Patricia E. Sharp

Buddhist Enlightenment and the Destruction of Attractor Networks

A Neuroscientific Speculation on the Buddhist Path from Everyday Consciousness to Buddha-Awakening

Abstract: *Buddhist philosophy asserts that human suffering is caused by ignorance regarding the true nature of reality. According to this, perceptions and thoughts are largely fabrications of our own minds, based on conditioned tendencies which often involve problematic fears, aversions, compulsions, etc. In Buddhist psychology, these tendencies reside in a portion of mind known as Store consciousness. Here, I suggest a correspondence between this Buddhist Store consciousness and the neuroscientific idea of stored (Hebbian) synaptic weights. These weights are strong synaptic connections built in through experience. Buddhist philosophy claims that humans can find relief from suffering through a process in which the Store consciousness is transformed. Here, I argue that this Buddhist 'transformation at the base' corresponds to a loosening of the learned synaptic connections. I will argue that Buddhist meditation practices create conditions in the brain which are optimal for diminishing the strength of our conditioned perceptual and behavioural tendencies.*

Correspondence:
Patricia E. Sharp, JP Scott Center for Mind, Brain and Behavior, Department of Psychology, Bowling Green State University, Bowling Green, Ohio 43403
Email: psharp@bgsu.edu

Introduction

The Buddhist Path Offers Relief from Suffering Caused by Ignorance of the True Nature of Reality

Buddhist philosophy asserts that, although human existence is marked by immense suffering, this suffering can be relieved by understanding its causes, and by following the Buddhist path to remove these causes. In Buddhist terms, the cause of suffering is 'ignorance' with regard to the true nature of reality. When we are relieved from this ignorance so that we 'see things as they really are', then we are released from human affliction and are free to interact with the larger world in a way which is flexible, open and joyous.

In describing the nature of this ignorance, the Buddhists speak of our inability to see the 'emptiness of appearances'. Here, the term 'appearances' refers to experiential (conscious) phenomena, and includes nearly all such phenomena, from perceptions of simple objects such as tables and trees, to larger concepts such as justice and democracy. These 'appearances' also include any emotions and sensations which may accompany our perceptions and ideas. The term 'emptiness', in this context, means, roughly, that there is no concrete, solid reality underlying these appearances. Upon examination, they have no real substance, but are merely *conditioned*, often quite repetitive *thoughts*.[1]

At the core of the Buddhist analysis is the recognition that our minds are capable of generating phenomena which appear to us as real, but which actually have little or no basis in reality. Perhaps the most obvious example of this is when we dream at night. In this case we may have, for example, an image of ourselves helplessly balanced on a narrow ledge, about to fall to our death. Dreams like this can seem so real that we are awakened in panic.

From the Buddhist point of view, the appearances that we have while awake also require examination. Although it seems that most Buddhist philosophers believe that there is a 'real', outside, material world, they also emphasize that our own training and constitutional make-up contribute a great deal to the way we perceive and relate to these real-world objects. In general, these dispositional tendencies that we contribute to our own perceptions can cause problems.

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[1] Note, this does not mean that Buddhist philosophers generally hold the classic idealist position that there is no external world. I believe it is accurate to suggest that most Buddhist thinkers believe that there are entities other than mind, but that our ability to apprehend these entities is always inextricably tied to our own actions, constitution and training. See Dreyfus and McClintock (2003) for further discussion of this point.

Although traditional Buddhist discourse may sound esoteric and, at times, fundamentalist to contemporary western scientists, the case can be made that there are, nonetheless, remarkable parallels between the Buddhist and the modern neuroscientific conceptions for how our constitution and experiences shape our perceptual and cognitive worlds. Both traditions assert that our experiences and actions leave lasting marks on how we perceive objects, people, events, and ourselves. Both traditions also assert that these imprints can often cause great difficulties. Examples of this from the western psychological/neuroscientific approach include the induction of chronic stress and anxiety which can follow traumatic events, and the obsessive addiction which can follow the chronic use of drugs of abuse.

In western neuroscientific terms, our habitual perceptions and emotional reactions can be seen, at least in part, as being due to Hebbian cell assemblies which were stamped in during earlier experiences through long-term potentiation (LTP) of the synaptic connections between the neurons involved in those experiences. Later, the resulting attractor networks tend to be reinstated under any internal or external conditions which are in some way similar to those of the original training experiences.

In Buddhist terms, this 'ripening of the karmic seeds' (recollection of past events) is due to previous experiences which laid down 'karmic imprints' (initial learning).

One difference between the Buddhist and the neuroscientific traditions, however, is that Buddhist teachings take a somewhat broader view of the ways in which our previously-conditioned habits can cause problems. In fact, they tend to view almost all conditioned perceptions, concepts and actions as potentially problematic.

For example, at the perceptual level, our tendency to instantly categorize each visual pattern into canonical objects such as 'tree', 'table', 'face' is seen as limiting, because this unmindful, instantaneous categorization may prevent us from seeing the unique beauty and individuality of each part of the world. Put simply, these habitual responses can lead to boredom and inflexibility. In contrast, the neuroscientific tradition seems to take a more honorific attitude toward our object recognition capabilities, along with the Hebbian plasticity thought to underlie these abilities.

Buddhist philosophy tends to take a dim view of habitual thought patterns at higher conceptual levels as well, even in cases in which the involved concepts would seem to be positive. For example, the Buddhist attitude is sceptical regarding the idea of self-esteem. In western culture we are often encouraged to develop a self-confident attitude,

so that we view ourselves as competent, successful, bright, and so on. In contrast, the Buddhist view is that this sort of construction of ourselves leads to endless craving (to become even more successful) and fear (that we could fall from our esteemed position in the world). Buddhist teachings assert that such notions of ourselves are merely repetitive thought patterns which are seen to be 'empty' upon examination. That is, when we look into ourselves to try to find the solid, inner rock of competence or successfulness, all we find is a series of repetitive self-referential *thoughts*. When we cling to the concept of self in this way, by repeating these thoughts, it causes rigidity in our actions as well as fear, jealousy and aggression toward others.

Here, I will argue that the Buddhist path offers instructions for gently loosening the strength of many of the patterns of synaptic connectivity that form the basis of our habitual perceptions and thought patterns. Data on brain activity during meditative states will be used to suggest that certain forms of meditation induce: 1) acute state changes in which high levels of cortical acetylcholine (a neurotransmitter involved in arousal and learning) enhance the reception of external sensory input, while simultaneously dampening feedback connections responsible for rehearsal of previously-learned patterns (Giocomo and Hasselmo, 2007; Hasselmo and McGaughy, 2004); 2) a longer-lasting tendency to reside in these high acetylcholine states, so that the enhanced preferential reception of novel, incoming information tends to persist beyond the periods of formal meditation; and 3) neural plasticity which provides partial rewiring (undoing) of at least some of the previously-conditioned patterns of Hebbian synaptic connectivity (the conditioned attractors themselves).

Consciousness, Attractor Networks, Neural Synchrony, and Synaptic Plasticity

Both contemporary neuroscience and traditional Buddhist philosophy assert that mind (consciousness) and body are closely intertwined. Buddhist practitioners have primarily focused on the 'mind' aspect of the mind/body complex, by examining conscious (phenomenal) experience, which is, of course, available only through private introspection. In contrast, contemporary neuroscience has concentrated largely on the physical (brain) aspects of the mind/body complex. The analysis provided in this target article will rely on the idea that, since mind and brain somehow go together (ignoring issues involving parallelism *versus* causality *versus* identity, and so on), it should, in principle, be possible to find a mapping between the introspective insights derived

from the Buddhist tradition, and at least some of the biological/functional insights derived from neuroscience.

