



Review

The role of primordial emotions in the evolutionary origin of consciousness

D.A. Denton^{a,b,*}, M.J. McKinley^c, M. Farrell^c, G.F. Egan^c^a Office of the Dean, Faculty of Medicine, Dentistry & Health Sciences, University of Melbourne, Parkville, Vic. 3010, Australia^b Baker Heart Research Institute, 75 Commercial Road, Melbourne 3004, Australia^c Howard Florey Institute of Experimental Physiology & Medicine, University of Melbourne, 3010, Australia

ARTICLE INFO

Article history:

Received 13 March 2008

Available online 12 August 2008

Keywords:

Emotion

Evolution

Consciousness

ABSTRACT

Primordial emotions are the subjective element of the instincts which are the genetically programmed behaviour patterns which contrive homeostasis. They include thirst, hunger for air, hunger for food, pain and hunger for specific minerals etc.

There are two constituents of a primordial emotion—the specific sensation which when severe may be imperious, and the compelling intention for gratification by a consummatory act. They may dominate the stream of consciousness, and can have plenipotentiary power over behaviour.

It is hypothesized that early in animal evolution complex reflex mechanisms in the basal brain subserving homeostatic responses, in concert with elements of the reticular activating system subserving arousal, melded functionally with regions embodied in the progressive rostral development of the telencephalon. This included the emergent limbic and paralimbic areas, and the insula. This phylogenetically ancient organization subserved the origin of consciousness as the primordial emotion, which signalled that the organisms existence was immediately threatened. Neuroimaging confirms major activations in regions of the basal brain during primordial emotions in humans. The behaviour of decorticate humans and animals is discussed in relation to the possible existence of primitive awareness.

Neuroimaging of the primordial emotions reveals that rapid gratification of intention by a consummatory act such as ingestion causes precipitate decline of both the initiating sensation and the intention. There is contemporaneous rapid disappearance of particular regions of brain activation which suggests they may be part of the jointly sufficient and severally necessary activations and deactivations which correlate with consciousness [Crick, F. & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6, 119–126].

© 2008 Elsevier Inc. All rights reserved.

1. Emotions—the subjective elements of instinct

Emotions are a mystery. Introspectively, persons are aware that an emotion can surge up and have totalitarian occupancy of the stream of consciousness. It may be intense enough to submerge any coherent will, or rationality hitherto operative.

Emotion is inexorably bound to instinct. The great Harvard psychologist, James (1918), stated “In speaking of instincts, it has been impossible to keep them separate from the emotional excitements which go with them. . . They shade imperceptively into each other”.

* Corresponding author. Address: Office of the Dean, Faculty of Medicine, Dentistry & Health Sciences, University of Melbourne, Parkville, Vic. 3010, Australia. Fax: +61 3 9347 0846.

E-mail address: eirap@unimelb.edu.au (D.A. Denton).

A pivotal view of this paper is that the primordial emotions are the subjective element of the instinctive behavioural patterns.

In terms of the difficulty in defining emotion, there are over 90 definitions in the literature, ranging over views of Watson, Jung, Freud, Darwin, Delgado, McDougall and others, representing several disciplines (see Denton 2006; Kleinginna & Kleinginna, 1981). If the word “emotion” was represented by a pyramid, then at the base are the primitive or primordial emotions, in the middle the distance receptor evoked emotions such as anger, hate, fear, love, and at the apex are the emotions such as experienced with the aesthetic delight of great art or music.

Concerning the definition of emotion, the shorter Oxford English Dictionary, inter alia, defines it as “A disturbance of the mind, mental sensation or state, or instinctive feeling”. Their definition includes emotion arising from bodily states. Webster’s International Dictionary notes the origin of the word from medieval French “*Mouvoir*” and the sense of move out or move away, and, inter alia, defines it as a “*physiological departure from homeostasis which is subjectively experienced in strong feeling. . . and bodily changes preparatory to overt acts which may or may not be performed*”. The element of intention and movement is incorporated in the word as inherent in its derivation from medieval French.

The primordial emotions include thirst, hunger for air, hunger for food, pain, hunger for specific minerals, sexual arousal and orgasm, sensations accompanying impediment of visceral function, as, for example, micturition or defecation, desire for sleep after severe deprivation, and avoidance of change of body core temperatures etc. (Denton, 2006). These subjective elements of instincts subserve the vegetative systems. They are genetically programmed and guard the physico-chemical constancy of the internal environment of the body—the homeostatic process. Obviously, this constancy is guarded also by hormonal systems which retain or excrete body substances in apt fashion. But over and above excretory control, and of paramount importance, the constancy also is guarded by the systems which contrive the imperious sensations, and thereupon the desire and intention to seek materials of which the body is depleted, such as water, salts, air or food. Those involved in ingestive behaviour do it in a manner which is quantitatively appropriate for the deviation in the body physico-chemical status—a spectacular instance of complex genetic programming (Denton, 1983).

These primordial emotions are in most cases driven by sensors detecting deviation from normal within the body—the interoceptors (Denton et al., 1999a). A thesis we have advanced is that the primordial emotions have emerged as consciousness during evolution because they are apt for the survival of the organism (Denton, 2006; Denton, McKinley, & Weisinger, 1996; Denton et al., 1999a). Whereas they may be perceived often as a mild intrusion into consciousness, they can reach intensity which gives total occupancy of the stream of consciousness and plenipotentiary power over behaviour.

As stated the biological organization of a primordial emotion has two components—an imperious specific sensation and the compelling intention. The intention, like the primordial emotion, is specific. The genetic organization determines that severe thirst is generative of a powerful intention to drink—not to eat or copulate. Thus, for example, with suffocation, there is a “hunger for air” sensation which Banzett and colleagues of Harvard (1990) have described as “You feel you’re going to die”, and a compelling intention to fight for breath. Neuroimaging shows the concurrent air hunger and hypercapnia to evoke powerful activation in phylogenetically ancient areas of the brain (Brannan et al., 2001; Corfield et al., 1995).

The primordial emotions contrast with another class of emotions which are most often fired by the distance receptors (exteroceptors)—the eyes, ears and the nose. These distance receptor evoked emotions, like rage, fear, hate, envy, happiness, playfulness, affection, anxiety, depression and disgust, are those to which the term emotion is most commonly applied. They are very often determined by situational perception. That is, the outcome of interaction with a conspecific, or reaction to another species, such as, for example, a predator or a snake. Like the primordial emotions, substantial elements of their organization are hardwired as witness, for example, Hess’s experiments (1964) where electrical stimulation of the cat hypothalamus can cause rage, hissing, spitting and attack. Similarly, a strong sense of fear and apprehension or fearful behaviour is evoked in humans and lower mammals by stimulation of the amygdala (LeDoux, 1998). The neuroimaging of such emotions by Damasio and colleagues (2000) shows these distance receptor evoked emotions also set in train strong activations in the evolutionary ancient areas of the brain. However, it is obvious that any classification which is made within the diverse types of emotion is to an extent arbitrary (Damasio 2000, 2006).

2. The survival value of the emergence of consciousness

Emotions, being intrinsically subjective, are a major element of conscious processes. Consciousness being the zenith of brain evolution and function, has emerged in evolution because its advent gave high survival advantage. It has been honed on the anvil of natural selection. For an animal to be able to form images in the mind, and to choose an apt option for action in the light of appraisal of an immediate situation, including in many instances its memory of previous experiences, has great advantage. This may be a much better determinant of action than acting reflexly with higher probability of being killed. The surviving animal may pass on its particular genetic structure which coded for the neural organization which subserved development of the propensity for conscious perception and analysis of situations.

Accordingly, the primordial emotions are postulated as the evolutionary beginning of consciousness. They often signal that the very existence of the organism is threatened (Denton, 2006; Denton et al., 1996).

In terms of the evolution of the neuroanatomical development which underpins consciousness, it is proposed that complex reflex mechanisms organized within the rhombencephalon, mesencephalon and diencephalon which subserved responses to deviation from steady state in the milieu interieur were elaborated phylogenetically when rostral growth of

the brain occurred. The development of the telencephalon embodied allocortex (3 celled layers), transitional cortex (5 celled layers) and early isocortex (6 celled layers), and involved structures including anterior and posterior cingulate gyri, insula, parahippocampus and hippocampus, pyriform lobe, together with elaboration of the thalamus, probably zona incerta (Merker, 2007) and the development of reticulo-thalamo-cortical connections. Putatively they provided the early substrate for functions underpinning conscious awareness.

The behavioural developments coherent with earliest consciousness eventually allowed the exercise of options based sometimes on rudimentary memory of past events. For example, intention when directed not at an immediate goal within the animal's sensory perception, but towards a goal not present, involves a plan (Young, 1986). Planned behaviour is consonant with Longuet-Higgins' view (see Kenny, Longuet-Higgins, Lucas, & Waddington, 1973) that an animal having a goal, and carrying out a plan to achieve it, bespeaks it having a mind. A classic example would be an animal desiccating in the heat and seeking out a distant source of water, the place of which it remembered from previous experience of drinking, or having seen it in the course of travel.

