part of the surgical treatment of an arteriovenous malformation, was “urged to guess” the nature and location of stimuli in his blind field (Sanders et al., 1974). His guesses, to his great surprise and despite his insistence “that he saw nothing except in his intact visual field,” proved to be substantially correct. Subsequent work has shown that, besides mediating neuroendocrine and reflex responses, blindsight can subservise accurate performance on a range of direct and indirect tasks (Stoerig and Cowey, 1997). Indeed, on some measures, blindsight allows accuracy well beyond the performance of normal subjects making judgments close to the threshold of awareness. Its capacities include localization of the “unseen” target by hand or eye, and simple judgments about orientation, shape, and presence or absence of motion. A range of skeptic interpretations of these results, in terms of covert eye movements, scatter of light into the intact visual field, the survival of

islands of cortex, and the persistence of degraded but nevertheless conscious visual awareness, have been substantially rebutted (Weiskrantz, 1998), although blindsight continues to provoke lively debate (Zeki and Ffytche, 1998). This line of research, inspired by observation made in monkeys, has come full circle with ingenious experimental evidence that destriated monkeys, like destriated humans, may lack “phenomenal vision” and rely on blindsight for their well-preserved visuomotor skills (Cowey and Stoerig, 1995). Patient GY, studied by Zeki and Ffytche (1998), who has a V1 lesion, illustrated the complex relationship between awareness and discrimination, which can dissociate into anosagnosia (awareness without discrimination) and on the other to agnosagnosia (discrimination without awareness). Adolphs and colleagues (2005) similarly studied a patient with extensive bilateral brain damage who could not recognize sugar and saline, but preferred sugar, illustrating discrimination without awareness in the olfactory domain.

The study of neglect also illustrates the effects of unperceived stimuli on subsequent behavior, although the puzzle in such cases, superficially at least, lies as much in the subjects’ initial failure to perceive the stimuli as in their subsequent effects (Robertson and Marshall, 1993). Following brain lesions, most commonly affecting the right inferior parietal lobe, subjects may fail to attend to stimuli in contralateral space. The failure can affect imagined scenes as well as real ones (Bisiach and Luzzatti, 1978). The syndrome has been fractionated into several subtypes: primarily perceptual or primarily motor (Tegner and Levander, 1991); primarily perceptual or primarily representational; spatially or object-based, and affecting near or far space (Halligan and Marshall, 1991). Yet, despite the apparent failure of awareness of stimuli in the affected half-field among subjects with neglect, there is clear evidence for implicit processing of information about these stimuli. Thus subjects with left hemineglect, invited to express a preference for one of two line drawings which differ only in the plume of smoke rising from a house fire on the far left, tend to choose the fire-free home (Marshall and Halligan, 1988). In a similar vein, unidentified words presented on the neglected left-hand side of space can influence the identification of words presented later on the attended side (Berti and Rizzolatti, 1992). Rees and colleagues (2000) have demonstrated activation of visual areas contralateral to the unreported stimulus in a patient with the related syndrome of extinction, suggesting that the failure of awareness in these disorders in neglect is due to disturbance of a relatively late stage of stimulus processing.

These examples of the influence of unperceived stimuli on behavior have parallels in the domains of memory

Table 31.2

Paradigms for studying the neural correlates of conscious (upper row) and unconscious (lower row) processes

	Vision	Memory	Action
Stimulus constant, experience changes	Shifts of attention Visual imagery Hallucinations “Multistable” percepts	Declarative recall	Free choice Delusions of control
Experience constant, behavior changes	Visually guided behavior in: Blindsight Neglect Agnosia	Procedural memory	Automatic behavior, alien limb

Source: from Zeman (2002), adapted from Frith et al. (1999).

and action (Table 31.2). “Declarative memories” are those we can explicitly recall and articulate, including our memories for autobiographic episodes (Squire et al., 1990). “Procedural” memories, which include those acquired through classic conditioning, priming, and during acquisition of motor skills, are implicit, capable of influencing behavior without any need for conscious recollection. Declarative memories are associated with a network of limbic and neocortical areas, somewhat distinct from the subcortical and motor cortical regions implicated in procedural memory (Berns et al., 1997; Buckner and Koutstaal, 1998; Clark and Squire, 1998). Studies of the gradual learning of rules which can, initially, gain an influence over behavior in the absence of any conscious appreciation of the rule offer related insights (Berns et al., 1997). In the context of action, much of what we do is automatic, requiring little or no supervision by consciousness: once again, there are illuminating differences between the underlying functional neuroanatomy of effortful, willed, “conscious,” actions and of habitual or automatic acts. For example, as skills are acquired, global brain activation decreases, and there are shifts in regional brain activation, with decreasing involvement of prefrontal regions as the requirement for conscious supervision declines (Haier et al., 1992; Passingham, 1997; Petersen et al., 1998; Raichle, 1998).

In each case—perception, memory, action—exploration of the neural basis of unconscious processes provides a promising approach to understanding the neurology of awareness, complementing the direct pursuit of the neural correlates of experience, discussed above. Comparison of conscious and unconscious states, and of conscious and unconscious processes, exemplifies the “contrastive analysis” that informs much contemporary discussion of the neurology of consciousness (Table 31.3). We will return to the broader implications of both approaches in the section on contemporary models and theories of consciousness, below.

Concepts of impaired and altered consciousness

Other chapters consider the pathologies of consciousness in detail. This section will therefore merely outline a taxonomy of these disorders, drawing attention to links with points made in the previous sections and with the global theories of consciousness discussed in the following section. As before, it is convenient to discuss pathologies of state and of content in turn.

Pathologies of conscious state

A TAXONOMY OF IMPAIRMENTS

Pathologies of conscious state can be classified with respect to duration (brief, as in syncope or epileptic seizure, or more protracted, as in coma), underlying cause (for example hypoxia/ischemia, trauma, epilepsy, drugs, endocrine and metabolic disturbance, infection and inflammation, structural brain disease, psychogenic, *inter alia*) or clinical features (for example, brainstem death versus coma versus vegetative state or unresponsive wakefulness syndrome (Laureys et al., 2010) versus akinetic mutism versus minimally conscious state (MCS, recently subdivided into MCS $-/+$ (Bruno et al., 2011)).