Buddhist psychology teaches that there is a fundamental and thorough transformation of consciousness (mind) as one progresses along the Buddhist path (see below). This suggests that there must be a corresponding fundamental and thorough transformation of at least some aspect(s) of brain function. In order to speculate on what kind of brain changes might be hypothesized, it is first necessary to consider current speculation on just how consciousness (whether the consciousness is pre- or post-enlightenment, in the Buddhist sense) maps onto brain activity. In the remainder of this section I will provide a brief summary of some of these data, with special emphasis on aspects of the mind/brain relationship which are relevant to the analysis of the physiological correlates of Buddhist meditation.

Specific Aspects of Consciousness are Related to Activity in Specific Sets of Neurons

Most obviously, it seems clear that, somehow, conscious experience is related to the activity of neurons (or at least some neurons) within the central nervous system, and that the exact quality of any one instant of consciousness is related to just which neurons are active. Thus, for example, neurons in the visual system, when active, seem to give rise to sensations of a visual (rather than auditory, somatic, etc.) nature. The precise momentary pattern of activity in these neurons seems to determine the exact nature of the visual qualia experienced at any one instant (Block, 2007; Zeki, 2007).[2]

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[2] In this article I will omit any detailed consideration of exactly which aspect of neural network activity is translated into conscious states. That is, I will not here discuss whether consciousness is specifically related to quantum events (e.g. Hammeroff and Penrose, 1996) entailed in neural activity, or electromagnetic events related to cell depolarization, etc. These considerations can be safely ignored in relation to the concerns of this article.

I will also omit any discussion of the distinction between access consciousness (or global workspace) *versus* pre-consciousness or phenomenal consciousness, as discussed elsewhere (see Block, 2007). Thus, for example, it has been suggested that many brain regions, possibly including sensory areas such as primary visual cortex, do not, in themselves, generate conscious phenomena, but merely pass on the results of their neural processing to regions such as parietal and frontal cortex. According to this scenario, it would be only these latter areas whose activity is directly associated with consciousness. For the present purposes, this issue can be safely ignored. This is because, if the changes in attractor network strength postulated here do, in fact, take place in pre-conscious (non-conscious) brain regions, they could (according to the theory presented here), nonetheless, contribute to the meditation-induced changes in consciousness described by Buddhists. Thus, the altered patterns of activity (loosened attractors) in these pre-conscious areas would provide novel (not previously-conditioned) inputs to the access-consciousness

In addition, there are also neural circuits involved in emotional aspects of phenomenal consciousness (Burgdorf and Panksepp, 2006; LeDoux, 2000). For example, certain kinds of activity in the nucleus accumbens are thought to coincide with the experience of hedonic pleasure (as well as the development of craving for this pleasure) induced by drugs of addiction, as well as by natural rewards, such as food, sex, and social interaction (Koob and Le Moal, 2008; Robinson and Berridge, 2003; Wise, 2004). Similarly, it seems that neural activation of cells in the amygdala (including the extended amygdala; Heimer and Van Hoesen, 2006) may give rise to feelings of fear and anxiety (Walker *et al.*, 2003).

Thus it seems that any one instant of consciousness likely corresponds to activity in some specific *set* of neurons, and *vice versa*.

Attractor Networks, Neural Plasticity, and Degrees of Freedom

Estimates of the number of neurons in the human brain range somewhere between 80 billion (Kolb and Wishaw, 2006) and one trillion (Thompson, 2000). It would seem that this large number of neurons would, in principle, provide for nearly infinite combinatorial possibilities in terms of the number of unique subsets of co-active neurons which could possibly arise. Indeed, any effort to calculate this number far exceeds the representational capabilities of any modern computer. This would seem to suggest that we could, in principle, live an entire lifetime without ever having the identical (or even similar) experience twice. (Note, the number of possible phenomenological states would have to be adjusted downward if it is true that not all neurons are directly involved in generating conscious experience *per se*.)

In reality, however, it seems that the number of combinatorial possibilities actually realized in the brain is likely very much smaller than the number of in-principle possibilities. Evidence for this comes from a wide variety of observations. One type of evidence has been provided by studies which combined electrophysiological recordings of individual cells, along with optical imaging to examine activation patterns in large populations of cells surrounding the individual electrically-recorded cell (Arieli *et al.*, 1996; Tsodyks *et al.*, 1999; Kenet *et al.*, 2003). In these studies, visual stimuli were presented to cats while recording from primary visual cortex. Not surprisingly, the investigators found that presentation of simple visual stimuli evoked characteristic patterns of activity across the cortex, so that certain cortical

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regions, so that these latter regions would, in turn, likely exhibit a reduction in repetitive replay of previously-conditioned neural firing patterns.

columns were activated for any one stimulus, in accordance with the orientation and movement direction of that stimulus. In other words, the optical imaging method employed here can be used to reveal the functional maps originally discussed by Hubel and Wiesel (1962). Similarly, the activity of an individual cell recorded within this same area was also predictable, based on the characteristics of the presented stimulus. What is new in these studies is that the researchers also examined the *spontaneous* activity of these same cell populations during periods in which there were no stimulus presentations. In this case, they used the spontaneous activity of the single (electrophysiologically-recorded) cell to trigger examination of the surrounding (optically-imaged) cellular activity pattern. They found that this spontaneous activity mimicked the stimulus-evoked patterns, in that activity in the single cell was always accompanied by emergence of the same map-like pattern in the surrounding population as that which was present during stimulus presentations. In other words, even when the system is not being driven by external stimulation, it is still, apparently, constrained in such a way that there are only a small number of active neural coalitions which can arise. Thus, any one cell becomes active only within a certain limited set of combinatorial possibilities.

Evidence for the limited number of neural activity patterns exhibited by the brain is also provided by introspective and behavioural observations. Thus, our perceptions and memories often seem to reflect a limited set of stereotyped, or canonical possibilities, and our everyday mental activity can often seem to be dominated by repetitive thoughts related to our worries and/or desires.

This reduction in the degrees of freedom available in the actual brain is thought to be due, at least in part, to constraints imposed by the limited *connectivity* between brain cells. Thus, both developmental (genetic) and environmental (learning-related) influences make it so that there are subsets of neurons which are preferentially connected to each other. For example, genetic programmes make it so that cells within each sensory organ send connections through a limited set of subcortical and cortical pathways. In turn, these connections are then fine-tuned by experience, so that the number of possible connections is further reduced by experience-driven neural activity.

Thus, the mature brain is characterized by non-homogeneity in the strengths of synaptic connections. This means that there are various subsets of neurons which are strongly interconnected, and these strong mutual connections lead to repeated co-activation of the involved neurons. These sets of strongly connected neurons are referred to as attractor networks, and these networks tend to dominate

the overall possibilities for sets of neural firing patterns. Thus, the total set of possible co-active neural subsets is considerably narrowed by the formation of these attractor networks.

Figures 1 and 2 provide very simple artificial networks which illustrate the concept of neural attractor networks. The networks presented here are extremely simplistic, and the reader is referred elsewhere (e.g. Amit *et al.*, 1994; Hopfield, 1982; McNaughton and Nadel, 1990) for a more complete discussion of this concept.

Figure 1 shows the development, and resulting mnemonic properties of an artificial attractor network at the level of visual object recognition. Here, a stimulus square (left side of each panel) is presented to the model retina. This simple version of a retina consists of a set of neural receptor elements which are activated by light that falls on them. Note that the pattern of light from the square causes a square pattern of activation (action potentials) on the sheet of retinal receptor cells.