3. Edelman and Tononi's theory of the origin of consciousness

The issue of the first dawning of consciousness—"primary consciousness" has been discussed by Gerald Edelman in several of his books (Edelman, 1992; Edelman & Tononi, 2000). Panksepp (1998) has also made an important proposal. Both proposals differ from the one advanced by the authors in this article.

The nub of Edelman's theory is that primary consciousness emerged with the capacity of an animal's brain to "create a scene". That is, it is essentially an exteroceptor or distance receptor theory.

Thus, primary consciousness is experienced as a picture or mental image of ongoing categorized events which are distance receptor generated, i.e. the events are outside the organisms integument, and are detected by eyes and visual processes, ears and hearing, or the nose and smell.

The central element in creating a scene is the process of perceptual categorization. That is, the multitude of signals coming from the exterior simultaneously which might have no causal or particular connection to one another, are carved up into signals useful for a particular species. Perception involves discrimination of an object and event by one or more sensory modalities and separation of it from background inflow: it is picked out.

Categorization embraces the treating of non-identical inflow as equivalent, and an individual generalizes on the basis of category the action which it will take. Edelman and Tononi (2000) have added to this idea of perceptual categorization the notion of "concept", whereby different perceptual categorizations are combined to give a universal. Some common features are abstracted. This line of reasoning is illustrated by considering the extremely interesting experiments of Herrnstein and colleagues (1964) on pigeons. The birds are hungry and learn to peck at a coloured slide picture that included a human in order to cause opening of a food hopper. Pigeons can pick out from dozens of photographs those with a human figure in them. This is notwithstanding that they are full face, side face, an infant or elderly, naked or clothed, with back to camera, under a tree, and numerous other situations. If it pecks at a picture with a human in it, food is delivered, whereas if there is no human it does not get food. The bird gets it right about 80% of the time. Herrnstein, Loveland, and Cable (1976) proposed the animals form a broad and, indeed, complex concept. Remarkable behaviours bespeaking consciousness in birds are reviewed in their neuroanatomical context by Butler and colleagues (2005).

A most intriguing body of data on the behaviour of the New Caledonian crow involves their preparation of tools by their cutting of pandanus palm leaves in order to extract insects from plants (Hunt, 1996; Hunt, 2000).

Weir, Chappell, and Kacelnik (2002) have elaborated the studies by making experiments on the birds at Oxford University. Experimentally, food is placed in a small bucket with a handle, and the bucket is placed at the bottom of an upright transparent plastic tube. Contemporaneously a piece of straight wire is left in the cage. The crow will take the wire and promptly feed the end into a cleft, and bend it into a hook and holding it in its beak use it to lift the food containing bucket out of the plastic tube. The wire bending is the preparation of an object for an imagined eventuality, akin to Aristotle's definition of the artist, as Kenneth Oakley (1954) of the British Museum stated in his definition of man the toolmaker.

Edelman and Tononi (2000) have suggested that at a time in evolution roughly corresponding to the transition from reptiles to mammals, and from reptiles to birds, a major new anatomical connectivity emerged mediating re-entry. It dynamically linked posterior areas of the brain involved in perceptual categorization with anterior areas responsible for value based memory. These cortico-cortical fibres contrived the building of a remembered present—a scene that adaptively links immediate contingencies to the animal's previous history of value driven behaviour—of rewards and punishments. Specific connections of the cortex to thalamus, including to the intralaminar and reticular nuclei developed, and, correspondingly, thalamic nuclei such as the intralaminar send diffuse projections to many areas of the cerebral cortex.

Edelman (1998) suggests an animal having primary consciousness alone can evoke a mental image or scene. It is based on immediate multimodal perceptual categorization in real time as dictated by a sequence of real events in the environment. He proposes such an animal has biological individuality but no concept of self. Whereas, it has a remembered present, it has no concept of past or future.

Edelman sees perceptual categorization, along with control of movement, as the most fundamental process of the vertebrate nervous system. The synthesis of contemporary neuroanatomical and neurophysiological knowledge in his books is a cogent and imaginative exercise embodying fundamental features of emergent functions of the brains of early vertebrates. In

contrast to the primordial emotion theory, it represents an above-down neural integration of inflow from the external world with all the implications in relation to survival. By contrast, the notion of the primordial emotions being the first genesis of awareness is a below-upwards concept when the immediate existence of the organism is in play.

Grossman (1980) has stated. . . “whereas...the anterior thalamic and also mesencephalic and pontine brainstem are necessary for consciousness, they are probably not sufficient. Interaction of these rather small masses of neurones with, at least, a certain volume of limbic or neocortex must occur”.

The issue of how much cortical function, if any, is necessary for consciousness of the primordial emotions is focussed by the issue of the behaviour exhibited by hydranencephalics. Data on this issue has been examined by Shewmon and colleagues (1999) and by Merker (2007).

Shewmon et al. (1999) studied four children with near total absence of cerebral cortex but who nevertheless, possessed discriminative awareness, being able to distinguish familiar from unfamiliar people and environments. They showed social interaction, functional vision, orienting and musical preferences, appropriate affective responses and associative learning. In two of these cases there was a thin remnant of temporo-occipital cortex though the tissue was reported as severely gliotic and optic radiations were absent. The authors expressed the opinion, citing parallel literature, that the children’s consciousness could be inferred to be mediated subcortically. This was not because they had absolutely zero cortical neurones, but because the few that were present could not plausibly subserve the totality of the conscious behaviour. The question is whether diencephalic and brainstem plasticity could subserve a measure of consciousness in congenitally decorticated children. The children exhibited situationally appropriate signs of pleasure or excitement indicating a coherent interaction between environmental stimuli, motivational–emotional mechanisms and bodily actions (Merker (2007)). The fact is that the human brainstem is specifically human, in that the children smile and laugh in a specifically human fashion which is different from our closest relatives among the apes. As Merker (2007) points out, Gamper (1926) account of the anencephalic girl entrusted to his care, showed that the specific human smile was occurring in circumstances where post mortem showed no neural tissue above the level of the thalamus and the thalamus itself was not functional. There is a coherence between Merker’s proposition that the primary function of consciousness vastly antedates the invention of neocortex by mammals and may, in fact, have an implementation in the upper brain stem, and the theory advanced here that primordial emotions, which are largely subserved by diencephalic, mesencephalic and medullary mechanisms, were the origin of primary consciousness.

Enquiries of parents and carers of these sadly compromised humans by Merker and Denton (unpublished) are examining the possibility that, though motor behaviour may be seriously compromised in some, they may exhibit discomfort and agitation if presentation of water or other fluid is not timely and is delayed. Further, there is abatement of the behaviour after gratification of the apparent need for water intake. In so far as it is suggestive that this is the case in some instances, evaluation of the implication will be assisted by the collection of accurate MR scan data to define how much cortical tissue, if any, is present, above the level of the thalamus. However, even if agitation is shown under circumstances where thirst would occur in the intact baby or child, it could be possible that the sensing of this state in the anterior wall of the third ventricle could excite the reticular activating system and initiate a general arousal-agitation effect without it necessarily being a consciousness of thirst. But, the demise of that state immediately after the specific act of drinking does, at least, raise the question of gratification of a consciousness of specific need since a significant amount of the water drunk would not be absorbed for some 10–15 min.

The basic unresolved questions with hydranencephalic humans are also directly relevant to consideration of the persistent vegetative state (PVS) Laureys, Perrin, and Brédart (2007), Laureys, Boly, and Maquet (2006), Owen et al. (2006), and Owen et al. (2007). This has been analysed by Panksepp, Fuchs, Garcia, and Lesiak (2007), and they raise important ethical issues. They state “recent neuroscientific evidence brings into question the conclusion that all aspects of consciousness are gone in patients who have descended into a persistent vegetative state (PVS)”. They raise the issue that “raw emotional feelings (primary process affects) can exist without any cognitive awareness of those feelings. Likewise, the basic brain mechanisms for thirst and hunger exist in brain regions typically not damaged by PVS”.

Also,

“If affective feelings can exist without cognitive awareness of those feelings, then it is possible that the instinctual emotional actions and pain ‘reflexes’ often exhibited by PVS patients may indicate some level of mentality remaining in PVS patients. Indeed, it is possible such raw affective feelings are intensified when PVS patients are removed from life-supports. They may still experience a variety of primary process affective states that could constitute forms of suffering. If so, withdrawal of life—support may violate the principle of nonmaleficence and be tantamount to inflicting inadvertent ‘cruel and unusual punishment’ on patients whose potential distress, during the process of dying, needs to be considered in ethical decision-making about how such individuals should be treated, especially when their lives are ended by termination of life-supports. Medical wisdom may dictate the use of more rapid pharmacological forms of euthanasia that minimize distress than the *de facto* euthanasia of life- support termination that may lead to excruciating feelings of pure thirst and other negative affective feelings in the absence of any reflective awareness”.