Table 31.4 is a British taxonomy of the major persistent pathologies of conscious state (Working party of the Royal College of Physicians, 2003), classified by clinical feature and including the (functional) locked-in syndrome, which is of course not a pathology of consciousness but all too easily mistaken for one (Bruno et al., 2011). Coma (meaning deep sleep in Greek) is a state of continuous “eyes-closed” unconsciousness from which a person cannot be awakened, in the absence of a sleep–wake cycle. It varies in degree from moderate to profound unresponsiveness, and is associated with a comparably variable reduction in cerebral metabolism. It results from diffuse hemispheric or focal brainstem/diencephalic dysfunction, and is usually a transitional

Table 31.3

“Contrastive analysis”: examples of studies comparing conscious and unconscious brain activity

Study (context)	Comparison	Results
Laureys 2000 (vegetative state)	Vegetative state versus recovery	Increase in cortical metabolic rate and restoration of connectivity with recovery
John 2001 (anesthesia)	Anesthesia versus awareness	Loss of gamma-band activity and cross-cortical coherence under anesthesia
Sahraie 1997 (blindsight)	Aware versus unaware mode of perception in blindsight patient GY	Aware mode associated with DLPF and prestriate activation, unaware with medial frontal cortex and subcortical
Dehaene et al., 1998 (backward masking)	Perceived numbers versus backward masked but processed numbers	Unreported numbers underwent perceptual, semantic, and motor processing similar to but less intense than reported numbers
Kanwisher 2000 (binocular rivalry)	Attention to face or place when stimuli of both kind are simultaneously in view, or perception of face or place during binocular rivalry	Activity in FFA and PPA locked to presence or absence of awareness of face and place
Moutoussis and Zeki 2002 (invisible stimuli)	Perceived versus “invisible” but processed faces/houses	Similar but less intense activation of FFA and PPA by invisible stimuli
Engel 1999 (binocular rivalry)	Perception of one or other of a pair of rivalrous stimuli	Firing of cell processing currently perceived stimulus better synchronized than firing of cells processing suppressed stimulus
Tononi 1998a (binocular rivalry)	Perception of high- versus low-frequency flicker during binocular rivalry	More widespread and intense activation by perceived stimulus
Petersen et al., 1998 (task automatization)	Effortful verb generation task versus performance after training	LPF, anterior cingulate, and cerebellar activation shifts to left perisylvian activation with training

DLPF, dorsolateral prefrontal cortex; FFA, fusiform face area; PPA, parahippocampal place area; LPF, lateral prefrontal cortex.

state, *en route* to recovery, brainstem death, or a state of chronically impaired awareness with recovery of the sleep–wake cycle. The risk of confusing the locked-in state with coma is now well recognized by neurologists. In this syndrome, which follows brainstem lesions abolishing the descending control of voluntary movement, patients are only able to communicate using movements of the eyes or eyelids.

Brainstem death implies the irreversible loss of all brainstem functions. In the United Kingdom it renders legal the removal of organs for transplantation, provided that appropriate consent has been obtained. It is generally followed by cardiac death, within hours to weeks, though there are reported exceptions to this rule.

The vegetative state was first defined by Jennett and Plum in 1972. In this condition, characterized by “wakefulness without awareness,” patients regain their sleep–wake cycle, and may be aroused by painful or salient stimuli, but show no signs of discriminative perception or deliberate action, including attempts to communicate (Anon, 1994; *The Multi-Society Task Force on PVS, 1994a, b*; Zeman, 1997; Jennett, 2004). Recovery from a vegetative state often occurs: younger age and traumatic, rather than hypoxic-ischemic, causation

improve the outlook. After 1 month the condition is often termed “persistent,” and in patients in whom recovery appears highly unlikely it may be deemed “permanent,” although permanence cannot of course be predicted with certainty. The underlying pathology usually involves some combination of: (1) diffuse cortical injury, typically cortical laminar necrosis; (2) diffuse white-matter injury, typically diffuse axonal injury or leukoencephalopathy; or (3) thalamic necrosis. It has been suggested recently that the vegetative state should be redesignated the “unresponsive wakefulness syndrome” to remove the pejorative connotations of the term “vegetative” and to underline the behavioral definition of the syndrome via the absence of response (which does not, in itself, preclude the possibility of awareness).

MCS is “a condition of severely altered consciousness in which minimal but definite (‘reproducible but inconsistent’) behavioural evidence of self or environmental awareness is demonstrated” (Giacino, 2005). Reliable object use or communication implies emergence from the MCS. Techniques are being developed, as mentioned below, to facilitate communication with severely disabled patients in MCS who are to some degree aware but have great difficulty in communicating their

Table 31.4

The differential diagnosis of impaired awareness

Condition	Vegetative state	Minimally conscious state (MCS)	Locked-in syndrome	Coma	Death confirmed by brainstem tests
Awareness	Absent	Present	Present	Absent	Absent
Sleep–wake cycle		Present with EEG correlate	Present	Absent	Absent
Response to pain	±	Present	Present (in eyes only)	±	Absent
Glasgow coma scale	E4, M1–4, V1–2	E4, M1–5, V1–4	E4, M1, V1	E1, M1–4, V1–2	E1, M1–3, V1
Motor function	No purposeful movement	Some consistent or inconsistent verbal or purposeful motor behavior	Volitional vertical eye movements or eye blink preserved	No purposeful movement	None or only reflex spinal movement
Respiratory function	Typically preserved	Typically preserved	Typically preserved	Variable	Absent
EEG activity	Typically slow-wave activity	More alpha power and increased connectivity compared to vegetative state (Lehembre et al., 2012) and increased entropy (Gosseries et al., 2011)	Typically normal	Typically slow-wave activity or alpha coma	Absent
Cerebral metabolism (positron emission tomography)	Severely reduced	Reduced, but more in MCS+ compared to MCS- (Bruno et al., 2012)	Mildly reduced	Moderately to severely reduced	Severely reduced or absent
Prognosis	Variable: if permanent, continued vegetative state or death	Variable	Depends on cause but full recovery unlikely	Recovery, vegetative state, or death within weeks	Already dead

Adapted from the Working party of the Royal College of Physicians (2003). EEG, electroencephalogram.

awareness: such patients are at high risk of misdiagnosis as vegetative. Some improvements have been seen in MCS after thalamic stimulation (Schiff et al., 2007) or after mesencephalic reticular formation stimulation (Yamamoto et al., 2005).

These distinctions are useful and moderately robust in clinical practice. They are not immune to practical and theoretic problems. At a practical level, there are apparent examples of long survival in “brain-dead” patients (Shewmon, 1998), and there is evidence that the vegetative state has often been misdiagnosed in patients who are in fact aware (Childs et al., 1993; Andrews et al., 1996; Schnakers et al., 2009). In future, techniques like those developed by Owen and others (Owen and Coleman, 2008), permitting communication

with severely disabled but aware patients who are unable to express themselves by speech or gesture, will help to reduce the risk of misdiagnosis. Related approaches may make it possible to predict the presence or absence of awareness on the basis of physiologic features such as cortical effective connectivity (Rosanova et al., 2012). It is conceivable that brainstem death might become a treatable disorder as neural prostheses are developed. At a theoretic level, it is open to question whether patients in vegetative states are wholly unaware (Zeman, 1997).