Initially, before any learning takes place, each of these receptor cells is connected to a randomly-selected set of two or three neurons in the simulated sensory cortex. (Note, for the sake of clarity, only the connections from the currently-active retinal cells are drawn. Those from the currently-inactive retinal neurons are assumed to be present, but are omitted here.) Because of these initially random excitatory connections to the sensory cortex, there is a small set of these cortical neurons which happen to receive enough excitation to reach threshold and begin, themselves, to fire action potentials. In Figure 1 it can be seen that there were three neurons which happened to receive enough excitation to fire to the square stimulus during the initial presentation. In this way, these neurons now become the representation of 'square' for this neural system. Note also that, according to considerations presented above, we might assume that there is some unique experiential quality which accompanies the activity in these neurons. Thus, during the initial presentation of the square, the activity in these neurons generates the novel conscious experience of seeing a square.

There are also, initially, randomly-wired connections between the cortical cells themselves. Here, again, only those between the currently-active cells are shown.

Critically, the initial exposure to the square (upper panel in Figure 1) creates an enduring change in the wiring of this network in accordance with Hebb's rule (Hebb, 1949). Specifically, Hebb postulated that whenever cells that are synaptically connected fire at about the same time, those connections between them will increase in strength. This means that on later occasions, these synapses involved in the

initial exposure will be so strong that even a partial reinstatement of the original firing pattern will generate activity in the full set of cells involved in the original learning event.
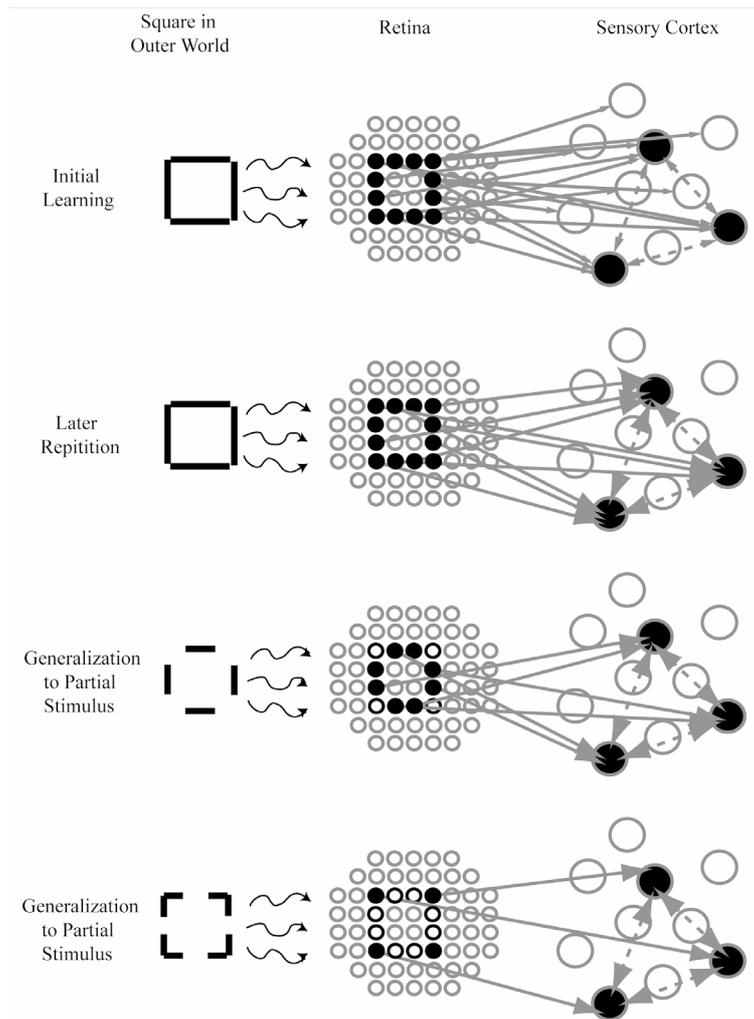

Figure 1: Simple artificial network to illustrate formation of an attractor network which recognizes a square. Each circle represents a neural element. The arrows represent axons and the excitatory synaptic connections they make with other neurons. The size of the arrowheads represents the excitatory strength of the synapse. Filled-in neurons are currently active.
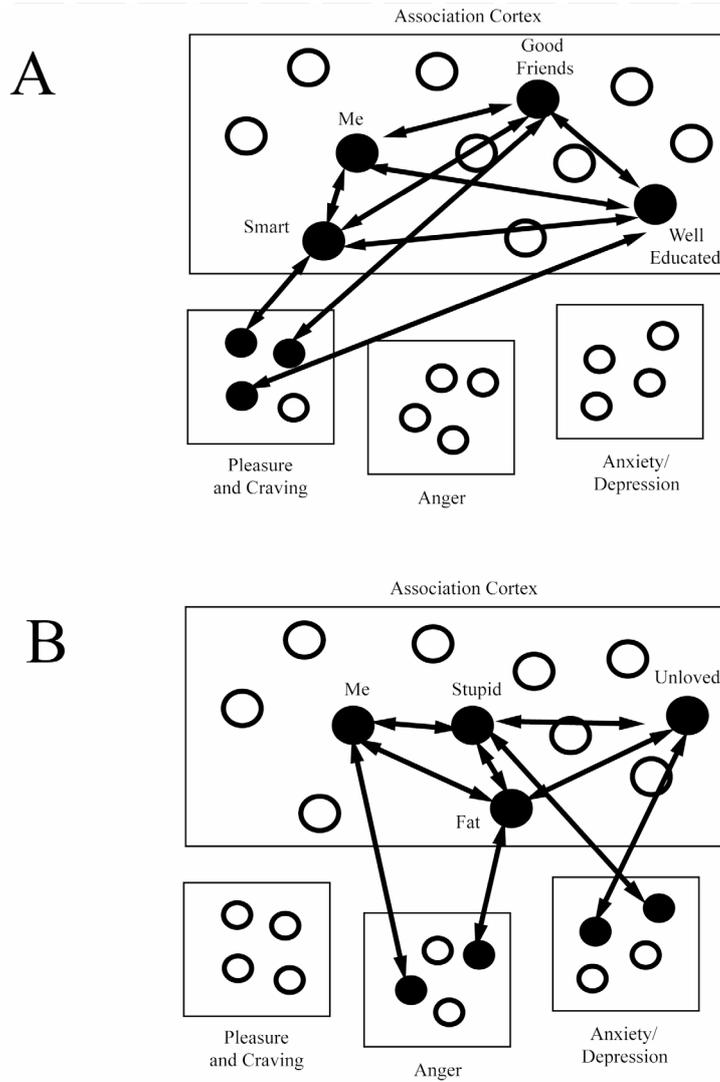
Figure 2: Illustration of attractor networks involving higher-order concepts and emotions. The circles represent neurons. The arrows represent the axons and synapses which make excitatory connections between the neurons. The filled-in circles represent currently-active neurons.

Since Hebb's initial suggestion, there has been overwhelming experimental verification of his idea (see, e.g. Bear, 2003, or Citri and Malenka, 2008, for review). A phenomenon known as long-term potentiation (LTP) of synaptic strength has been found to exist at synapses throughout many brain regions, and this form of long-lasting, activity-dependent plasticity typically follows Hebb's rule, requiring precisely-timed co-activation of the pre- and post-synaptic elements (Bi and Poo, 1998; Nelson *et al.*, 2002).

A corollary to this rule, added later (see Bear, 2003; Citri and Malenka, 2008; Dudek and Bear, 1993) is that synapses which are active pre-synaptically, but which do not succeed in firing the post-synaptic cell, will actually be weakened through a process known as long-term depression (LTD). For example, note that during initial exposure to the square (top panel) there were some axonal projections from active retinal cells which synapsed onto inactive sensory cortex cells (those that did not happen to fire during the presentation of the square). This uncorrelated activity between the pre- and post-synaptic sides of the synapses results in a weakening of those synapses.