The observations of Bard and Rioch (1937) and others on surgically decorticate animals provides further evidence bearing on integrative capacities resident in diencephalon, mesencephalon, and the medulla. For example, Bard and Rioch describe a cat which was decorticated in two stages, and observed thereafter for over 2 years. Post mortem showed the neopallium was entirely removed except a small portion of the gyrus splenium posterior attached to a caudal margin of the gyrus hippocampus. The olfactory bulbs and stalks were present but the stalks were injured. There was injury to some parts of the striatum and subthalamus and dorsal thalamus. Observation of this animal showed it orientated to a source of sound. Furthermore,

correlated with the anatomical integrity of a large part of the central olfactory system there was a definite response to certain odours. There was a striking sniffing, licking and moving about with head close to the floor when an odoriferous food (e.g. fish) was placed nearby. After a hearty meal this behaviour could not be evoked, and it was most intense when food had been withheld for some time. There was no ability to locate the source of odour and unless food was placed directly in front of the animal it was reached only by chance. The drinking behaviour of the animal was not recorded. In all four cats in Bard and McRiogh's study nose and chop licking was very pronounced, indicating it is a function of the lower centres. It was discovered accidentally four weeks after the second decerebration that inserting a thermometer into the vagina induced loud growling, lowering of the chest and head, elevation of the pelvis and tail and treading movements of the hind legs. After removal of the stimulus, the cat executed vigorous squirming movements on her side and playfully rubbed her cheek and occiput against the floor. It was apparent she was exhibiting one phase of typical feline oestrus behaviour. She exhibited the same behaviour when exposed to a sexually aroused male cat. The locomotion of the animal was good though not quite normal, and the occurrence of walking could sometimes be related with either hunger or a distended bladder or rectum. The cat slept as a normal cat but it was necessary to use a strong stimulus to wake her. She then went through typical stretching movements occasionally accompanied by yawning and might extend her forelegs and claws and scratch the floor analogous to a cat sharpening its claws on a post or tree.

Overall, the data on four decerebrated cats studied from the viewpoint of their emotional responses and with record of entire or near entire neopallium excision indicated that ventral portions of the striatum and lower centres with which they are connected such as hypothalamus, subthalamus and reticular substance of the brain stem are capable of elaborate feeding reactions of a complicated type. The behaviour was most elaborate in the individual animal described above which had some basal olfactory areas preserved. The animals had a very low threshold for rage reaction evoked by tactile stimuli, and also exhibited fear reaction to loud noises. The integrity of a large amount of sexual behaviour when in oestrus was evident in one animal which retained a portion of the rhinencephalon. Partial deficiencies were seen in all animals with a depression of spontaneous activity. The animals also had a great decline in care of the body and fur which became matted. A general feature was that there was a complete loss of their individual "personality" as evident preoperatively, and the response to external stimuli which could be received became entirely stereotyped.

From the viewpoint of the thesis of this article, the data indicate that relatively complex emotional behaviour patterns in response to specific stimuli may remain intact in the absence of the neopallium, and with often considerable damage also to underlying structures such as the striatum and the thalamus.

Whereas there was no report of any intentional behaviour in seeking food, or fluid for that matter, it remains a challenge to consider whether some measure of specific subjective sensation was present.

4. Panksepp and Homer Smith's theory on origin of consciousness

In relation to the theory of the primordial emotions being the origin of consciousness, there is an alternative view of Panksepp (1998). He also places the evolutionary genesis of consciousness in the brainstem, but bases its origin in the primitive motor systems in this part of the brain. In overview he puts much emphasis on "split brain" studies to propose the essential centre of existence is subcortical. Despite the instances of the left hand opposing the action of the right in, for example, a patient pulling up trousers as described by Sperry (1974), in the main the split brain patient functions as a coordinated individual during processes such as riding a bike, playing the piano and swimming (Zaidel, 1994). It requires special experiments to reveal the profound difference of perceptual awareness of the hemispheres. Panksepp proposes that the primordial self schema was laid out first in stable motor coordinates within the brainstem—i.e. in the periventricular and surrounding areas of the midbrain and diencephalon which are connected with the limbic and paleocortical zones. He sees these primal motor areas as likely to be the primitive neural mechanisms which generate affective states of consciousness. The primordial motor circuits generate a fundamental sense of "self" within the brain, and this allows animals to develop into the intentional and volitional creatures that they are. He thinks it is easy to overlook this motor foundation of consciousness when we are focussed on the diverse forms of sensory-perceptual awareness.

This idea of Panksepp is closely allied to an earlier general proposal of Homer Smith (1959). Smith suggested that consciousness first developed when animals developed the capacity to go from here to there in the search for food.

Homer Smith reflects that all animals are dependent on plants or other animals for food. Animal evolution has presented a pageant of predator and prey—eat or be eaten. This was the issue of evolution of consciousness.

Therefore, the mobile predatory phenomenon required the successful animal to solve the Cartesian problem of moving bodies, and in four dimensions. Space and accurate timing was a *sine qua non*.

Panksepp suggests that movement leads to the ineffable feeling of experiencing oneself as an active agent in the events perceived in the world.

In relation to Panksepp's idea on the origin of consciousness, there is, relative to the one on primordial emotion, the issue of what comes first? The proposal of the primordial emotions as the generative phenomenon embodies the idea of both the imperious sensation and the compelling specific intention. The idea implicit is that the former (the sensation) is generally causal of the latter (the intention)—that is the motor events. Reflex mechanisms in the brainstem at early stages of phylogeny subserve response to disturbance of the *milieu interieur*, but no conscious sensation is involved in reflex motor response. For example, it is possible that drinking by fish in salt water is purely reflex without any conscious intention. But during

migration of vertebrates out of the rivers and swamps to dry land, the thirst sensation signalling that the body was desiccating was causal of both intention and the motor events of seeking water. It seems plausible phylogenetically that the emergence of conscious sensation initiated by interoceptors within the body caused the conscious volitional employment of motor systems to bring about conditions of gratification of the imperious mental state. That is, the awareness of sensory inflow was the selection pressure favouring complex reflex motor mechanisms of the mid and hind brain to evolve to volitional control of motor systems involving consciousness.

On the issue of precedence, it is clear that the initial subjective element and the motor elements of instinct are deeply entwined. However, it is noteworthy in higher animals that destruction of the periventricular grey, the ascending sensory reticular activating system and the posterior pontine system causes coma. However, in the horrendous “locked in” syndrome, a lesion in the anterior pontine area destroys all motor activity except the ability to raise the eyebrows. The patient however, remains fully conscious despite midbrain destruction giving nearly complete motor loss.

It is of great interest that Searle used the thirst process as a main issue for discussion in both his Reith Lectures (Searle, 1985) and his book on “Intentionality” (Searle, 1983). He remarked that actions characteristically consist of two components, a mental component and a physical component. If successful, the mental component causes the physical component. “This form of causation I call intentional causation, and it is an intention to do something. . . the mental energy which is identified as powering action is an energy that works by intentional causation.

Although it is outside the scope of this review to discuss it, Damasio (2000), Parvizi and Damasio (2001) have built an extensive theoretical construct concerning the organization of consciousness. The book embodies discussions of emotion, and also very considerable emphasis on a cardinal role of feelings in the conscious process. We have proposed feelings to be essentially the cognitive elaboration of emotion resulting in a cast of mind or a “context” as Baars puts it in his general analysis of the “global workspace”. In Denton (2006) certain views of Damasio are discussed. In particular the view that “emotion was probably set in evolution before the dawn of consciousness”, and also his view, as stated in his book, that “one may wonder about the relevance of discussing the biological role of emotions in a text devoted to the matter of consciousness”. We would be dubious of the idea of emotion separated from consciousness. The position taken here, to reiterate what was said earlier, is that the primordial emotions, the subjective component of the instinct, is the result of very powerful selection pressure, and has high survival value in signalling that the existence of the organism is threatened. As a subjective amalgam of the imperious sensations and the compelling intention it is highly likely that a powerful selection pressure would have favoured its phylogenetic emergence. This pivot of its biological relevance rests irrevocably on the fact that it is conscious, the imperious sensation being causative of compelling and apt intention to ameliorate or resolve the life threatening situation.

5. The neuroimaging of primordial emotions

Neuroimaging provides knowledge of those areas of the brain which become activated or deactivated contemporaneous with the subjective experience of a primordial emotion—the areas subserving the imperious sensation and compelling intention. Francis Crick (1994) has stated that—

“It seems probable that at any one moment some active neural process in your head correlates with consciousness, while others do not. What are the differences between them”?

The direct experimental approach is greatly facilitated by the fact that with primordial emotion the intention of gratification is a key element of the subjective state. The consummatory act of gratification can involve a quite precipitous decline of the emotion with complete loss of the sensation and the intention. Thus, thirst may rapidly and completely disappear after rapid drinking to satisfaction, hunger for air disappear immediately after two or three deep breaths of fresh air, hunger disappear following access to food and rapid eating, high sexual excitement disappears with orgasm, and salt hunger disappears after rapid drinking of salt solution over 3–4 min. Now the rapid satiation process such as drinking in a thirsty animal has very high survival value. It is a clear advantage for a water depleted herbivore to be able to go to a water hole in the veldt and rapidly correct a deficiency of 2–5% body weight of water in 2–5 min and get out. This reduces its exposure to predators and risk of being killed (Denton, 2006). Those with this mechanism are more likely to have progeny.

Physiological metering of amount ingested is involved in rapid gratification. Experiments such as drinking with an open oesophageal fistula, or tubing of the known deficit of water into the stomach prior to access to water, have made clear that effective rapid gratification with central “switch off” of thirst depends on a “gestalt” of sensory inflow (7th, 9th and 10th cranial nerves) in the correct temporal sequence (Denton, 1983).