The classic impairments of consciousness mentioned so far are relatively severe and well defined. In the hinterland of coma lie a range of more subtle impairments of consciousness that have attracted an inconsistent and

confusing terminology, including terms such as delirium, confusional states, acute organic brain syndrome, stupor, and catatonia. For example, akinetic mutism is a state of profound apathy with some evidence of preserved awareness, characterized by attentive visual pursuit and an unfulfilled “promise of speech.” It is often associated with damage to the medial frontal lobes and as part of catatonia.

Delirium, confusion, and acute organic brain syndrome are probably best considered as a single, highly heterogeneous, nosologic entity, characterized by the acute or subacute onset of a “clouding of consciousness,” accompanied by incoherence of thought, impairment of working memory and delayed recall, abnormalities of perception, often including hallucinations, disturbance of emotion and of behavior, which may become either hypo- or hyperactive (Lipowski, 1990; Lindsay et al., 2002). These features are, in delirium, the result of diffuse brain dysfunction, commonly due to metabolic derangement, organ failure, infection, or the effects of drugs or drug withdrawal. The “clouding of consciousness” that is often considered characteristic of delirium can be dissected into a number of components. These include disturbance of the sleep–wake cycle associated with abnormalities of arousal or alertness; an inability to sustain attention that is the neuropsychologic hallmark of “confusional states,” and abnormalities of awareness, that, in delirium, often include fleeting hallucinations and delusions. This complex of features indicates that the distinction we have drawn between “wakefulness” and “awareness” is not always respected by the brain and its disorders: “attention,” in particular, is a composite function, related to both arousal and awareness, functions jointly disrupted in delirium. Their joint disruption is partly the result of the widespread brain pathology that underlies delirium, but also reflects the joint role of certain brain regions, especially the thalamus, in mediating both arousal and awareness.

Stupor is a related disturbance of consciousness “whose central feature is a reduction in, or absence of, relational functions: that is action and speech” (Sims, 2003). Akinetic mutism is a neurologic cause of stupor. It is a state of profound apathy with some evidence of preserved awareness, characterized by attentive visual pursuit, and an unfulfilled “promise of speech.” It is often associated with damage to the medial frontal lobes and can occur as part of catatonia, mentioned below. The distinction between neurologic and psychiatric causes of stupor, such as affective disorder, psychosis, and dissociative disorder, can be extremely difficult.

Catatonia is another “disorder of consciousness” falling awkwardly between the disciplines of neurology and psychiatry (Fink and Taylor, 2003). It is characterized by motor features, varying from catalepsy or

“waxy flexibility” to motor stereotypies, including “echo” phenomena, accompanied by a markedly altered mental state involving alteration of both arousal and awareness. Its most common causes are psychiatric, including bipolar disease, depression, and schizophrenia, but it occurs in neurologic disorders including, for example, the neuroleptic malignant syndrome and encephalitis lethargica. The value of a combined neuropsychiatric approach to these clinical phenomena should be self-evident.

There is, finally, a group of candidate disorders or alterations of conscious state whose status is deeply unclear. These include dissociative or functional coma and stupor, fugues, trances, and alteration of consciousness during hypnosis (Halligan et al., 2001; Vuilleumier, 2005). It is uncertain at present to what extent these phenomena are best understood as perturbations of conscious state and to what extent as modulations of social behavior. Elucidation of their neural correlates may help to clarify their nature (for recent review, see Bell et al., 2011).

The possibility that the various classic states of reduced or absent consciousness, among them SWS, the varieties of coma, including anesthetic coma and the vegetative state, and loss of awareness during complex partial seizures (Blumenfeld, 2012) may have important underlying common neurobiologic features has been raised by recent research (Baars et al., 2003) and will be discussed further below.

STATE BOUNDARY DISSOCIATION

The impairments of conscious state considered so far represent more or less protracted deviations from the normal, healthy alternation of sleep and wakefulness. The parasomnias are disorders of behavior, autonomic nervous system functioning, and experience occurring in relation to sleep (Table 31.5). The newly revised *International Classification of Sleep Disorders* (ICSD-2) recognizes that parasomnias can emerge during entry into sleep, within sleep, or during arousals from sleep (American Academy of Sleep Medicine, 2005). Parasomnias occur in all non-REM and REM sleep stages. They have been described illuminatingly as the result of “state boundary dissociation,” the breakdown of the boundaries that normally separate the principal conscious states described above, allowing elements of these states to commingle (Fig. 31.13; Mahowald and Schenck, 1992).

Thus sleep paralysis, caused by the persistence of the atonia of REM sleep into wakefulness, results from a partial breakdown of the normal separation between these two states. In REM sleep behavior disorder, the muscle tone of wakefulness intrudes into REM sleep, allowing the release of dream-enacting behaviors. Hypnagogic hallucinations, intrusions of dream mentation into wakefulness, are expressions of a similar overlap.

Table 31.5

A classification of the common parasomnias and related conditions, by sleep stage

Sleep/wake transition disorders	NREM arousal disorders	REM sleep parasomnias	Others
Sleep starts	Confusional arousals	Nightmares	Sleep bruxism
Exploding head syndrome	Sleep terrors	Sleep paralysis	Sleep enuresis
Rhythmic movement disorders	Sleep walking	REM sleep behavior disorder	Sleep-related panic attacks
Restless legs syndrome			Sleep-related hallucinations
			Periodic leg movements in sleep
			Sleep-related choking episodes
			Sleep-related groaning
			Sleep-related eating disorder
			Sleep-related dissociative disorders
			Sleep-related headaches

NREM, nonrapid eye movement; REM, rapid eye movement.

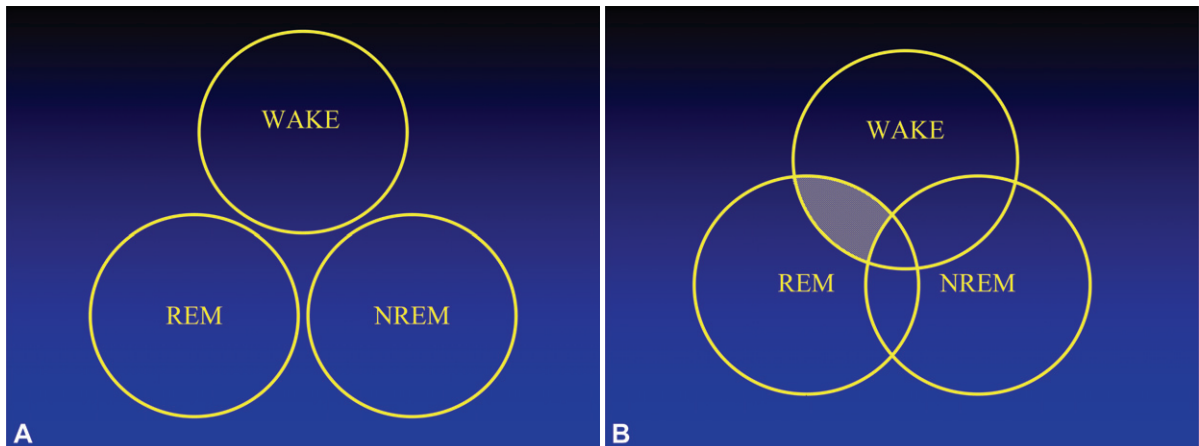


Fig. 31.13. (A, B) State boundary dissociation. The states of wakefulness, rapid eye movement (REM), and non-REM (NREM) sleep are normally distinct. Many parasomnias can be understood as the result of a fusion of two or more states: for example, overlap between the phenomena of REM sleep and wakefulness (shaded) gives rise to REM sleep behavior disorder; overlap between NREM sleep and wakefulness occurs during sleep walking and night terrors. (Reproduced from Mahowald and Schenck, 1992.)