The results of this Hebbian learning are illustrated in the lower three panels of Figure 1 (note only currently-active axons and synapses are shown). Here, the synapses which were active both pre- and post-synaptically during initial learning have become stronger through LTP, while those that were active only pre-synaptically have been weakened, through the process of LTD. Here, the strengthened synapses are shown using larger arrowheads, while the weakened synapses have been omitted entirely, for clarity.

This set of interconnected cells shown in the lower three panels of Figure 1 constitute an attractor network. Specifically, they are a set of strongly interconnected cells which, due to these strong connections, tend to always become activated together. Thus, these strong synaptic weights, worn in by experience, form a sort of 'rut' in the brain architecture. They decrease the degrees of freedom in the network (Buzsaki, 2006).

The lower two panels in Figure 1 show how this attractor network acts to facilitate object recognition, even under circumstances in which there is only a partial version of the original training square. Here, because the synaptic connections involved in the original learning have become so strong, activation of even a subset of the original neurons causes a reinstatement of the whole pattern. Note that the same three cortical neurons fire in response to each of the partial

squares shown in the lower two panels, even though there is *no overlap* in the *retinal* activation pattern for these two versions of the square.

Within the western tradition of psychology, this robust object recognition tends to be celebrated, while in relation to the Buddhist perspective, this could be viewed as a failure to discern detail.

Figure 2 illustrates this same attractor network idea in a simple artificial network meant to correspond to a higher conceptual level of information processing. In particular, the cortical association area represented here might serve as a model for certain areas which appear to preferentially code for concepts related to self (see Austin, 2006, chapter 52 for review). The upper panel (A) shows an example of an attractor state that might be active when we are in a good mood.

Note that the model neurons in associative cortex are shown here connected to neurons in a separate brain region labelled 'Pleasure and Craving'. Cell activity in the nucleus accumbens, along with its dopaminergic afferents, is thought to somehow orchestrate both reward and craving, at both the behavioural and experiential levels (Robinson and Berridge, 2003; Wise, 2004). Thus the nucleus accumbens may map onto the 'Pleasure and Craving' region depicted in Figure 2. Importantly, there is evidence that connections between accumbens cells and other cognitive and sensory brain regions can be built up during experience, via Hebbian plasticity mechanisms like those outlined above (Hyman *et al.*, 2006). The strong connections which cause this attractor to 'boot up' were, presumably, built in during experiences in which we were surrounded by loving family and friends who gave us praise and support. These circumstances would, presumably, cause co-activation of the associative cortical cells which represent the positive autobiographical thoughts, and, at the same time, the positive regard itself may induce activity in the nucleus accumbens.

The existence of an attractor network something like this would imply that we may frequently experience positive thoughts about ourselves, and these would be accompanied by some mix of pleasure and craving, as orchestrated by the nucleus accumbens. At a behavioural level, this type of accumbens activation generates intense behavioural activation and reward-seeking. This idea is reminiscent of the Buddhist emphasis on the problems related to ego or self (Klesha-Mind, as described below). Buddhist teachings place a strong emphasis on the idea that the tendency to fixate on a delusional, constructed image of ourselves, along with the concomitant craving and obsession, is a major source of our suffering and isolation.

The lower panel (B) of Figure 2 shows an attractor network like that which might be booted up when we are in a bad mood. This network was presumably built up during hostile experience in the world. In this case, the active neurons in the association cortex are those which code for negative self-related concepts. These cortical cells are shown here as interconnected with cells involved with anger (perhaps located in hypothalamic or other brainstem regions), as well as those related to anxiety and depression (perhaps in the extended amygdala). Presumably, each of these emotional responses may be evoked in the hostile social situation in which these insults were received. Work using research animals has shown that anxiety/depression symptoms evoked by activity in these structures tends to become conditioned (via Hebbian mechanisms) to contexts which resemble those involved in the original traumatic experience(s) (reviewed in Davis *et al.*, 2006; Walker *et al.*, 2003).

Attractors like those illustrated in Figures 1 and 2 are present at every level of information processing, and are thought to be responsible for learned perceptual abilities, as well as explicit memories and motor habits. Thus, for example, Hebbian long-term plasticity is thought to underlie the response properties of neurons in primary visual cortex (Bear, 2003; Hubel and Wiesel, 1959; 1962; Fregnac and Schultz, 1999), spatial and episodic memory in the hippocampus (Marr, 1971; McNaughton and Morris, 1987), and motor learning in the cerebellum (Marr, 1969), to name just a few.

Close Neural Synchrony is Orchestrated by Gamma Oscillations, and this Synchrony Provides the Basis for Both Conscious Phenomena and LTP

Thus far I have outlined evidence that both the emergence of individual conscious phenomena, as well as the synaptic plasticity necessary to develop attractor networks, depends on synchronous activity in subsets of neurons. What remains to be specified is just how close in time the action potentials from different cells must be, in order to be considered synchronous with regard to the above effects. Also, how does the brain manage to arrange for the required level of synchrony?

A large volume of data from a variety of sources suggests that the timeframe for both the emergence of conscious percepts, as well as for optimal Hebbian plasticity, consists of a window of just a few milliseconds, and that this level of synchrony is provided by ambient gamma-frequency oscillations (Bi and Poo, 1998; Buzsaki, 2006, chapter 9; Crick and Koch, 1990; Engel *et al.*, 1999; Llinas *et al.*,

1998; Markram *et al.*, 1997; Nelson *et al.*, 2002; Singer and Gray, 1995; Singer, 1998; Traub *et al.*, 1998). That is, cells must be co-active within approximately 1–3 milliseconds of one another for optimal Hebbian plasticity and also for the emergence of identifiable, individual phenomenal events. This window corresponds to intervals of excitatory depolarization which are provided by neural oscillations within the gamma frequency range.

To understand this situation, it must first be recognized that all neurons are constantly engaged in membrane voltage oscillations of one form or another (see Buzsaki, 2006). This means that the neurons are constantly oscillating between membrane voltages which bring them close to their threshold for firing an action potential, and voltages which may be far below this threshold. There is a wide range of frequencies over which these voltage oscillations may take place. The frequency for a given neuron at any one time is influenced by a complex combination of the cell's intrinsic properties, as well as the variety of extrinsic influences impinging on the cell at that moment.

Of relevance here is that active involvement in stimulus processing seems to evoke oscillations within the gamma frequency range (often approximately 40–60 Hz). These oscillations arise very specifically and transiently within subsets of neurons involved in processing individual stimuli. Because of the relatively high frequency of the gamma oscillations, different cells firing within a given peak in the oscillation must, necessarily, fire within a few milliseconds of one another.

The connection between this gamma-induced firing synchrony and conscious perception has been revealed in a series of powerful experiments by Singer and colleagues (reviewed in Engel *et al.*, 1999; Singer, 1998; Singer and Gray, 1995). These investigators looked at activity in sets of neurons in each of two different locations within visual cortical areas. The researchers used stimulus configurations which could activate cells in both locations (based on stimulus properties such as location within the visual field, directional orientation, direction of movement, etc.) They observed, first, that stimulus presentation induced *local* gamma oscillations and firing synchrony. Of relevance here is that when cells in the two different areas were activated by the same stimulus, the firing was also synchronous *across the two areas*. Alternatively, if two clearly distinct stimuli were used (one for each of the two recorded brain locations), then the firing across these two brain areas was not synchronous. For example, when a single, long, horizontal bar was moved across the visual field so that it activated cells in each of two cortical columns with collinear horizontal receptive fields, then cells in the two columns fired synchronously.

In contrast, if two different bars, moving in different directions were used to activate cells in the two areas, both sets of cells fired at gamma frequency, but the two sets were not in synchrony with each other. In other words, when cells represent a unitary perceptual element, they synchronize.