Knowledge of the processes underlying this rapid “switch off” of thirst is not well advanced. The rapid drinking will give a cascade of neural inflow from the cranial nerves cited in specific temporal sequence. Present knowledge does suggest that this would be relayed from the nucleus of the tractus solitarius to the pontine parabrachial nucleus. If, indeed, it were true that a substantial neural correlate of consciousness of thirst is subserved by neural aggregates in the anterior cingulate (Brodmann 32 and 24) the question is how their activation hitherto generating thirst, inhibited by behavioural gratification. Presumptively in the thirst state, these aggregates in anterior cingulate, insula and other regions are activated, and could be involved as part of a jointly sufficient and severally necessary excitation subtending the thirst consciousness. Arguably they are primarily activated by the areas in the anterior wall of the third ventricle which sense change in the osmotic pressure of the plasma, and also the [Na] of the cerebrospinal fluid. Since the state of high osmotic pressure of the blood will continue for

at least 10–15 min until significant amount of the water drunk is absorbed, and osmotic pressure is progressively reduced, a formal possibility is that some other mechanism strongly inhibits the hitherto excited cortical areas in the face of continued inflow from the anterior wall of the third ventricle or alternatively afferent outflow from the anterior wall of the third ventricle is inhibited. In the case of the former, such a mechanism could involve known projection from the pontine parabrachial nucleus to the amygdale, bed nucleus of the stria terminalis and lateral hypothalamus. The interconnections of these nuclei to other nuclei as well as the parabrachial influence on the prefrontal, the ventral tegmental area and the nucleus accumbens, collectively constitute a forebrain reward system, including involvement of dopamine (See Krause & Sakai, 2007 for a review of these anatomical connections and putative role of dopamine in the case of saline ingestion in response to sodium deficiency).

In considering thirst as an integrated physiological process it can be recognized that there are many mechanism which can be involved in genesis. As well as the predominant causation by rise in the osmotic pressure of the blood, thirst can also be initiated by fall in the volume of the circulation with afferent baroreceptor inflow operating from the parabrachial nucleus, presumably by activating the centres in the anterior wall of the third ventricle. Also the situation of a dry mouth for one of several reasons can result in afferent inflow which gives a sensation akin to thirst. A dry mouth as a result of dehydration with diminished or absent saliva flow can be a significant concurrent afferent sensory input, and contribute significantly to consciousness of thirst in the circumstance of body desiccation in the heat. However, it is clear that “dry mouth” is a peripheral phenomenon which feeds through S1 to amplify the central process. It is not a prime mover as witness the robust thirst of a water deprived ruminant like, sheep, goat, cattle or camel, where the continuous flow of saliva underpinning the ruminant digestive process, albeit reduced, ensures the mouth is constantly wet, despite decreased saliva flow. We have examined the neuroimaging effects of obviating dry mouth during maximum thirst (See Denton, 2005).

6. Neuroimaging of thirst

Consideration of neuroimaging of thirst gives insight into some of the general issues raised above.

Moderate thirst was produced in 10 volunteers by rapid intravenous infusion of 0.51 M NaCl (Denton et al., 1999a). Subjects were imaged at the stage of maximum thirst. In the light of the characteristic “dry mouth” sensation which occurs with thirst as a consequence of large diminution of saliva flow, the subjects were permitted to wash out their mouths with water via a glass straw, and then the water was expelled without any swallowing occurring. The subjects were imaged again. Shortly afterwards they were permitted to drink as much water as they desired. Three minutes later they were imaged (Fig. 1). Thirst sensation, which had decreased 33% after washing out the mouth with water, declined precipitously to baseline score with *ad lib* drinking. A crucial point is that there is little or no change of plasma Na concentration or osmotic pressure in the 5–10 min after drinking (Denton et al., 1999b). This change only occurs later with absorption of water from the gut. Thus, those elements activated in the brain by change of sodium concentration and osmotic pressure would continue to have effect until 15–30 min later—a time when significant water absorption had occurred. However, the regions which were activated by the consciousness of thirst did not remain activated within 3 min consistent with complete loss of thirst sensation. A crucial observation (Fig. 1) is that the strong activation of the Brodmann area 32 area, anterior to the genu of the corpus callosum, persisted after wetting the mouth, whereas some areas in BA24 did not. This BA32 area did not remain activated 3 min after drinking water to satiation, as had other areas of BA24. This, with other observations made with fNMR, suggest that activation in this BA32 area may be one of the “neural correlates of consciousness” of thirst (Crick & Koch, 2003; Egan et al., 2003; Koch, 2004).

In general discussion of this concept of “neural correlates of consciousness” Koch (2004) notes that a vast number of processes must be in place for consciousness to occur. It is clear there will be enabling factors as well as specific factors. The former are represented by systems active for any form of consciousness to occur, whereas the specific are required for a particular conscious percept. Thus the capacity to experience anything is dependent on the continuing regulation of the cortex and its satellites by an aggregate of nuclei in the brainstem, the basal part of the forebrain, and the thalamus. The axons of the cells of these nuclei project widely and release acetylcholine and other neurotransmitters crucial to wakefulness, arousal, and sleep. Jointly, the ascending fibres create the essential conditions for any consciousness to occur. The fact of regional specialization of the cortex is shown, for example, by the data that the neural correlates of consciousness of colour differ from those of motion or faces (Zeki, 1993).

The area V5 is shown by cellular recording to be specialized for motion, whereas the majority of cells in V4 are to a greater or lesser extent colour selective (Zeki, 1993). Lesions of the lingual and fusiform gyrus give rise to colour blindness, the data overall consonant with the fusiform gyrus being the main locus of consciousness of colour. Experimental work of Zeki in collaboration with Frachowiak (Zeki, 1993) using PET neuroimaging of humans viewing a Mondrian art work indicted this area with colour stimulation and caused them to name it human V4. There was very much less activity in the area when the same colour pattern was viewed as shades of grey. The change in this area in the PET imaging experiment was consistent with it being a neural correlate of consciousness of colour. With regard to an integrated visual image in the brain, Zeki emphasised that there is integration of the results of different operations in different specialized parts of the brain to generate a unified visual image in the brain and this is the result of ongoing activity in several re-entrantly connected visual areas.

Many other areas subserving special senses and showing variation of activity with change of conscious perception have been identified and have contributed to recognition of special areas. Neuroimaging studies have revealed also the changing

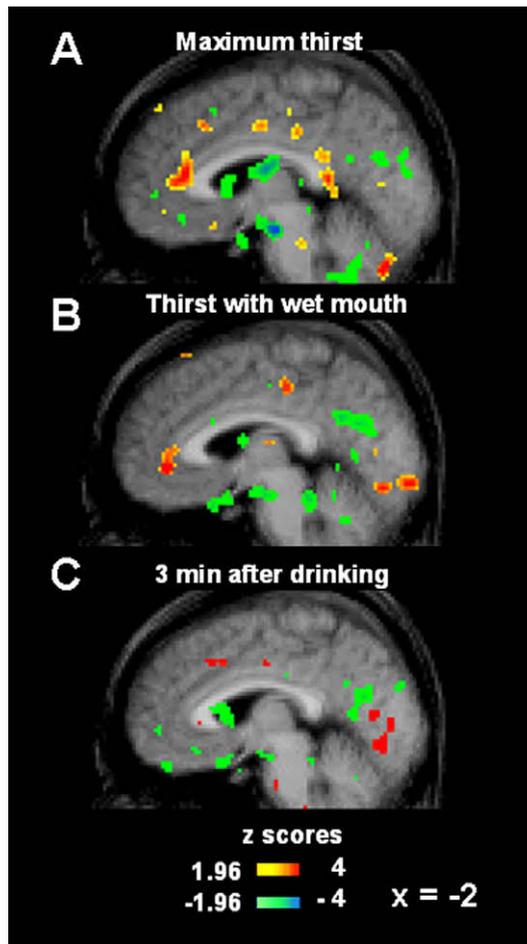


Fig. 1. Positron Emission Tomography (PET) measures of regional cerebral blood flow (rCBF) were made before (baseline), during and after systemic infusion of 0.51 M NaCl in 10 healthy men. (A) Contrasting the period of maximum thirst with baseline scans produced activation in Brodmann Area (BA) 32 of the anterior cingulate cortex and midcingulate and posterior cingulate region. (B) Activation was still present in BA 32 when scans acquired after rinsing the mouth with water were contrasted with baseline. (C) The contrast between the immediate post drink period and baseline did show disappearance of the activation in BA 32 contemporaneous with the loss of thirst. Activations are rendered on an average of the 10 subjects' anatomical images after normalization to the Talairach and Tournoux stereotactic reference system (Talairach & Tournoux, 1988). The sagittal section is 2 mm to the left of the anterior commissure. Figure adapted from Denton et al. (1999a), Denton et al. (1999b).

patterns of excitation with differing conscious states showing a plasticity in so far as some areas involved in one state may also be involved in a coalition with other areas in a different conscious state.