Sleep walking occurs as a result of incomplete arousal from SWS, with motor activity appropriate to wakefulness occurring in conjunction with mentation of a kind that normally occurs in SWS (Bassetti et al., 2000).

Pathologies of awareness

If “awareness” is taken to refer to the contents of experience, several of the pathologies referred to in the previous section profoundly affect it. The vegetative state has already been characterized as a condition of “wakefulness without awareness.” In the MCS the capacity for experience has recovered to some degree but remains severely limited.

Many of the focal deficits described in neuropsychology can also be regarded as pathologies of awareness, as these typically affect the contents of experience. They have been described in the domains of emotion, visual, auditory and other sensory modalities, memory, action, and language. The emotion of fear, for example, can be profoundly affected by selective damage to the amygdala (Young et al., 1995). In vision, equally selective deficits have been described, for example, the loss of color vision following focal brain damage, central achromatopsia (Zeki, 1990), the loss of motion vision, akinetopsia (Zeki, 1991), selective impairment of face recognition, prosopagnosia, and the selective loss of the capacity for visual imagery (Farah, 1984). In the auditory domain

conditions like amusia and auditory agnosia are recognized (for review, see [Goll et al., 2010](#)).

Much of neuropsychology and cognitive neuroscience therefore has a bearing on the “science of awareness.” Many psychiatric disorders, especially those involving psychotic experience, profoundly affect the contents of consciousness and are also, in this sense, “pathologies of awareness” ([Frith, 2004](#)).

Pathologies of self-awareness

These are as at least as various as the meanings of “self-consciousness,” discussed above. The senses distinguished there should provide a helpful approach to understanding the diversity of disorders of self-awareness.

Thus, the selective loss of proprioception, whether due to a disorder of the central or the peripheral nervous system, impairs self-awareness in the sense of self-perception. The experience of phantom or alien limbs, xenomelia ([McGeoch et al., 2011](#)), and perhaps the alteration of self-perception that occurs in “depersonalization and derealization” are disorders of self-awareness in a similar sense of the term.

Anosognosia, failure to appreciate the presence of disease, is a disorder of self-monitoring ([Adair et al., 2003](#)). It occurs, for example, for memory deficit in Alzheimer’s disease, and for limb weakness in association with the phenomena of hemineglect and extinction. Self-monitoring of errors (emergent awareness) is disturbed in frontotemporal dementia ([O’Keefe et al., 2007](#)).

Selective loss of mirror self-recognition, the fourth sense of self-consciousness, is a rare occurrence, but has been described in dementia. Impairments of the “awareness of awareness” or “theory of mind” are more common and have been a focus of recent research. It is suggested that the core cognitive deficit in autism is failure to acquire the appreciation of the mental states of others that most of us acquire without effort as small children ([Baron-Cohen, 1995](#); [Frith and Frith, 1999](#)). Similar deficits occur in the course of some degenerative disorders, notably frontotemporal dementia ([Gregory et al., 2002](#)). It has been suggested that a distributed network of brain regions in the parietal lobe, paralimbic regions, and frontal lobes subserve this socially crucial form of self-awareness ([Abu-Akel, 2003](#)).

Finally, “self-knowledge,” the last sense of self-consciousness distinguished above, can be affected by a variety of neurologic disorders, for example those affecting autobiographic memory ([Evans et al., 1996, 2003](#); [Manes et al., 2001](#); [Kopelman, 2004](#)). Unawareness of personality change in frontotemporal dementia ([Rankin et al., 2005](#)) might be regarded as another example of impaired self-knowledge in this final sense.

CONTEMPORARY MODELS AND THEORIES OF CONSCIOUSNESS

The Renaissance of empiric research on consciousness has stimulated several rather general accounts of its mechanisms. A common denominator of these theories is their ambition to do justice to the subjective features of experience, showing how these might plausibly emerge from the candidate mechanisms; most of the theories also incorporate an account of the functions of consciousness in the control of behavior. Some aim to specify anatomic foundations and physiologic mechanisms; others have focused on the computational tasks that conscious processes might perform; a third group of theories has addressed the possible social origins and roles of consciousness. These approaches are not mutually exclusive: visual experience has subjective qualities, a neural basis, a computational role in controlling behavior, and a social context. We shall review a selection of the more prominent proposals in each of these groups, focusing on the emergence of “core” or “primary consciousness,” our moment-to-moment awareness of ourselves and our environment, leaving the fundamental question of whether any such theory is capable, in principle, of giving a complete account of consciousness, until the final section.

Anatomy and physiology: the “where” and “how” of consciousness?

The majority of theories take it for granted that structures in the upper brainstem, thalamus, and basal forebrain play a critical role in arousal, while thalamic and cortical activity substantially determines the content of consciousness. Most assume that the NCC will prove to be some variety of “neuronal cell-assembly,” defined by the Canadian psychologist Donald [Hebb \(1949\)](#) as a “diffuse structure comprising cells in the cortex and diencephalon . . . capable of acting briefly as a closed system, delivering facilitation to other such systems.” Most theories also assume that the loosely linked, but temporarily coherent, network of neurons subserving consciousness at a given time will be widely distributed in the brain, and will engage a range of cognitive capacities. But agreement on the role of neuronal assemblies in the genesis of consciousness leaves scope for disagreement about many important details: Must the assembly be of a certain minimum size, and undergo a particular duration, intensity, or pattern of activity to give rise to consciousness? Need it incorporate particular neuronal types, cortical layers, or cortical regions? Must there be a particular set of interregional connections? Must a certain set of psychologic functions be engaged?

Tononi and Edelman (1998b) have developed a model that envisages the emergence of “primary consciousness,” the construction of our multimodal perceptual world, from a “dynamic core of strongly interacting elements,” cortical modules that are at once internally complex, potentially independent, and yet highly interconnected; these interactions depend on a process of re-entry, via reciprocal links between regions of the thalamocortical system; this permits the integration of current sensory processing with previously acquired affect-laden memories. Tononi and Edelman (1998b) argue that this model of a constantly shifting “dynamic core” of neural elements subserving consciousness accounts for many of its properties – its continuity and changefulness, its coherence and its pace of change, the existence of a focus of attention and a more diffuse surround, the wide access of its contents to a range of psychologic operations. The notion that consciousness depends upon a combination of modular specialization and functional integration has been elaborated conceptually and mathematically into the information integration theory of consciousness. This proposes that consciousness can be conceptualized as integrated information requiring both a large repertoire of available states (information) and their coherent interaction (integration).