These workers theorize that it is this synchrony which somehow gives rise to the conscious perception of a single entity. In contrast, asynchronous activity between two different areas apparently gives rise to the perception of two different elements.

Findings of stimulus-induced, close synchrony across brain regions have been replicated in numerous additional brain areas, including the olfactory, auditory and somatosensory cortex, motor systems, and subcortical areas (see Engle *et al.*, 1999, for review).[3]

In addition, as mentioned above, detailed studies of the exact timing requirements for the induction of LTP have revealed that this plasticity is most powerfully induced by coincident activity within intervals which are orchestrated at gamma frequency (reviewed in Nelson *et al.*, 2002; Traub *et al.*, 1998). This requirement for precise timing is known as Spike Timing Dependent Plasticity (Abbot and Nelson, 2000; Bi and Poo, 1998), and has been the subject of a great deal of empirical work over the last decade.

Thus, gamma provides the vehicle for the establishment of attractor networks via Hebbian plasticity, and it also thus provides the vehicle for the subsequent reinstatement of activity in these networks during later presentations of the same or similar stimulus conditions. When these networks are active under the conditions imposed by gamma-frequency oscillations, they give rise to phenomenal events in consciousness. According to Spivey and colleagues (see Spivey and Dale, 2004), our ongoing stream of consciousness is determined by the constant ebb and flow of activity in these networks.

These observations will be relevant below, where evidence is reviewed to show that Buddhist meditation induces very powerful gamma oscillations.

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[3]   Note, much of the early work on this synchronous cell activity was performed on anaesthetized cats, so that there could be some question as to the relevance of these findings in relation to consciousness. However, considerable subsequent work on awake monkeys and humans (e.g. Maldonado *et al.*, 2008; Melloni *et al.*, 2007; Uhlhaas *et al.*, 2008) suggests that the conclusions from the original work on cats are, indeed, relevant in relation to consciousness.

A Speculative Mapping Between Buddhist Introspective Accounts of Mind and Neuroscientific Accounts of Brain

The Buddhist introspective tradition provides an account of mind (Everyday Consciousness) in which all events and aspects of consciousness are placed into eight categories. This 'Everyday Consciousness' refers to the pre-enlightened version of mind, which is the mind that most of us experience on a day-to-day basis.

Buddhist tradition also provides a description of the enlightened mind (Buddha-Awakening). Although there seem to be very few living individuals who claim to be enlightened, this description is nonetheless useful for the general Buddhist practitioner, because it provides a roadmap, and a source of confirmation for one's progress on the Buddhist path.

EVERYDAY CONSCIOUSNESS	BUDDHA-AWAKENING
Unstable Consciousness	Primordial Awareness that Knows the Nature of Reality Exactly As It Is
Eye Consciousness	
Ear Consciousness	Primordial Awareness that Knows the Nature of Reality to Its Full Extent
Nose Consciousness	
Tongue Consciousness	
Body Consciousness	Mirrorlike Primordial Awareness (Ability to see others' thoughts and feelings clearly)
Mind Consciousness	
Stable Consciousness	Discriminating Primordial Awareness (Ability to clearly discern differences without delusion or labelling)
Klesha-Mind (Manas)	
All-Base (Store) Consciousness	Primordial Awareness that Accomplishes All Action (Ability to act clearly and effectively)

Table 1: Categories within Everyday Consciousness and Buddha-Awakening

These accounts of the enlightened mind typically include five categories of consciousness. Note, this seems to imply that the eight Everyday Consciousnesses are collapsed into the five categories of Buddha-Awakening over the course of Buddhist practice. Thus, it seems that the mind is so thoroughly restructured that the old categories are no longer discernable, and, in the enlightened state, only five categories are necessary. In fact, although the full account of Buddha-Awakening includes five categories, these can be viewed as just

different aspects of the fundamental property of the enlightened mind, known as *primordial awareness*. This primordial awareness provides the basis for seeing the 'true nature of reality'.

Table 1 provides a listing of the types of consciousness in each of the everyday and awakened minds. The terminology for both 'Everyday Consciousness' and 'Buddha-Awakening' used here follows the usage in Thrangu Rinpoche's (2002) text on mind and the path to enlightenment.

Everyday Consciousness and its Neural Correlates

Table 2 provides a list of each of the types of consciousness, along with a tentative guess regarding the brain structures and processes to which each of these may correspond.

The unstable consciousnesses

The first six consciousnesses are characterized as unstable, in that events (perceptions, ideas, concepts, feelings) within these consciousnesses constantly arise and then vanish. In other words, events within these first six constitute our ongoing stream of consciousness.

Of these six, the first five are each associated with one of the five senses. Each of the sense consciousnesses are regarded as pre-conceptual. They represent the initial perception of objects and events from the outer world, and they take place in the instant prior to any judgment or categorization. They are also unaccompanied by any emotional component. Since these pre-conceptual sense consciousnesses are less relevant to the present considerations, I will omit any detailed description of these, except to say that Buddhist accounts state that the physical basis for each of these sense consciousnesses resides in a 'subtle faculty' located within each of the relevant sense organs. I reflect this Buddhist assertion in Table 2 (right column), but also allow for the possibility that the physical plant for pre-conceptual conscious sensory experience may extend to certain additional nervous system regions, such as primary sensory cortical areas.

The last of the unstable consciousnesses is mind consciousness. It is within mind consciousness that our everyday thoughts arise. These include judgments, such as 'this is good', 'that is bad', 'I am miserable', 'I am fine', 'that is a cat', 'this is a chair', 'the most recent U.S. Supreme Court decision was unfair', etc.

MIND	BRAIN
Everyday Consciousness	Strong Attractor Networks
Eye Consciousness	Electrochemical Events in Retina (and possible additional regions?)
Ear Consciousness	Electrochemical Events in Cochlear Hair Cells (and possible additional regions?)
Nose Consciousness	Electrochemical Events in Olfactory Receptor Cells (and possible additional regions?)
Tongue Consciousness	Electrochemical Events in Taste Receptor Cells (and possible additional regions?)
Mind Consciousness	Electrochemical Events in Central Nervous System
Klesha-Mind (Manas)	Stored Information in Cortex Plus Activity in Nucleus Accumbens
All-Base (Store) Consciousness	The Entire Set of Synaptic Connections and Their Relative Weights (Strengths) Worn in by Experience and Heredity
Buddha-Awakening	Loosened Attractor Networks
The Five Primordial Awarenesses (See Table 1)	All Sensory and Central Brain Regions Interconnected Through Transformed Synaptic Weights

Table 2: Speculative Mapping Between Buddhist Categories of Consciousness and Brain Regions/Activities

Unlike the five sense consciousnesses, mind consciousness does not directly perceive objects from the outer world. Rather, the basis for the arising of phenomena in mind consciousness can be either a perceptual event from one of the sense consciousnesses, or can be another, preceding phenomenon in mind consciousness itself.

In the former case, in which a preceding sense consciousness gives rise to a phenomenon in mind consciousness, this means that mind consciousness also perceives objects from the outer world, just not directly. Defining characteristics of these indirect perceptions of outer objects are, first, that they are not as clear as those within the original sense consciousness. Thus when we recall an object from memory (using mind consciousness), the level of detail will not be as great as when we perceive the object directly using our eyes. Second, the perceptions of objects that take place within mind consciousness are, at

least partly, mind consciousness's own inventions. That is, although they may resemble the original percept from the sense consciousness, they also reveal a strong influence of the structure of mind consciousness itself.

As noted above, thoughts within mind consciousness itself can also form the basis for the arising of subsequent thoughts (phenomena). Thus, we can become 'lost in thought' when mind consciousness gives rise to a causally-connected succession of thoughts, ideas, images, etc.