There is evidence of localization also with higher cognitive functions such as self awareness though there is inadequate data as to precision of this, as, for example, compared with visual areas. Platek, Keenan, Gallup, and Mohamed (2004) have summarized evidence supporting that information about the self is processed in the right hemisphere. They found significant activation in the right superior middle, and inferior frontal gyri when such activation associated with self-face processing was compared with activation associated with familiar face processing. This right side locus of cerebral activity with reaction to self was supported by Wada test data where reaction to self was much more evident if the left hemisphere was anesthetized as compared with the result with right hemisphere anesthetization. Lobectomy data also supported the proposal that the right hemisphere is pre-eminent in this regard. The authors also proposed that the attribution of mental states to others presupposes self awareness and their data from neurosurgery experiments supported the proposal of their self processing and mental state attribution involve shared neuro-cognitive networks. That is, in order to infer the mental experiences of other individuals one must have a sense of ones own experiences -essentially species that are self aware can use their experiences to model the mental state of others.

Returning now to our considerations of maximum thirst, we have set out earlier our reasons for suggesting that there are evolutionary considerations for designating the rapid gratification of deficiency of body water to have a particular status in exploring "neural correlates of consciousness." It is behaviour of very high survival value. Thus in this neuroimaging study with infusion of 0.51 M NaCl, maximum thirst sensation evoked 13 highly significant activations (and nine deactivations) in anterior middle and posterior cingulate and parahippocampal gyri, insula, claustrum, thalamus, amygdala, diencephalon and

midbrain. It should be noted that attribution to claustrum by neuroimaging is uncertain as there is not adequate resolution to distinguish the area from putamen and insula between which it lies. A further PET study of subjects showed clearly this pattern of change in the anterior–mid cingulate (Fig. 2). An fMRI study (Fig. 3) also clearly showed activation in the anterior wall of the third ventricle (lamina terminalis) which had not been seen in the PET studies—reflecting the greater resolution with fMRI (Egan et al., 2003). With fMRI, drinking water caused a large sharp decline in the BOLD activation in the anterior cingulate region, but no change in the region of the anterior wall of the third ventricle, the area (organ vasculosum of the

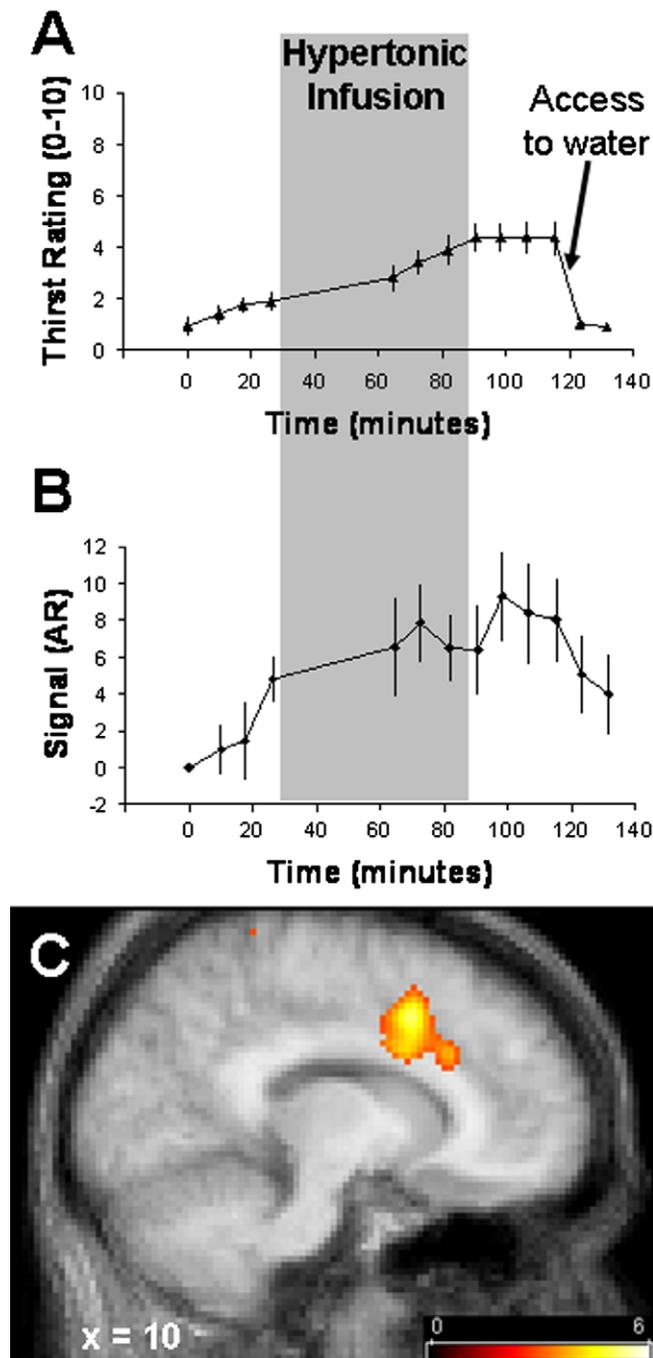


Fig. 2. (A) A systemic infusion of 0.51 M NaCl in 10 healthy mean was associated with increased ratings of thirst that rapidly decreased after drinking. (B) PET measures of rCBF in voxels activated during maximum thirst show a pronounced decrease in signal intensity after drinking. (C) The voxels activated by maximum thirst were located in the mid cingulate cortex, approximately 10 mm from the midline into the right hemisphere. Figure adapted from Farrell et al. (2006).

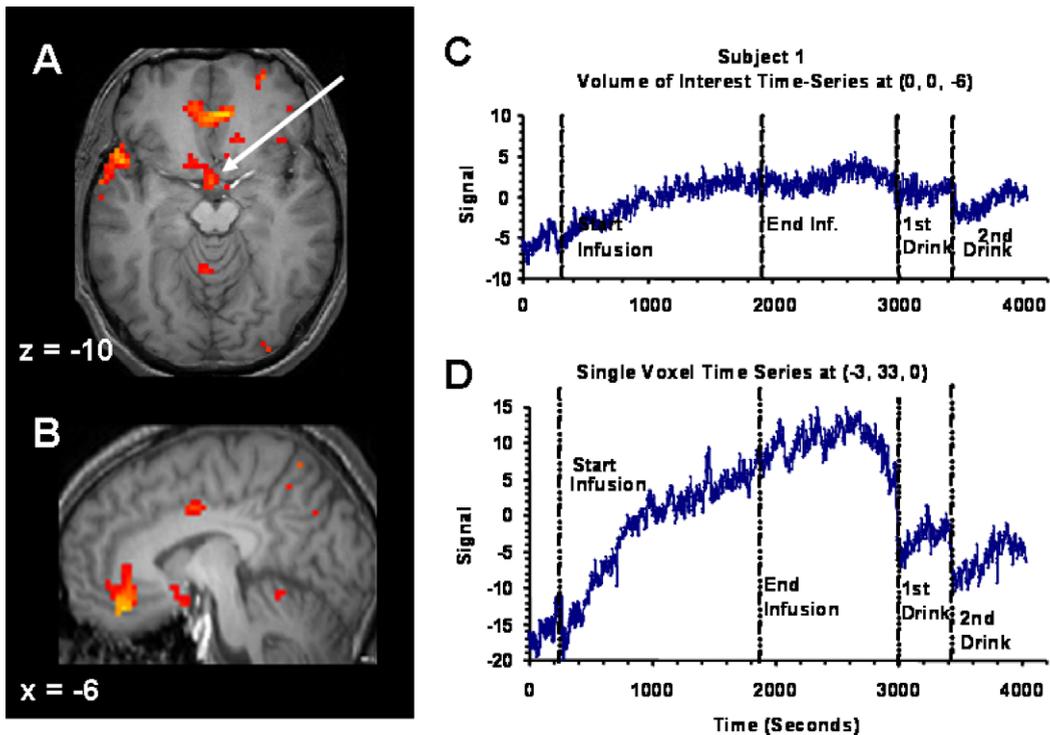


Fig. 3. Functional magnetic resonance images (fMRI) using blood oxygen level-dependent (BOLD) contrast were acquired over 60 min prior to, during and after systemic infusion of 0.51 M NaCl in a healthy male. Activations were generated by contrasting the period of maximum increase of thirst with scans acquired during the pre-infusion baseline state. (A) Maximum thirst activations were present in a region of the hypothalamus incorporating the lamina terminalis (indicated by arrow). (B) The anterior cingulate cortex (BA 32) was also activated during maximum thirst. (C) The BOLD signal from a voxel in the hypothalamus increased during the infusion and remained elevated after drinking. (D) The time course of the BOLD signal from a voxel in the anterior cingulate cortex indicates a rise in response to the hypertonic infusion, that was reversed after drinking. Co-ordinates in (A) and (B) are distances in mm from the anterior commissure according to the Talairach and Tournoux stereotactic reference system (Talairach & Tournoux, 1988). Figure adapted from Egan et al. (2003).

lamina terminalis) where the osmoreceptors are located (McKinley, Denton, & Weisinger, 1978). Significant activation occurred in the phylogenetically ancient areas of the cerebellum with both maximum thirst, and following satiation (Parsons et al., 2000). Correlation of thirst score with 99 scans made in the experiment showed a principal region of activation in the posterior cingulate (BA31) (Denton et al., 1999a).