Crick (1994) and Koch (1998) have proposed a theory along related lines with some differences of emphasis. They argue that, in the case of visual awareness, the NCC must be an “explicit, multi-level, symbolic interpretation of part of the visual scene.” “Explicitness” implies that the NCC must reference those features of the visual scene of which we are currently aware, for example, by a synchronized elevation of the firing rate of the cells which reference the features; the NCC for vision will be “multilevel” in the sense that several levels of processing in the hierarchy of cortical visual areas are involved; it is “symbolic” in the sense that the NCC represents the relevant features of the visual scene. Crick and Koch (1995) anticipate that the NCC at any given time will involve a sparse but spatially distributed network of neurons, and that its activity will stand out against the background of neuronal firing for at least 100–200 ms. Crick and Koch suggest that the neurons involved in the NCC may have “some unique combination of molecular, pharmacologic, biophysical and anatomic properties”: for example, Crick has speculated that “bursty” pyramidal cells in layer 5 of the cortical visual areas may play a critical role in the NCC. With the aim of honing the definition of the NCC for vision, Crick and Koch (1995) have made the controversial proposal that neurons within area V1, primary visual cortex, do not directly participate in the NCC for visual awareness, despite supplying much of the information that is processed in visual areas downstream. The idea has two main sources: the empiric

observation that several characteristics of our visual experience correlate more closely with the activity of neurons in higher visual areas, such as V4, than in V1; and the theoretic view that only cortical regions that can directly influence action, via interconnections with the frontal lobes, can directly contribute to consciousness.

A number of other proposals offer variations on the themes of these two theories, some emphasizing the importance of particular brain regions, others the importance of particular processes, generally defined in broad psychologic terms. Thus, arguing on the basis of evidence from experimental and clinical neuropsychology, David Milner (1995) has proposed that the “dorsal/where” stream of visual processing is dedicated to the “online” control of visually guided behavior, while the “ventral/what” stream is responsible for the creation of our conscious visual world. Three other distinguished contributors to the field have suggested versions of the principle, mooted by both Edelman and Crick, that consciousness is conferred on otherwise unconscious neural processes by virtue of some further interactive process – of “commentary,” “comparison,” or “remapping.” These theories thus describe the emergence of a “core self” from an unconscious “protoself” (Panksepp and Northoff, 2009). Larry Weiskrantz (1997) has argued that what is missing in both blindsight and in the amnesic syndrome is “the ability to render a parallel acknowledged commentary” on activities – sensorimotor control, procedural memory – that the subject can in fact still perform. Weiskrantz helpfully draws a distinction between two views of the “commentary stage”: that it merely enables the acknowledgment of consciousness which is itself somehow achieved by other means, and that making the commentary actually endows us with consciousness: “it is what is meant by being aware and what gives rise to it.” Weiskrantz favors the second, more radical view, and draws attention to the parallel between this proposal and the ideas of the philosopher David Rosenthal (1986), the originator of “higher-order thought” theories of consciousness. Jeffrey Gray (1998) makes the analogous suggestion that awareness arises from a “second pass” in which the unconscious data provided by sensory processes are compared with expectations generated by past experience and current intentions. In a similar vein, Antonio Damasio proposes that awareness occurs when the brain represents the effects of sensory events on the organism by a process of “second-order mapping” (Damasio, 1994, 2000, 2010). In other words, mere sensation is insufficient for awareness: it must first be transformed by a process that makes explicit the impact of the knowledge on the knower. Weiskrantz implicates frontolimbic areas in the commentary stage, Jeffrey Gray locates the critical

comparison in his theory to limbic regions of the temporal lobes and the basal ganglia, while Damasio locates the neural representation of the self in the upper brainstem, thalamus, deep forebrain nuclei, and somatosensory cortex. Recently Critchley and Seth have proposed that subjective feeling states are the result of updating of visceral, motor, and autonomic input through a salience network and the feedback that is generated by predicted feeling states. Von Economo neurons in the anterior insula are postulated to play an important role in accessing this interoceptive information (see [Critchley and Seth \(2012\)](#) for model).

Along related lines, [Baars et al. \(2003\)](#) have recently drawn together the threads from studies of the conscious resting state, sleep, coma, anesthesia, and disorders of consciousness ([Fig. 31.14](#)) to identify a network of frontoparietal regions with an especially close relationship to consciousness: activity in these regions is tonically high in the resting conscious state, and selectively depressed

in all four states of unconsciousness. These authors propose that these brain regions subserve “self systems” in the brain: when they are damaged or deactivated the “observing subject” is no longer available to respond to the “objects of consciousness” within the brain. They provide the neuronal home to the “global workspace” envisaged by the information-processing theories described in the following section.

The theories discussed so far emphasize the anatomic organization of the brain networks and the nature of the psychologic processes involved in consciousness. The notion that a certain kind of distributed neuronal activity may be crucial has also been raised. The most popular current candidate for a key role in the physiology of consciousness is neural activity synchronized in the gamma frequency range of 35–45 Hz. There is evidence to suggest a role for coherent gamma-band activity in arousal, sensory segmentation, selective attention, working memory, and in aspects of “higher-order consciousness,”