Also worth mentioning is that, as long as we are not yet enlightened, mind consciousness will cling to an endless series of repetitive, often senseless, thoughts which are conditioned by past experience. In this way, mind consciousness provides the mechanism for neurotic attachment, and is the root for affliction and suffering.

With regard to the physical basis (faculty) for mind consciousness, according to Thrangu Rinpoche (2002), Buddhist teachings assert that, unlike the sense consciousnesses (which are each assumed to reside in their respective sense organ, such as eye, ear, etc.), there is no particular location to which the mind consciousness can be localized. In light of contemporary neuroscientific considerations, however, it seems reasonable to suggest that mind consciousness might correspond to the biochemical activity of large parts of, or perhaps all of, the cerebral cortex. In addition, the fact that mind consciousness also includes emotions, such as happiness, desire, craving, fear, anger, etc. we may also want to consider that the faculty which provides the basis for mind consciousness would include subcortical structures as well. Indeed, perhaps the entire central nervous system should be included here.

Within the various central nervous system structures involved in mind consciousness, it seems that the basis for the endless stream of repetitive thoughts mentioned above could be the constant shifting activation of attractor networks like those illustrated in Figure 2.

The stable consciousnesses

Of the total eight forms of everyday consciousness, the last two are referred to as stable consciousnesses. This means that these consciousnesses are always present, unlike the other six. Thus, for example, particular events within eye consciousness come and go while our eyes are open. Similarly, the thoughts and feelings within mind consciousness constantly arise and fade. In contrast, both of the stable consciousnesses are always present, even when we sleep or are under the influence of an anaesthetic.

Klesha-Mind: the seventh type of consciousness is referred to, in different texts, either as Klesha-Mind or Manas. This form of consciousness is related to the idea of self and self-preservation. The idea of Klesha-Mind is complex and multi-faceted. I will provide only a brief outline here, and the reader is referred elsewhere (e.g. Thrangu Rinpoche, 2002; Thich Nhat Hanh, 2006) for more detailed accounts.

Klesha-Mind involves, in part, the subset of stored imprints which have to do with our concept of ourselves. Presumably, this includes a set of autobiographical facts related to our physicality, personal history, and attributes, such as those suggested in Figure 2. In addition, Klesha-Mind includes a set of connected emotional and motivational mechanisms, also suggested in Figure 2, which orchestrate feelings such as craving (for things which are to our benefit) and aversion (for those things which are not part of us, or which may hurt us). The survival instincts and addictive, acquisitive tendencies included in Klesha-Mind are viewed as ever-present. Thus, even when we are asleep, we are ready to jump up to defend against an intruder, or attend to conditions of extreme cold, hunger, etc.

All-Base Consciousness (Store Consciousness): Buddhist teachings assert that the eighth form of consciousness, All-Base consciousness, forms the basis for all the other consciousnesses (Thich Nhat Hanh, 2006). In psychological terms, I believe All-Base (Store) consciousness corresponds, quite simply, to memory. However, in this case, the concept of memory must be extended to include a kind of inherited 'memory' which is responsible for species-specific knowledge and behavioural tendencies built in automatically during development.

Thus, in terms of brain structures, it seems that All-Base consciousness may correspond to the axons and synapses which, together, serve to connect the neurons within the nervous system. One aspect of these connections is the fact that the strength of any one synapse constantly changes as a result of experience. In other words, these synaptic connections form the basis for memory storage in accordance with Hebb's famous (1949) postulate.

One reason for asserting the correspondence between the Buddhist All-Base, or Store, consciousness and synaptic connections is the Buddhist assertion that All-Base consciousness forms the connection between different parts of mind, so that the mind becomes a unified whole. As stated by Thrangu Rinpoche:

> Though each of the particular consciousnesses has its own specific functions and defining characteristics, you can, from the absolute point

of view, only talk of the mind as a singularity. The mind is one; its essence is one. It has its specific defining characteristics and functions, but only a single expression which is clear and cognizing. When the eyes see an object and the mind immediately apprehends that object without having to check or confirm it through any other process, or when mind consciousness understands ear consciousness immediately, a connection of mutuality is indicated. Though the mind is divided into different categories, the connection comes about due to the single nature of the all-base consciousness. Being the basis for all aspects of mind, it is designated as the eighth consciousness. (Thrangu Rinpoche, 2002, p. 35)

Thus, All-Base consciousness provides connections between different parts of the mind, just as axons and synapses provide connections between different parts of the brain.

However, there is an additional, critical aspect of the All-Base consciousness which typically receives much more emphasis within Buddhist texts. This is the ability of the All-Base to seize and store experience and then, later, replay that experience when the conditions are right. The following description is provided by Thrangu Rinpoche:

The all-base consciousness expresses itself in two different ways. Firstly, it is the 'all-base that seizes karmic imprints'. That means all karmic imprints, such as the perceptions of the eyes, ears, nose, tongue, or those of the body, as well as all mental activities including those of a studious nature, are grasped by the all-base so they will not be forgotten. In this way memories are made: something is seized and thereafter not forgotten. None of the consciousnesses of the six collections can seize their imprints. These consciousnesses dissolve as soon as they arise. However, the corresponding karmic imprints are stored within the all-base. They are collected there and thus not forgotten. If we learn something today the corresponding information is stored in the form of karmic imprints within the all-base, and this is why it is possible to remember it tomorrow or at a later date. In this respect — that of the functions of seizing, storing, and not thereafter forgetting — the all-base consciousness is called 'all-base that seizes karmic imprints'.

The second aspect of the all-base consciousness is called the 'all-base of complete ripening'. This designates the possibility of allowing the karmic imprints that were once stored in the mind to reappear again. The future reappearance of karmic imprints is the function of the all-base of complete ripening. (Thrangu Rinpoche, 2002, pp. 35–36)

These descriptions of the All-Base, or Store, consciousness sound remarkably similar to modern descriptions of content-addressable memory (e.g. Hebb, 1949; Marr, 1971). In this, transient perceptions and thoughts are orchestrated by momentary activity in cell assemblies. This transient 'rehearsal' leads to lasting changes in synaptic

strength, so that the involved neurons become more strongly con-nected, thus resulting in the formation of lasting attractor networks like those shown in Figures 1 and 2. It seems that it is the *pattern of synaptic weights* (developed as a result of both genetic and environ-mental influences) which constitutes the neural analogue to the Bud-dhist All-Base (Store) consciousness.

Buddha-Awakening and its Neural Correlates

> The concepts of letting go and nonclinging are simple. Our condition-ing and habit of mind are strong, though, and it is easy for us to get caught over and over again in our daily lives. We need to acknowledge this and accept that it is the nature of being human… We must find a way to recondition our minds, and ultimately free ourselves from condition-ing altogether. (Shankman, 2008)

The primordial awareness of the dharmadhatu

At the core of the primordial awareness of the dharmadhatu is 'the ability to know the nature of reality exactly as it is'. That is, we are delivered into a state in which each situation appears to us as novel and clear, unencumbered by our conditioned tendencies to code all events in terms of our own ego needs, fears, aversions, and desires. As we move closer to this primordial awareness, we gradually leave behind the endless, repetitive, delusional thoughts and perceptions of Everyday Consciousness. In general, we are liberated from dualistic thinking in which items and events are categorized into 'this' and 'that'.

Of central importance here is that, according to Buddhist teaching, the mechanism for this liberation is 'nothing other than transforma-tion of the all-base mind' (Thrangu Rinpoche, 2002), also referred to as 'transformation at the base' (Thich Nhat Hanh, 2006). Thus, in this process we cleanse our karmic imprints, so that we are free from the struggle and delusion of Everyday Consciousness. Recall that I have suggested that these karmic imprints can be equated with the stored pattern of synaptic weights like those responsible for attractor net-works such as those illustrated in Figures 1 and 2.