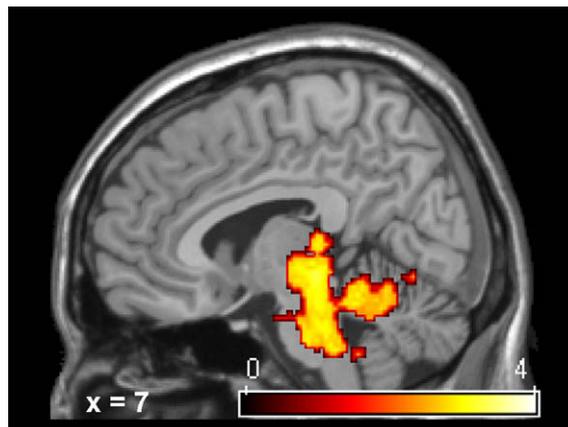


Fig. 4. Measures of rCBF were collected with a pulsed arterial spin labelling (PASL) magnetic resonance imaging sequence in 15 healthy subjects, immediately after eating to satiation following an 18 h fast and then 90 min after eating. Satiation activations were identified by contrasting images acquired immediately after eating with those acquired 90 min after eating, which acted as control. An extensive region of midbrain, brainstem and cerebellum was activated during the satiation period. Sagittal slice is 7 mm lateral to the anterior commissure in the right hemisphere. The activation is rendered on the Montreal Neurosciences Institute template brain. Image has been generated from unpublished data.

Electrical stimulation of anterior cingulate areas in monkeys causes water drinking about 2–5 min later, evidence in support of this region having a topographical relation to thirst and drinking in a primate (Robinson & Mishkin, 1968). As discussed elsewhere (Denton, 2006) the anterior cingulate is activated in several different areas with different primordial emotions. There may be topographical dedications, but as Vogt and Gabriel (1993) have pointed out, surprisingly little is known about the contribution of individual or structural aggregates of neurones of the cingulate cortex to function.

With hunger, Tataranni and colleagues (1999) showed activations in the hypothalamus and insula regions and several other limbic and paralimbic areas including the anterior cingulate, claustrum, hippocampus and parahippocampus, and in the motor nuclei represented by caudate and putamen, as well as the cerebellum. Early data from a hunger-satiety study we are making with arterial spin labelling fMRI is shown in Fig. 4. The comparison of post eating immediately following 18 h of food deprivation with baseline state indicated a principal involvement of basal brain areas.

“Hunger for air” or extreme breathlessness is a powerful primordial emotion (Banzett et al., 1990). Experiments where air hunger and hypercapnia occurred simultaneously showed powerful activations (Fig. 5) in the midbrain tegmentum, periaqueductal grey, the pons, and posterior hypothalamus, putamen, and cerebellum, with multiple foci in the anterior and middle cingulate gyrus, insula, claustrum, amygdala, and temporal gyrus (Brannan et al., 2001). The medulla, and thus the Botzinger complex was not in the field of image analysis. Large deactivations occurred in the anterior cingulate region, the posterior cingulate and the lateral prefrontal cortex, possibly indicative of inhibition of cognitive processes with the extreme emotion of hunger for air. With technically sophisticated experiments in which air hunger effect was dissociated from effects of high CO₂ (Banzett et al., 2000), the data reflected that the insula had a dominant role in air hunger. The air hunger experiments of Corfield et al. (1995), Brannan et al. (2001), and Liotti et al. (2001) also showed strong activation in the insula. The investigations of Craig (2003b) and Derbyshire (2003) emphasise the role of insula and limbic system in response to pain and visceral distension. Craig, Chen, Bandy, and Reiman (2000) describes pain as a homeostatic emotion akin to temperature change, itch, hunger and thirst, and also visceral distension and muscular ache. It reflects an adverse condition in the body that demands a behavioural response.

Craig (2003a), Craig (2003b) has made a detailed and imaginative analysis of afferent inflow pertinent to homeostatic control. This is via Laminar I neurons and he proposed that small diameter (A δ and C) primary afferents, which parallel sym-

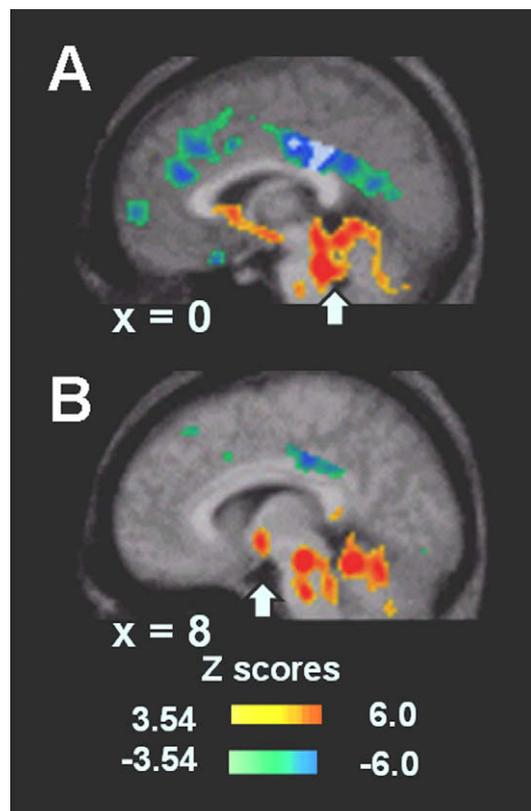


Fig. 5. Air-hunger activations were identified by contrasting PET measures of rCBF from scans acquired during inhalation of 8% CO₂ with scans acquired during inhalation of a N₂/O₂ mixture. (A) Air-hunger activations included an extensive region of the midbrain and brainstem (indicated by arrow) that incorporated the midbrain tegmentum, periaqueductal grey and pons. (B) Air hunger was also notable for activation in the hypothalamus (indicated by arrow). The x values represent the lateral position in mm of the sagittal slice with respect to the anterior commissure, according to the Talairach and Tournoux stereotactic reference system (Talairach & Tournoux, 1988). Figure adapted from Brannan et al. (2001).

pathetic efferents, conduct information regarding all manner of physiological conditions including the mechanical, thermal, chemical, metabolic and hormonal status of skin, muscle, joints, teeth and viscera. He states the main target of the inflow of the Lamina I and the nucleus tractus solitarius (NTS) is the parabrachial nucleus (PBN) which is the main integrative site for all homeostatic afferent activity. This integrative organization includes also the participation of the periaqueductal grey (PAG) and the hypothalamus. The lamina I neurons also project via the thalamus to the interoceptive cortex (the dorsal margin of the insula) and the anterior cingulate cortex (ACC). He remarks that the direct activation of these areas by distinct homeostatic modalities corresponds with *simultaneous generation of both a sensation and a motivation reflecting the survival needs of the body* (our italics).

7. Some putative cortical organizations subserving consciousness

Consistent with the earlier statements in this article on the survival value of consciousness, and considering briefly some aspects of the cortical organization in general terms, Baars (2005) proposes consciousness is a fundamental biological adaptation. He says that the brain correlates of consciousness appear to be phylogenetically ancient and go back at least to the earliest mammals. In all mammals, alertness and sensory consciousness are required for the goal directed behaviours that make species survival and reproduction possible.

Panksepp (2005) proposed consciousness refers to brain states that have an experiential feel to them, and it is envisaged as a multi-tiered process that needs to be viewed in evolutionary terms with multiple layers of emergence (see also Bogen, 1995).

Panksepp et al. (2007) says, in an organizational sense, cortical systems may be seen in the following context. He focuses on the primary affects from bodily hungers to emotional delights. “If we get the foundational issues right then the secondary and tertiary layers of consciousness—the ability to have thoughts about the world and thoughts about thoughts—should become easier hard problems”. He suggests the more ancient, medially concentrated interceptive motivational—emotional urges of the brainstem were foundational for the more lateral zones that harvest external information for the guidance of behaviour. He says “very medial homeostatic detectors (i.e. for hunger, thirst etc.) regulate adjacent core emotional systems that generate many distinct instinctual emotional intentions in action – to use Searle (1983) “felicitous phrase”.

He summarizes, “if we envision three key mesencephalic—diencephalic functions as concentric circles with (1) body need detectors situated most medially (Denton, 2006), (2) emotional instinctual systems concentrated in subsequent layers (Panksepp, 1998), and with all surrounded by (3) more externally directed somatosensory and somatomotor processes for attentive target selections and directed actions, we have a working image of primary process phenomenal consciousness”. He suggests affective consciousness, comprised heavily of the two highly interactive medial layers may suffice for some levels of experience, but probably without self awareness. He adds that all mind scientists should remember that “primary consciousness arises from the somatovisceral operating systems of the upper brain stem (Watt & Pincus, 2004), and that there is something deeply personal about this kind of neural activity. This is where our bodily needs are felt (Denton, 2006)” (Panksepp, 2007).

Feinberg (2001) sees the functional outcome of the structure which has been determined by evolution as a “non-nested” system. This is distinct from a “nested system” with the mind as a radically emergent system of the brain as Sperry conceived (Sperry, 1966). Possibly the fact that a basal brain mechanism and sensation like hunger for air can have immediate totalitarian occupation of the stream of consciousness bespeaks a “non-nested” system of brain organization.