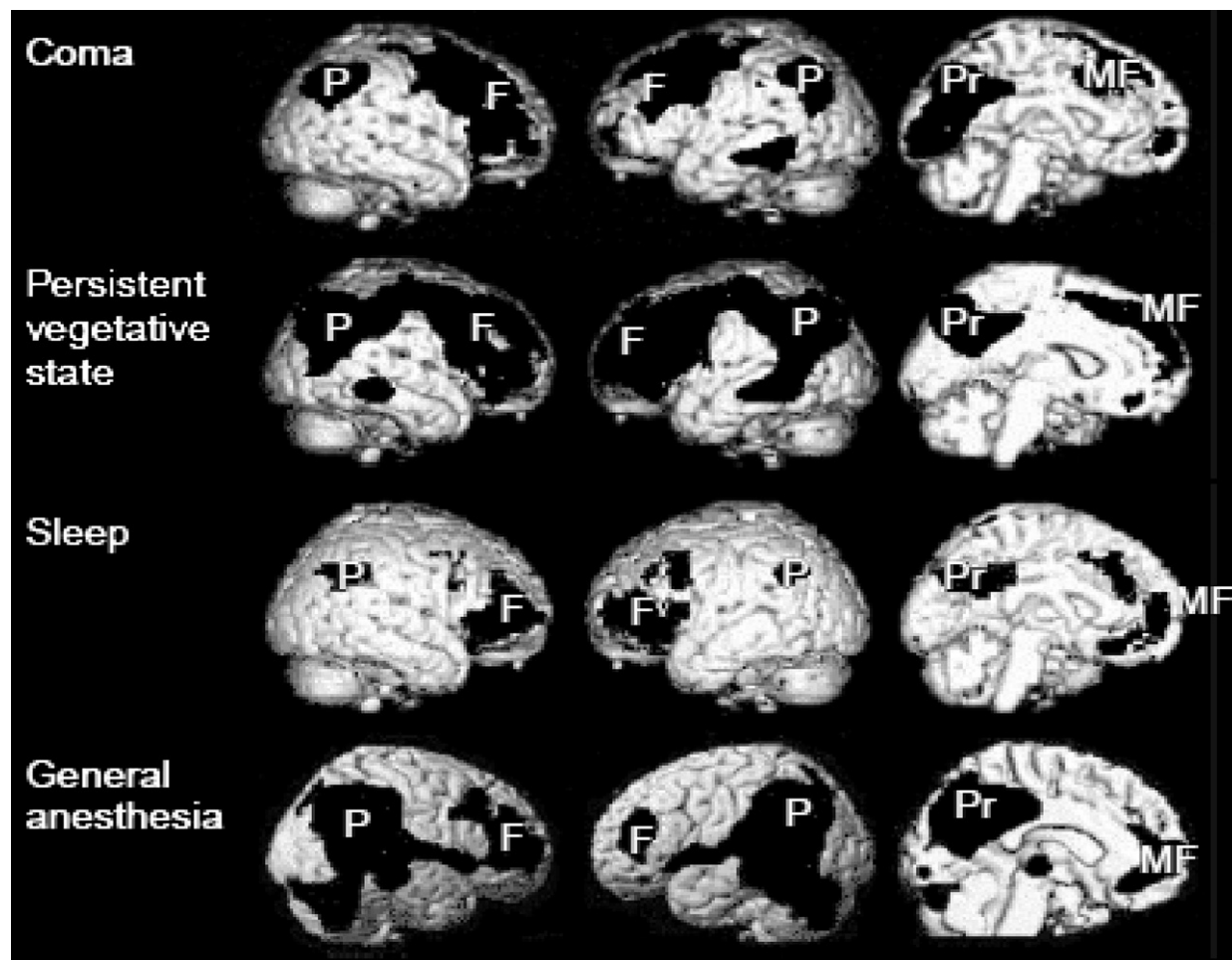


Fig. 31.14. The anatomy of the global workspace: a set of lateral frontal (F), parietal (P), and medial frontal (MF) regions, together with the precuneus (Pr), which shows depressed activity in a range of states of diminished awareness may provide the anatomic basis for the “global workspace.” (Reproduced from [Baars et al., 2003](#).)

motivation, action planning, and symbolic processing (Engel et al., 1999).

These theories are already diverse, although united by many common themes and principles. It would be misleading to fail to mention that the field has its share of intriguing outliers. For example, while most theories emphasize the importance of interaction between brain regions and psychologic processes in the genesis of consciousness, Zeki has proposed that individual visual areas may be associated with individual “microconsciousnesses” (Zeki and Bartels, 1998); Victor Lamme (2006) has proposed that recurrent processing within sensory areas may be of critical importance for the occurrence of consciousness. While most of these theories work within the boundaries of standard neuroscience, Roy John (2005) has suggested that mechanisms akin to those discussed throughout this section give rise to a “resonating electrotonic field” that is the proximal physical substrate for awareness. Finally, quantum theorists of consciousness have argued that we need to appeal to the basic physical features of the subatomic constituents of the brain to understand how it gives rise to awareness (Penrose, 1994). These theories provide a reminder that the current scientific consensus on the mechanisms of consciousness is far from universal: it remains possible that its explanation will require novel departures in scientific theory.

Cognitive/information-processing approaches

What is consciousness for? Almost all theories assume that consciousness plays a role in the control of behavior, specifically in circumstances that involve novel challenges or unpredictable events to which we need to devote a substantial part of our psychologic resources. In such circumstances instinctual or automatic behaviors may be inadequate: the capacities to select and acquire appropriate responses, from a wide and adaptable repertoire, often on the basis of fine perceptual distinctions, will be advantageous. Functional theories propose that consciousness is bound up with these capacities, linking the evolution of awareness to the emergence of flexible patterns of learned behavior from more rigid instinctive patterns of response as the “synaptic bridge” that links sensation to action gradually lengthened in the course of cerebral evolution. These are, broadly, “integrative” theories of consciousness.

The most widely endorsed suggestion, made in Baars’ (2002) and Dehaene’s and Naccache (2003) closely related “global workspace,” or “global neuronal workspace” (Dehaene and Changeux, 2011) theories, is that consciousness is the expression of a mode of brain processing that allows information of crucial current

importance to be broadcast widely through the brain, harnessing the activities of a wide range of potentially independent processors to the task in hand. Thus when we are conscious of information we are in a position to report on it by a variety of means, to use it to guide action of other kinds and to memorize it. In switching from an unconscious to a conscious mode of processing we trade automaticity, speed, and high-capacity parallel processing for flexibility of response under relatively slow, serial control. Theories of this kind follow the lead of William James in associating consciousness with selective attention and “primary” or “working” memory: attention controls admission to the global workspace where information, once admitted, commands working memory and gains access to resources distributed throughout the brain. Whether a clear distinction can really be drawn between the two modes of information processing in the brain envisaged by these theories will be a key question for consciousness research over the coming years.

Social theories

The theories outlined so far have focused on brain anatomy and physiology, psychologic processes within the individual brain and computation algorithms. But there are several reasons for suggesting that consciousness has an important social dimension. First, we have seen that the Latin root of “consciousness” referred, originally, to knowledge shared with another. Second, the sharing of knowledge with oneself, in awareness, and the sharing of knowledge with others, in social exchanges, may be interconnected: there is a theoretic argument and empiric evidence that awareness of self and awareness of others are acquired in parallel (Strawson, 1974; Parker et al., 1994). Third, language is a vital contributor to human awareness, and language, clearly, is a social phenomenon. Proponents of social theories sometimes claim that the social dimension of consciousness explains the bafflement we tend to feel when we try to explain how the brain can generate experience: on these views experience is as much a social construction as a biologic and psychologic phenomenon (Rose, 1998; Singer, 1998).

Humphrey (1978) provided a lucid example of theories which propose a social function for awareness. He suggested that the purpose of consciousness is to allow social animals to model each other’s behavior on the basis of their insight into its psychologic motivation. In other words, our knowledge of our own mental states supplies us with insight into the mental states underlying the actions of others; the ability to predict these actions is a major determinant of our biologic success. More recently, such knowledge has been described in terms

of the possession of theory of mind: some social theories broadly associate this with consciousness. The identification of mirror neurons – cells that are activated by performing actions oneself and by watching others perform the same actions – provides one potential mechanism for the rapid identification of the mental states of others.