The central idea being presented in this article is that this 'transfor-mation of the All-Base' corresponds to a loosening of, or release from, certain of the attractor networks which have been established during our lifetime of experiences and actions.

Thus, one possibility is that meditation could evoke a neural state in which the brain is comparatively open to the ongoing stream of novel input from the outer world, while at the same time, less given to the rehearsal/reinstatement of previously-learned patterns. Interestingly,

it has been suggested that the neurotransmitter acetylcholine may acutely induce exactly this pattern of changed relative synaptic efficacy (Giocomo and Hasselmo, 2007; Hasselmo and McGaughy, 2004).

Specifically, it has been suggested that acetylcholine may dampen local feedback and recurrent synaptic connections which are largely responsible for both learning and reinstatement of conditioned patterns like those shown in Figures 1 and 2, while at the same time enhancing afferent input which is responsible for conveying new information from the outer world. Within Figure 1, the *recurrent connections* consist of the connections between the neurons within sensory cortex, while the *afferent inputs* to this area consist of the connections from the retina to the sensory cortex. In Figure 2, the cortical *recurrent (feedback)* connections consist of the synaptic connections between neurons within the association cortex (for example, those between the 'Me', 'Smart', and 'Well Educated' neurons). In contrast, *afferent connections* in Figure 2 would consist of inputs to this area from more primary sensory regions (not shown in Figure 2). This pattern of afferent and recurrent connections is repeated throughout each level of the cerebral cortex. Thus, the principle cells within each cortical region receive inputs from 'earlier' processing regions (afferent input), and also receive recurrent inputs from other cells within the local region (recurrent connections). According to Hasselmo and colleagues (see Giocomo and Hasselmo, 2007; Hasselmo and McGaughy, 2004, for review) acetylcholine consistently, throughout the cortex, serves to amplify the strength of the afferent inputs, while dampening the efficacy of the recurrent connections. Thus, according to this idea, when cortical acetylcholine levels are high, the cortex is in a state of heightened responsiveness to ongoing sensory stimuli, with reduced interference from previously-learned memories. This enhances both processing and learning in relation to afferent inputs.

As reviewed below, there is evidence that acetylcholine levels are likely very high during periods of meditation. Thus, it is possible that meditation may provide practice periods during which this state of heightened and flexible attentiveness to outside influences is induced. In addition, it could be that these practice sessions also somehow allow for a shift toward this open attentiveness as a default state, so that the adept meditator becomes increasingly flexible and open in everyday interactions.

A second possibility is that, at least in certain critical brain regions, there could be neural plasticity induced during meditation which involves lasting changes in our established pattern of synaptic

weights. For example, Hebbian connections responsible for conditioned craving, or perhaps those responsible for learned aversions and fears could be transformed during meditation practice, so that these conditioned networks loosen their grip on our emotions and behavioural reactions. Importantly, the high levels of synchronous gamma activity present during meditation, as well as the postulated high levels of cortical acetylcholine during meditation both contribute to enhanced LTP (see above and Giocomo and Hasselmo, 2007; Hasselmo and McGaughy, 2004).

If it is true that Buddhist meditation practice somehow lessens the impact of previously-established Hebbian connectivity patterns, then this would perhaps result in an increase in the precision of the relationship between brain activity and the outer world. Thus, the brain would be free to produce novel firing patterns in response to novel external input. In other words, the brain would do a better job of reflecting the world, in all its diversity and vicissitudes. This may correspond to the Buddhist sense of 'knowing reality as it is'.

In addition, there would be less tendency for perseveration and repetition (over time) of particular activity patterns. In other words, there would not be certain strong networks which would repeatedly arise spontaneously to compete for and win dominance over momentary brain activity.

Meditation Practice
and its Possible Neural Correlates

The ordinary mind of an ordinary sentient being, as it were, disappears. Consequently, discursive thoughts become dormant, and roving thoughts vanish into the space of awareness… Adhering to the experiences of vacuity and luminosity, while looking inwards, the appearance of oneself, others, and objects vanish. This is the substrate consciousness… one has come to the essential nature of the mind. (Dudjom Lingpa, as quoted in Wallace, 2007a)

Buddhist Meditation

There are a wide variety of contemplative practices included within the Buddhist traditions. Here, I will outline what is perhaps the most basic, foundational practice.

Specifically, within Tibetan Buddhism, perhaps the most commonly-used form of meditation is shamatha-vipashyana. This seems to be the form of meditation most commonly taught to beginners, and it is also said that the basic shamatha meditation is all that is needed to go all the way to enlightenment (Shankman, 2008). The term shamatha

refers to a calming of the mind, while the term vipashyana refers to insight about the nature of mind.

In this shamatha-vipashyana meditation, one typically focuses on some object, such as the breath. A typical instruction might be to just simply notice each time there is an out-breath. The idea here is to gradually learn to become sufficiently mindful so that it is increasingly possible to 'stay with the breath'. Typically, especially in the beginning, there are many thoughts which arise during this effort, and we often forget entirely about the breath for long periods of time within the meditation session. The practice consists of simply learning to notice when this thinking takes place, label it as 'thinking', and return to the breath.

The term vipashyana refers to the fact that the vigilant watching of thoughts which arise allows us to gain insight about our habitual thought patterns, the inconsequentiality of these constantly-arising thoughts, and the nature of thought itself.

More relevant to the current discussion is the shamatha aspect of this meditation practice. Shamatha refers to a state of mind in which the usual ceaseless arising of one thought after the next gradually subsides. Somehow, as a result of the constant interruption of everyday thoughts, in accordance with the meditation instructions, the mind comes to rest in a state of tranquility, devoid of any discernable content. In this state the meditator is fully awake and conscious, but is said to be experiencing the substrate of consciousness itself, or the true nature of mind (Wallace, 2007a).

Brain Correlates of Meditation Practice and the Enduring Results of the Practice

Periods of shamatha apparently provide practice sessions in which no attractor states are booted up

As outlined above, it has been theorized that any one conscious thought or perception may depend on the closely-synchronous co-activation of sets of neurons which constitute the cell assemblies corresponding to that particular mental event.

If it is true that conscious percepts and ideas are generated by synchronous activation of neurons within attractor networks, then it seems that the shamatha meditation state, in which there is a dissolution of conceptual and discursive thought, may correspond to brain states in which there are no activated attractor states. Thus, the absence of identifiable thoughts and percepts suggests the absence of attractor states.

This means that, despite the fact that the brain of the meditator is, presumably, equipped with Hebbian synaptic weights which have been worn in through experience, the shamatha meditation practices apparently somehow temporarily override the resulting attractor networks, so that there are no identifiable thoughts during these states. This suggests that, during these meditative periods, the brain apparently skates through a series of undifferentiated, novel patterns in which, presumably, there is still some brain activity (membrane oscillations, action potentials, synaptic activity), yet none of this activity corresponds to identifiable thoughts, ideas, concepts, etc.

Buddhist meditation is accompanied by strong, synchronous, global neural membrane oscillation within the gamma frequency range

Given that conditioned attractor networks are a very powerful source of control over neural activity patterns, how can these attractor networks be overridden during meditation? One possible clue comes from the numerous investigations of brain EEG activity during various types of meditation (reviewed in Cahn and Polish, 2006; Austin, 2006). One consistent finding is that meditation is typically accompanied by strong oscillatory signals within each of the theta/alpha (4–9 hertz) and gamma (>30 hertz) frequency ranges. (Note this means that the fast gamma oscillations are nested within the slower theta/alpha oscillations.)