The concept of a global neuronal workplace as an integrating system (Baars, 1988; Dehaene, Kerzberg, & Changeux 1998) involves, *inter alia*, various segments of the brain seen as a massively distributed system of specialized processes, acting in parallel with most of them unconscious at any given moment. The contemporary content of consciousness is broadcast to a collection of specialized unconscious processors which, in turn, can compete and cooperate to gain subsequent access to the global neuronal workspace and consciousness.

The broad issues of the neuronal organization subserving conscious cognitive processes, perception and intention has been dissected in an interesting and entertaining fashion by Dennett (1991). He proposes what he terms a Multiple Drafts basis of neuronal function in categorical contrast to the idea that somewhere, conveniently hidden in the obscure “center of the mind-brain, there is a ‘Cartesian Theatre’”. This is a place where it all comes together, and consciousness happens. Accordingly, our conscious minds would be located at the termination of all in-bound processes just before the initiation of all out-bound processes. He says the Multiple Drafts model avoids the mistake of supposing that there must be a single narrative (the ‘final’ or ‘published’ draft you might say) that is canonical—that is the actual stream of consciousness of the subject. According to his model of the Multiple Drafts, “all varieties of perception—indeed, all varieties of thought or mental activity—are accomplished in the brain by parallel multitrack processes of interpretation and elaboration of sensory inputs. Information entering the brain is under continuous editorial revision”.

8. Conclusion

It is, of course, evident that this is an early stage of accrual of knowledge to allow speculation on the phylogenetic processes giving rise to primary consciousness or the first dim awareness. Neuroimaging during changing states in lower animals will probably be essential to gain insight on change of brain function when changes in the body cause altered

behaviour. This is a vast field to explore in terms of fundamental processes ensuring normal regulatory function of organisms and the continuity of their existence. The neuroimaging data in humans is consonant with the hypothesis that the evolutionary ancient areas of the brain—both in brain stem and the telencephalon—play a dominant role in the primordial emotions. This may be consistent with our proposal of the primordial emotions as being the earliest dim awareness—the initial subjectivity or consciousness. It is basically a below up notion. The brain stem centres and the reticular activating systems functionally melded with the evolving limbic areas to give first dim awareness. However, in parallel, it is clear that distance receptor evoked emotions like fear with acute activation of the amygdala cause major arousal through excitation of lower brain areas including the reticular activating system and also activation of motor systems. Elegant studies by [Damasio and colleagues \(2000\)](#) of different recalled emotions of the type which predominantly involve distance receptors in their initial evocation by perceptual categorization of the inflow indicate that diencephalic, mesencephalic and medullary areas, as distinct from arousal mechanisms localized in the reticular activating system, may be topographically dedicated to different emotions.

Studies of these vegetative organisations discussed here could open a different type of avenue than, for example, vision, for fruitful exploration of the question of Francis Crick and Christof Koch. That is, which active neural processes in a specific situation correlate with consciousness and which do not? Clearly in the physiological situations involving rapid gratification, there will be such a dichotomy. Explicitly, active areas in images of the brain would reflect both concurrent conscious and unconscious processes underlying the induction of thirst. With induction of thirst, there will be activations in the anterior wall of the third ventricle (the organ vasculosum of the lamina terminalis) indicating the sensing of the change of osmotic pressure of the blood. There will be nuclei in other areas of the hypothalamus concerned, for example, with the release of antidiuretic hormone as a result of the rise of osmotic pressure of the blood, and there will be other areas affected by small effects on blood pressure, heart rate, blood volume etc. These stimuli would not reverse until 20–30 min after satiation by drinking water when enough water would be absorbed to significantly change the chemistry of the blood and other physiological variables. A qualification to this latter statement is that the secretion of antidiuretic hormone ceases immediately after drinking, and, indeed, its secretion is sensitive to conscious influences such as fright.

However activated areas e.g. limbic, putatively subserving the conscious sensation of thirst, would disappear very rapidly with the disappearance of the sense of thirst associated with the gratification of the intention to drink water to satiation. Thus, the appearance of activations, in particular areas, (e.g. in Brodmann 32 and 24 etc.), with emergence of thirst and their rapid reduction with satiation by drinking is suggestive of them being a neural correlate of the consciousness of thirst. This effect of drinking in causing large reduction of activation in BA32 and BA24 has been seen in separate studies ([Denton et al., 1999a](#); [Denton et al., 1999b](#); [Egan et al., 2003](#); [Farrell et al., 2006](#)) using different imaging techniques.

It should be noted that with PET imaging there are limitations of sensitivity in allowing identification of basal brain nuclei likely to be activated in their role of control of homeostatic processes. Further, appearance or the reduction or disappearance of deactivated areas may also correlate with change of conscious state.

The contemporaneity of change in brain activation with rapid satiation and immediate loss of thirst is suggestive that the basic biological process of gratification with its high survival value constitutes an important avenue for observing neural processes correlating with consciousness.

Acknowledgments

This work is supported by the Robert J. Jr. and Helen C. Kleberg Foundation, the Harold G. and Leila Y. Mathers Charitable Trust, the Search Foundation, the Derek Denton Endowment, and the Brown Foundation. We are also deeply indebted to Dr. Robert Shade, Professor Peter Fox and Mr. Frank Zamarrilla for collaboration in the experiments, and also Professor Jean-Pierre Changeux, the late Dr. Francis Crick, Professor Christof Koch, and Dr. Roger Guillemin, for discussion.

References

- Baars, B. J. (1988). *A cognitive theory of consciousness*. Cambridge University Press.
- Baars, B. J. (2005). Subjective experience is probably not limited to humans: The evidence from neurobiology and behavior. *Consciousness and Cognition*, 14, 7–21.
- Banzett, R. B., Lansing, R. W., Brown, R., Topoulos, R., Yager, D., Steele, S. M., et al (1990). Air hunger from increased PCO₂ persists after complete neuromuscular block in humans. *Respiratory Physiology*, 80, 1–18.
- Banzett, R. B., Mulnier, H. E., Murphy, K., Rosen, S. D., Wise, R. J. S., & Adams, L. (2000). Breathlessness in humans activates insular cortex. *Neuroreport*, 11, 2117–2120.
- Bard, P., & Rioch, D. McK. (1937). A study of four cats deprived of neocortex and additional portions of the forebrain. *Bulletin of the Johns Hopkins Hospital LX*, 73–148.
- Bogen, J. E. (1995). On the neurophysiology of consciousness. Part 1: Overview. *Consciousness and Cognition*, 4, 52–62.
- Brannan, S., Liotti, M., Egan, G., Shade, R., Madden, L., Robbillard, R., et al (2001). Neuroimaging of cerebral activations and deactivations associated with hypercapnia and hunger for air. *Proceedings of the National Academy of Sciences USA*, 98, 2029–2034.
- Butler, A. B., Manger, P. R., Lindahl, B. I. B., & Arhem, P. (2005). Evolution of the neural basis of consciousness: A bird-mammal comparison. *BioEssays*, 27, 923–936.
- Corfield, D. R., Fink, G. R., Ramsay, S. C., Murphy, K., Harty, H. R., Watson, J. D., et al (1995). Evidence for limbic system activation during CO₂-stimulated breathing in man. *Journal of Physiology*, 488, 77–84.
- Craig, A. D. (2003a). Interoception: The sense of the physiological condition of the body. *Current Opinion in Neurobiology*, 13, 500–505.
- Craig, A. D. (2003b). A new view of pain as a homeostatic emotion. *Trends in Neuroscience*, 26, 303–307.
- Craig, A. D., Chen, K., Bandy, D., & Reiman, E. M. (2000). Thermosensory activation of the insula cortex. *Nature Neuroscience*, 3, 184–190.