There is no doubt that a comprehensive theory of consciousness needs to take account of its social dimension. But most commentators agree that this is the wrong level of explanation for the simpler forms of consciousness, providing an avenue by which to understand varieties of self-awareness or “higher-order consciousness” rather than addressing the more basic phenomenon of perceptual awareness.

A theory of theories?

The reader may be wearying, by this stage, of the variety of proposals on offer, and eager for a satisfying synthesis. Unfortunately, it is early days in the science of consciousness, and there is no clear consensus view. It may be worth trying to encapsulate the common ground between the majority of models we have mentioned in a few lines. Admittedly vague, such a summary would run somewhat as follows: awareness, as defined at the start of this chapter, requires an appropriate background of brain activation by the nonspecific brainstem and diencephalic activating systems that set the state of consciousness. This must be linked to moderately prolonged, moderately high-intensity, locally differentiated yet well-synchronized and widely integrated activity in a transient neocortical cell assembly interconnecting sensory, limbic, and executive regions in insular, parietal, temporal, and frontal regions. Activity within the widespread resulting cortical–subcortical cell assembly facilitates the flexible selection (and acquisition) of appropriate responses, from a varied and adaptable repertoire, sometimes on the basis of fine perceptual distinctions. These responses include the various forms of self-report. Through these processes “knowledge that is in the network” becomes “knowledge for the network” (Cleeremans, 2005). To be undergoing brain activity of these kinds, potentially enabling these highly flexible forms of interaction with the environment is, most contemporary theories suggest, to be conscious.

THE PHILOSOPHY OF CONSCIOUSNESS

Anyone reviewing the discoveries of the past century that bear on the brain mechanisms of wakefulness and awareness would surely conclude that we have learnt a great deal about consciousness. But many observers are left with the sense that there remains an “explanatory gap” between the findings of brain science and the phenomenon of consciousness. Why should these

wonderfully elaborate, yet entirely physical, neural processes give rise to the qualities of experience at all? Husserl expressed this sense of puzzlement powerfully: “Between consciousness and reality there yawns a veritable abyss of meaning” (Id 1, 93, in Carman, 1999). More specifically, why should particular subsets of brain activity give rise to particular experiences, like those of smell and taste, seeing, hearing, and touching? Brain science, David Chalmers has argued, is poised to answer the “easy,” mechanistic, problems of consciousness, but the philosophically “hard” problem remains (Chalmers, 1996). Even once we have achieved a comprehensive understanding of the inner workings and outward behavior of an organism, it seems that we can always ask these further questions: is it conscious, and, if so, what is its experience like? A solution to the “hard problem” must render transparent the opaque relationship between observable events and felt experiences.

In this final section we shall introduce the standard philosophic approaches to understanding the relationship between mind and brain in terms of three strong, widely shared, intuitions about consciousness. We shall close by suggesting, as others have done, that to solve the problem of consciousness we may need to refashion our concept of awareness and to broaden the boundaries of explanation.

Three intuitions about consciousness

We focus on western philosophic approaches. We note that in eastern (Indian) philosophy, in contrast to the western tradition, mind and consciousness are distinguished: while the mind is physical and characterized by a link to intention and the contingent reality of sensation, consciousness is nonphysical, and reflects the irreducibly cognitive aspect of the universe (Rao, 1998, 2005). Three central intuitions recur repeatedly in western philosophic discussions of consciousness (Zeman, 2001, 2002). Philosophic accounts of consciousness can be helpfully judged against them.

The first intuition is that consciousness, in the sense of awareness or experience, is a robust phenomenon, rich and real, that deserves to be explained by science and not “explained away.” Sensory experiences, for example, like those of color, sound, or pain, the simplest and most vivid instances of awareness, are phenomena that any full description of the universe must take seriously. Indeed, experiences of this kind are arguably our point of departure in gaining knowledge of the world. Consciousness, in this sense, is “the sea in which we swim” (Velmans, 2000). Almost everyone interested in the science and philosophy of consciousness would agree on these points in principle: but, of course, there is

scope for plentiful disagreement about what is meant by the “reality” of awareness.

The second intuition is that consciousness is bound up with our physical being. Everyone knows that fatigue, alcohol, knocks on the head, and countless other physical events can modify the state and contents of consciousness. The survey of the neurobiology of consciousness given above reinforces this prescientific view: consciousness is firmly rooted in the brain, and the structure of experience appears to be mirrored by the structure of neural processes. It has become reasonable to suppose that every distinction drawn in experience will be reflected in a distinctive pattern of neural activity.

The third intuition is that consciousness makes a difference to our behavior. It seems self-evident that much of our behavior is explained by mental events. If we could not see, or hear, or touch, if we could not experience pain or pleasure, if we lacked conscious desires and intentions, we would not and could not behave as we do. If this is true, it is natural to suppose that consciousness is a biologic capacity that evolved in the service of action.

The fact that these three intuitions are “natural” and widely shared does not guarantee that they are true. But they help to identify the main points of disagreement between the contending theories of consciousness in the philosophy of mind – and to explain our reactions to them. We shall focus on three of these approaches: the view that conscious and neural events are closely correlated but fundamentally distinct classes of phenomena; the view that underlying neural events are identical with the corresponding conscious experiences; and the view that experiences are best understood in terms of the functions served by neural events.

Philosophic approaches

DUALISM

Dualism, the view that there are separate classes of mental and physical entities, processes or properties, is deeply entrenched in our vocabulary, our thinking, and our institutions. In medicine, for example, we often find ourselves sorting disorders into “organic” and “psycho-genic” categories, a distinction that assumes, against all the evidence, that the “psyche” is inorganic (White et al., 2012). We then use the results to divide medical labor between those who care for bodies – physicians – and those who care for minds – psychiatrists. The dichotomy between mind and brain is reinforced by traditional physical separation of these two medical specialisms.

René Descartes (1976) is usually identified as the chief historic representative of philosophic dualism. In the *Discourse on the Method*, published in 1637, he argued that, while it was possible to be mistaken about all other beliefs, it was not possible for him to be

mistaken in his belief that he was a “thinking thing.” This inference seems reasonably secure. He went on to conclude, much more questionably, that “I [am] a substance of which the whole essence and nature consists in thinking, and which, in order to exist, needs no place and depends on no material thing.” Thus Descartes drew a radical distinction between immaterial “thinking things,” minds, and “extended things,” physical objects, surely a much less secure conclusion.

Contemporary dualists have replaced Descartes’ “supernatural substance dualism” with the naturalistic view that mental attributes are a special, but natural, class of properties of physical things, namely organisms. In David Chalmers’ (1996) version, for example, conscious events are distinct from, but closely related to, neural events, to which they are yoked by fundamental “psycho-physical laws.” In Chalmers’ vocabulary, a sophisticated computer, capable of reporting and acting on information sensed in its surroundings, would be “aware*,” that is to say, in a physical state analogous to the state of the human brain during conscious experience, but not necessarily “aware” in the crucial, experiential, sense: this latter, subjective, form of awareness would only follow if additional psychophysical laws linked the computer’s physical state to experiences like ours. The philosopher Ned Block has developed a distinction similar to Chalmers’ distinction between “awareness*” and “awareness,” using the terms “access consciousness” and “phenomenal consciousness” (Young and Block, 1996).