In addition, a recent study of highly-trained, long-time Tibetan Buddhist practitioners during loving kindness and compassion meditation (which, like shamatha, involves an absence of images, memories, or referents) has suggested that these oscillations are *synchronized* throughout much of the cortical mantle (Lutz *et al.*, 2004). Thus, this work suggests that the neural cells throughout the cortex, and, likely, at least some subcortical areas as well (Manns *et al.*, 2000; Jones, 2004), are all brought into a pattern of synchronous trans-membrane electrical oscillation during certain meditative states.

Also notable is that the amplitude of the gamma-frequency oscillations observed in accomplished meditators, which presumably reflects both the number of involved neurons as well as the precision of their synchrony, is 'the highest reported in the literature in a non-pathological context' (Lutz *et al.*, 2004). Indeed, a number of EEG researchers have commented on the fact that the unusually high amplitude of EEG activity during meditation is reminiscent of that observed in association with seizure activity (Buzsaki, 2006, chapter 8) and, in fact, it has been suggested that meditation could be a danger for those

susceptible to epileptic seizures (see Lansky and St Louis, 2006, for review). Thus, the above work suggests that meditation induces precisely synchronous cell membrane oscillations and action potentials within the gamma frequency range, across a massive number and spatial distribution of central nervous system neurons.

It is curious that, even though Singer and colleagues have provided evidence that conscious events result from simultaneous activity of neurons synchronized within the gamma-frequency time window, in the case of at least some forms of meditation, this synchrony exists in the absence of any identifiable thoughts. How can this massive synchrony give rise to no thought, rather than thought?

One possibility is that, since the synchronization is global, and since it takes place under circumstances in which thoughts are constantly disrupted through repeated return to the meditation object (e.g. the breath), it could be that a state develops in which the individual attractors are continuously 'swamped'. According to this idea, since the synchrony is global, no one attractor can 'win' in any given instant. Thus, the set of neurons which happen to fire within any one gamma cycle would be a novel set (not previously co-active together), and would not correspond to identifiable thoughts or percepts.

The high levels of gamma activity during meditation may induce synaptic plasticity in many cortical areas

Importantly, these transient meditation-induced states of no attractor activity would also be expected to have lasting consequences if it is assumed that synaptic plasticity (LTP and/or LTD) takes place during the meditative episodes. Specifically, each of the transient and unique patterns of randomly co-active neurons might be expected to induce some LTP in the involved synapses. At the same time, the lack of synchronous co-activity between neurons involved in previously-trained attractor networks would be expected to result in LTD (Bear, 2003). As reviewed above, the synchronous gamma activity observed during meditation does, indeed, set the optimal condition for the induction of synaptic plasticity.

The synchronous theta/alpha and gamma EEG activity during meditation is likely induced by subcortical cholinergic neuron activity

There is a system of sub-cortical nuclei which are thought to work together to control state changes in consciousness and behaviour over the course of the sleep–wake cycle (Steriade and McCarley, 1990). The mechanism for this control is thought to involve cerebral EEG

states (Steriade, 2004) which, in turn, serve as gates to either facilitate or diminish arousal, attention, and responsiveness to external stimulation, depending on the frequency of the entrained EEG oscillations.

Among these sub-cortical nuclei are a set of cholinergic nuclei (nuclei containing cells which release acetylcholine as their neurotransmitter), including the pedunculopontine nucleus, the laterodorsal tegmental nucleus, the septal and diagonal band nuclei, and certain basal forebrain cells. These cholinergic cell groups become active both during attentive wakefulness and also during rapid-eye-movement (REM) sleep (reviewed in Jones, 2004). A great deal of empirical work has shown that activation of these cholinergic nuclei serves, first, to block the slow wave oscillations and sleep spindles characteristic of slow wave sleep, and, second, to generate the theta and gamma frequency oscillations characteristic of attentive wakefulness and REM sleep.

If it is assumed that cholinergic mechanisms are also responsible for the initiation of theta and gamma activity during meditation, this suggests that the process of meditation itself somehow activates these cholinergic cell groups (as do many other wakeful activities). In the case of meditation, it seems likely that forebrain influences somehow brought into play by the meditation instructions are the likely source of activation for the cholinergic cell groups. One unique aspect of this cholinergic influence during meditation, however, is that, apparently, the cholinergic activation is not limited to a small set of task-specific or sense modality-specific cholinergic neurons, as is often the case (Buzsaki, 2006; Fournier *et al.*, 2004). Rather, it seems that meditation practice somehow initiates global, synchronous activation of the cholinergic cell groups which, in turn, pace the synchronous cortical theta and gamma oscillations.

Of relevance here, theoretical work, reviewed above, on the influence of cortical acetylcholine suggests that, within each local cortical region, high levels of acetylcholine reduce the activity of feedback synapses involved in memory consolidation and reinstatement, while increasing the activity (and plasticity) in synapses which process input from sensory and other distant cortical regions (Hasselmo and McGaughy, 2004; Giocomo and Hasselmo, 2007). Thus, high acetylcholine reduces the tendency to rehearse previously-formed attractor networks and enhances the tendency toward new learning.

Summary of Meditation-Induced Effects on the Brain

It appears that meditation practice somehow induces uniformly high levels of acetylcholine throughout the cortical mantle. This high acetylcholine, in turn, induces powerful, synchronous gamma-frequency oscillations throughout cortex. It is postulated here that this synchronous gamma activity may serve to 'swamp' conditioned attractor networks, so that the meditator experiences periods of lucid non-thought. Attractor network activity would also be weakened due to the acetylcholine-induced dampening of the feedback loops necessary for their activation.

It seems possible that, whatever the mechanism is for the acute induction of the high acetylcholine/gamma activity during meditation itself, this mechanism could become stronger during repeated meditation practice. Thus, the meditation practitioner may be becoming better at inducing these states of open attentiveness, and this may extend into waking periods other than formal meditation. Support for this idea is provided by the fact that the accomplished meditators recorded in the Lutz *et al.* (2004) study cited above also showed significantly and substantially higher levels of *resting* (prior to meditation) gamma frequency activity.

In addition, the combination of high acetylcholine and gamma set the conditions for neural plasticity (LTP and LTD), especially for the afferent inputs to each region. As outlined above, this may allow for a gentle undoing of at least some of the learned patterns within these afferent connections.

Note that since the recurrent and local feedback connections throughout cortex are dampened during high acetylcholine conditions, these connections are, presumably, also somewhat protected from the synaptic rewiring (LTP and LTD) during this time. This is important, because it could allow for the maintenance of essential learned skills and memories.

Conclusions

The ideas presented here have dealt with a core Buddhist concept related to the 'emptiness' of 'appearances', and the possibility of liberation from these appearances. It is important to note that many other central Buddhist ideas have been left out of consideration here. These include themes such as mindfulness, self, compassion, virtue, impermanence, and bliss, to name a few.

In describing the proposed meditation-induced state and trait changes, I have stopped short of specifying precisely which brain

regions and conditioned behaviours, memories, and perceptual pro-
cesses may be involved. Buddhist philosophy suggests that these
changes must be quite wide-ranging. However, any lasting changes
must, at the same time, be somewhat subtle and/or selective, since
Buddhist practice does not erase conditioned habits so thoroughly as
to leave the meditation practitioner helpless to perform necessary life
skills.

It is hoped that this essay can be part of a larger effort to investigate
these and additional topics from a combined introspectionist and
neuroscientific point of view. As called for elsewhere (Petitmengin,
2009; Varela and Shear, 1999; Wallace, 2007a,b) this line of investi-
gation could be part of a reinstatement of introspection as a proper
part of psychological and neuroscientific methodology.

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