- Crick, F. (1994). *The astonishing hypothesis: The scientific search for the soul*. London: Simon & Schuster.
- Crick, F., & Koch, C. (2003). A framework for consciousness. *Nature Neuroscience*, 6, 119–126.
- Damasio, A. R. (2000). *The feeling of what happens*. London: Heinemann.
- Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. I. B., Ponto, J. P., et al (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, 3, 1049–1056.
- Dehaene, S., Kerzberg, M., & Changeux, J.-P. (1998). A neuronal model of a global workspace in effortful cognitive tasks. *Proceedings of the National Academy of Sciences USA*, 95, 14529–14534.
- Dennett, D. (1991). *Consciousness explained*. London: Allen Lane, Pergamum Press.
- Denton, D. A. (1983). *The Hunger for Salt*. London: Springer-Verlag.
- Denton, D. A. (2005). *Les Emotions Primordiales et L'Eveil de la Conscience*. Paris: Flammarion.
- Denton, D. A. (2006). *The primordial emotions: The dawning of consciousness*. Oxford University Press.
- Denton, D. A., McKinley, K. J., & Weisinger, R. S. (1996). Hypothalamic integration of body fluid regulation. *Proceedings of the National Academy of Sciences USA*, 93, 7397–7404.
- Denton, D. A., Shade, R., Zamarripa, F., Egan, G., Blair-West, J., McKinley, M., et al (1999a). Neuroimaging of genesis and satiation of thirst: An interoceptor driven theory of origins of primary consciousness. *Proceedings of the National Academy of Sciences USA*, 96, 5304–5309.
- Denton, D. A., Shade, R., Zamarripa, F., Egan, G., Blair-West, J., McKinley, M., et al (1999b). The correlation of regional cerebral blood flow (rCBF) and change of plasma sodium concentration during genesis and satiation of thirst. *Proceedings of the National Academy of Sciences USA*, 96, 2532–2537.
- Derbyshire, S. W. G. (2003). A systemic review of neuroimaging data during visceral stimulation. *American Journal of Gastroenterology*, 98, 13–20.
- Edelman, G. M. (1992). *Bright air, brilliant fire: On the matter of the mind*. New York: Basic Books.
- Edelman, G. M. (1998). Building a picture of the brain. *Daedalus (Journal of the American Academy of Arts and Sciences)*, 127, 37–69 [Spring].
- Edelman, G. M., & Tononi, G. (2000). *A universe of consciousness: How matter becomes imagination*. New York: Basic Books.
- Egan, G., Silk, T., Zamarripa, F., Williams, J., Federico, P., Cunningham, R., et al (2003). Neural correlates of the emergence of consciousness of thirst. *Proceedings of the National Academy of Sciences USA*, 100, 15241–15246.
- Farrell, M. J., Egan, G. F., Zamarripa, F., Shade, R., Blair-West, J., Fox, P., et al (2006). Unique, common, and interacting cortical correlates of thirst and pain. *Proceedings of the National Academy of Sciences USA*, 103, 2416–2421.
- Feinberg, T. E. (2001). Why the mind is not a radically emergent feature of the brain. *Journal of Consciousness Studies*, 8, 123–145.
- Gamper, E. (1926). Bau und Leistungen eines menschlichen Mittelhirnwesens (Arhinencephalie mit Encephalocoele). *Zeitschrift für die gesamte Neurologie und Psychiatrie*, 102, 154–235 and 104, 49–120.
- Grossman, R. G. (1980). Are current concepts and methods in neuroscience adequate for studying the neural basis of consciousness and mental activity. In H. M. Pinsky & W. D. Willis, Jr. (Eds.), *Information processing in the nervous system* (pp. 331). New York: Raven Press.
- Herrnstein, R. J., & Loveland, D. H. (1964). Complex visual concept in the pigeon. *Science*, 146, 549.
- Herrnstein, R. J., Loveland, D. H., & Cable, C. (1976). Natural concepts in pigeons. *Journal of Experimental Psychology, Animal Behaviour Processes*, 2, 285–302.
- Hess, W. R. (1964). *The biology of mind*. Chicago: University of Chicago Press.
- Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, 379, 249–251.
- Hunt, G. R. (2000). Human-like, population level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus moneduloides*. *Proceedings of the Royal Society of London B*, 267, 403–413.
- James, W. (1918). *The principles of psychology* (1890). American Science Series (Vols. 2). New York: Henry Holt and Co.
- Kenny, A. J. P., Longuet-Higgins, H. C., Lucas, J. R., & Waddington, C. H. (1973). *The nature of mind*. Edinburgh: Edinburgh University Press.
- Kleinginna, P. R., Jr., & Kleinginna, A. M. (1981). A categorized list of emotion definitions, with suggestions for a consensual definition. *Motivation & Emotion*, 5, 345–379.
- Koch, C. (2004). *The quest for consciousness*. Colorado: Roberts & Co.
- Krause, E. G., & Sakai, R. R. (2007). Richter and sodium appetite: From adrenalectomy to molecular biology. *Appetite*, 49(2), 353–367.
- Laureys, S., Boly, M., & Maquet, P. (2006). Tracking the recovery of consciousness from coma. *Journal of Clinical Investigation*, 116(7), 1823–1825.
- Laureys, S., Perrin, F., & Brédart, S. (2007). Self-consciousness in non-communicative patients. *Consciousness and Cognition*, 16, 722–741.
- LeDoux, S. (1998). *The emotional brain. The mysterious underpinning of emotional life*. New York: Touchstone (Simon & Schuster Inc.).
- Liotti, M., Brannan, S., Egan, G., Shade, R., Madden, L., Abplanalp, B., et al (2001). Brain responses associated with consciousness of breathlessness (air hunger). *Proceedings of the National Academy of Sciences USA*, 98, 2035–2040.
- McKinley, M. J., Denton, D. A., & Weisinger, R. S. (1978). Sensors for antidiuresis and thirst—osmoreceptors or CSF sodium detectors. *Brain Research*, 141, 89–103.
- Merker, B. (2007). Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Sciences*, 30, 63–134.
- Oakley, K. P. (1954). Skill as a human possession. In C. Singer (Ed.), *History of technology* (Vol. 1). London: Oxford University Press.
- Owen, A. M., Coleman, M. R., Boly, M., Davis, M. H., Laureys, S., & Pickard, J. D. (2006). Detecting awareness in the vegetative state. *Science*, 313, 1402.
- Owen, A. M., Coleman, M. R., Boly, M., Davis, M. H., Laureys, S., & Pickard, J. D. (2007). Using functional magnetic resonance imaging to detect covert awareness in the vegetative state. *Archives of Neurology*, 64(8), 1098–1102.
- Panksepp, J. (1998). *Affective neuroscience. The foundations of human and animal emotions*. New York: Oxford University Press Inc..
- Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition*, 14, 30–80.
- Panksepp, J. (2007). Emotional feelings originate below the neocortex: Toward a neurobiology of the soul. In B. Merker (2007) *Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. Behavioral and Brain Sciences*, 30, 63–134.
- Panksepp, J., Fuchs, T., Garcia, V. A., & Lesiak, A. (2007). Does any aspect of mind survive brain damage that typically leads to a persistent vegetative state? Ethical considerations. *Philosophy, Ethics, and Humanities in Medicine*, 2, 32.
- Parsons, L. M., Denton, D., Egan, G., McKinley, M., Shade, R., Lancaster, J., et al (2000). Neuroimaging evidence implicating cerebellum in support of sensory/cognitive processes associated with thirst. *Proceedings of the National Academy of Sciences USA*, 97, 2332–2336.
- Parvizi, J., & Damasio, A. (2001). Consciousness and the brainstem. *Cognition*, 79, 135–160.
- Platek, S. M., Keenan, J. P., Gallup, G. G., Jr., & Mohamed, F. B. (2004). Where am I? The neurological correlates of self and other. *Brain Research Cognition Brain Research*, 19, 114–122.
- Robinson, B. W., & Mishkin, M. (1968). Alimentary responses to forebrain stimulation in monkeys. *Experimental Brain Research*, 4, 330–366.
- Searle, J. R. (1983). *Intentionality: An essay in the philosophy of mind*. Cambridge, UK: Cambridge University Press.
- Searle, J.R. (1985). *Minds, Brains and Science. The 1984 Reith Lectures*, London, British Broadcasting Corporation. Penguin Books, 1989. Cambridge, Mass: Harvard University Press.
- Shewmon, D. A., Holmes, G. L., & Byrne, P. A. (1999). Consciousness in congenitally decorticate children: Developmental vegetative state as self-fulfilling prophecy. *Developmental Medicine and Child Neurology*, 42, 364–374.
- Smith, H. W. (1959). The Biology of consciousness. In C. Brooks & P. Cranefield (Eds.), *The historical development of physiological thought* (pp. 109–136). New York: The Hafner Publishing Co..
- Sperry, R. W. (1966). Brain bisection and the mechanisms of consciousness. In J. C. Eccles (Ed.), *Brain and conscious experience*. New York: Springer-Verlag.
- Sperry, R. W. (1974). Lateral specialization in the surgically separated hemispheres. In F. O. Schmitt (Ed.), *The neurosciences. Third study program* (vol. 5). Cambridge, Mass: MIT Press.
- Talairach, P., & Tournoux, J. (1988) *A stereotaxic coplanar atlas of the human brain*. Stuttgart: Thieme.
- Tataranni, P. A., Gautier, J.-F., Chen, K., Uecker, A., Bandy, D., Salbe, A.D., et al (1999). Neuroanatomical correlates of hunger and satiation in humans using positron emission tomography. *Proceedings of the National Academy of Sciences USA*, 96, 4569–4574.

- Vogt, B. A., & Gabriel, M. (1993). *Neurobiology of cingulate cortex and limbic thalamus*. Boston, MA: Birkhauser.
- Watt, D. F., & Pincus, D. I. (2004). Neural substrates of consciousness: Implications for clinical psychiatry. In J. Paanksepp (Ed.), *Textbook of biological psychiatry* (pp. 75–110). Wiley.
- Weir, A. S., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science*, 297, 981.
- Young, J. Z. (1986). *Philosophy and the brain*. Oxford: Oxford University Press.
- Zaidel, D. W. (1994). A view of the world from a split brain perspective. In E. M. R. Critchley (Ed.), *The neurological boundaries of reality* (pp. 161–174). London: Farrand Press.
- Zeki, S. (1993). *A vision of the brain*. Oxford, UK: Blackwell Scientific Publications.