Theories like these certainly respect our first intuition, taking consciousness seriously. Chalmers’ theory also does justice to the second intuition, by granting that mental events are causally dependent on their neural substrate. But they fall foul of the third intuition, as there seems to be no scope for the nonphysical properties of conscious events to make a difference to the physical trajectory of behavior.

MIND–BRAIN IDENTITY THEORY

The suggestion that conscious events are identical to corresponding neural events offers a reductionist, physicalistic solution to the mind–body problem. It was proposed by Lucretius in the ancient world and Thomas Hobbes in the 17th century. Other recent examples of reductive explanations have reinvigorated materialistic theories of the mind. Often-cited instances include the reduction of heat to the kinetic energy of atoms, the explanation of light in terms of electromagnetic radiation, and perhaps of deeper relevance to consciousness, the analysis of “life” as the property possessed by complex, highly integrated, physical systems that are able to utilize energy from their surroundings to sustain and reproduce themselves. Why should consciousness be an exception to the

stream of successful reductions of phenomena once considered, like life, to be beyond the reach of science?

Some well-known philosophic thought experiments suggest that it might indeed be an exception. Current physical theory teaches that light, as a physical entity, is nothing more than a certain type of radiation. To know everything about such radiation would be to know everything about light. But it is not clear that if we knew everything about the physicochemic properties of an organism we would thereby know everything about its experience. For example, how far can science take us towards an appreciation of the subjective experience of an animal equipped with a sense we lack, like the echolocatory sense of bats and dolphins (Nagel, 1979)? Or, to come closer to home, could a blind student of the visual system ever gain the knowledge, that the sighted naturally possess, of “what it is like to see” (Jackson, 1982)? Some philosophers have taken these examples to show that conscious experience has subjective properties that are not fully specified by, and cannot be reduced to, the neural structures and processes on which they depend.

In terms of our three intuitions, mind–brain identity theories, with their claim that conscious events “simply are” brain events, do justice to the physical basis of experience and allow for its functional role. But they fail to satisfy the first intuition, that the properties of experience are robust phenomena in need of explanation. In John Searle’s (1992) uncompromising words: “the deeper objection [to physicalism] can be put quite simply: the theory has left out the mind.”

FUNCTIONALISM

Dualism is rooted in the intuition that awareness is “rich and real,” a phenomenon that goes beyond its physical substrate. Identity theory is rooted in the intuition that awareness is intimately bound up with events in the brain. Functionalism is most closely related to our third intuition: that consciousness makes a difference to our lives. Indeed, this theory might be caricatured as the view that consciousness does not just make a difference to our lives: it is that difference. In other words the essence of awareness lies in the functions that it serves, the transformations of input into output with which it is associated.

This approach owes much to the developing science of artificial intelligence. Daniel Dennett (1991) has emphasized the analogy between the activity of the brain, and the awareness associated with it, with the implementation of a software package in a computer to create a “virtual machine”: “human consciousness . . . can best be understood as the operation of a . . . virtual machine . . . in the parallel architecture of a brain.” Taking vision as an example, functionalism suggests that visual experience

consists in the countless acts of discrimination and classification that sight permits, and in their consequences for the rest of our mental life: functionalism reinterprets our experience in terms of a series of acts of judgment.

This approach has many attractions. Like identity theory, it finds a place for consciousness in the natural world. It accounts for – indeed it originates with – our conviction that consciousness has effects. It escapes the superficiality of its intellectual predecessor, behaviorism, by taking seriously what goes on within our heads. It allows for the occurrence of consciousness in other organisms or machines that perform the same cognitive computations as we do.

But, at least at first sight, functionalism appears to be vulnerable to the same fundamental objection as identity theory: that it fails to account for the qualitative properties of consciousness. We seem to be able to ask of a virtual machine, just as we can of a neural assembly, why should it be conscious at all, and, if it is conscious, why should its consciousness be like this?

The debate between proponents of these three broad theories – identity theory, dualism, functionalism – continues. For the time being there is no alternative but to continue to use all three vocabularies of experience, biology, and behavior in our efforts to understand the mind.

Broadening the explanatory horizon

Describing the process by which mechanistic models replaced animistic ones to become the standard approach to biologic explanation, the historian of medicine, Charles Singer (1928), wrote: “The course of physiological advance may be described, briefly, as the expulsion of the mental element from process after process associated with vital activity.” This advance was of course highly successful. But as our mental lives are a crucial aspect of our biology, the process of expulsion eventually had to stop. The current fascination with consciousness reflects the mounting intellectual pressure to explain how “vital activity” in the brain generates a mental element with rich subjective content (for a review, see Zeman, 2012). As Merleau-Ponty (1964) wrote, “the distinction between subject and object is blurred in my body.”

This explanation may require a rethinking of what we mean by “the mental,” that is, of what we are seeking to explain, as well as a reassessment of the role played by the brain. The traditional quest has been for a brain mechanism, or set of mechanisms, that will account for the occurrence of experience much as Descartes conceived it – an essentially private, invisible, and immaterial process. Both this conceptualization of experience and the exclusive emphasis on the brain have been called into question.

With regard to the brain, while its activity clearly plays a key role in the genesis of experience, it is only part of the story. The mind is typically embodied, embedded, and extended: that is to say, typical episodes of experience involve interactions between the brain and the body that contains it; depend upon a long history of individual development, conditioned powerfully, in the case of human consciousness, by cultural inheritance; and are played out in a physical environment, through a process that is extended in both time and space. The brain is highly relevant to the study of consciousness, but we probably need to look beyond it if we are to give a full explanation of awareness.

On the second count, we should not assume that the target of our explanation is the kind of immaterial function envisaged by René Descartes. After all, we determine whether others are conscious by interacting with them, or simply watching them: 10 seconds spent scrutinizing an expert mountaineer ascend a cliff would leave little doubt about his consciousness. Instead of regarding consciousness as a mysterious emanation from the brain, perhaps we should think of it as the exercise of a capacity for sophisticated forms of interaction with the world, enabled by the brain. This is broadly the approach taken by O'Regan, Noe, and others, who have argued that sensation is not "generated" by the neural processes but consists in the real or virtual exercise of exploratory skills (O'Regan and Noe, 2001; Noe, 2004).

Whether this challenging approach will succeed in bridging or dispelling the "explanatory gap" between the mind and brain remains to be seen. It is certain, however, that the study of consciousness, one of the major challenges for human understanding, has entered an immensely exciting phase.

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