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THE ELECTROMAGNETIC FIELD THEORY OF CONSCIOUSNESS:
A TESTABLE HYPOTHESIS ABOUT THE CHARACTERISTICS OF CONSCIOUS
AS OPPOSED TO NON-CONSCIOUS FIELDS

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ABSTRACT

The electromagnetic field theory of consciousness proposes that conscious experiences are identical with certain electromagnetic patterns generated by the brain. While the theory has always acknowledged that not all of the electromagnetic patterns generated by brain activity are conscious, until now it has not been able to specify what might distinguish conscious patterns from non-conscious patterns. Here a hypothesis is proposed about the 3-D shape of electromagnetic fields that are conscious, as opposed to those that are not conscious. Seven predictions arising from this hypothesis are described. Existing empirical evidence shows that four of these predictions have already been successfully tested. Requirements for experimental testing of the other three are discussed.

1. INTRODUCTION

The definition of consciousness is famously difficult. Not only is it true that, as Searle (1993) says, “Like most words, “consciousness” does not admit of a definition in terms of genus and differentia or necessary and sufficient conditions”: but also, ‘consciousness’ is even worse than most words in that the phenomenon it describes is so private that it is impossible to know for sure whether it even exists in any entity other than oneself. Nonetheless, as Searle (ibid) goes on, “it is important to say exactly what we are talking about, because the phenomenon of consciousness that we are interested in needs to be distinguished from certain other phenomena such as attention, knowledge and self-consciousness. By “consciousness”, I simply mean those subjective states of sentience or awareness that begin when one wakes up in the morning from a dreamless sleep and continue throughout the day until one goes to sleep at night or falls into a coma, or dies, or otherwise becomes, as one would say, “unconscious.” I will take this as a working definition for the purposes of this essay, in hopes that a better definition may eventually be possible as a result of the experiments proposed here.

The problem about developing a better definition of consciousness is that in order to define something, you have to know what it is. While we can each experience from moment to moment the contents of our own consciousness, we do not yet know what consciousness in general – as opposed, for example, to matter in general – is. There are presently a large number of theories about what consciousness is. There are dualist or semidualist theories, which say that at least some aspect of consciousness is not physical (and therefore not accessible to science). There are quantum mechanical theories, which say that consciousness is physical, but just as ontologically mysterious or hard to understand in everyday terms as everything else about quantum mechanics. Finally, there are at the moment three main non-quantum physicalist theories which are distinctive enough to drive a particular experimental program.

1. The *psychoneural identity theory* was originally proposed by the philosophers Place (1956), Feigl (1958) and Smart (1959) and rebranded some decades later as “the astonishing hypothesis” (Crick 1994). This idea is summarised as follows (Crick 1994, p.3) : “The Astonishing Hypothesis is that “You”, your joys and your sorrows, your memories and your ambitions, your sense of personal identity and free will, are in fact no more than the behavior of a vast assembly of nerve cells and their associated molecules. As Lewis Carroll’s Alice might have phrased it: “You’re nothing but a pack of neurons.”” It is never specified by this hypothesis exactly what makes the behaviour of some neurons conscious and others not, but the unspoken consensus at present seems to be that particular patterns of action potential firing may be the key. Thus the experimental paradigm dictated by this theory tends to involve the recording of single units, which are an extracellular measure of the firing of individual neurons. While neurophysiologists as a group usually prefer not to think about consciousness at all, the scientific tribe who are most comfortable with the psychoneural identity theory do tend to be neurophysiologists.
2. The second major idea about the nature of consciousness that presently drives a particular experimental approach is *functionalism*. Both the provenance and the defining assertion of functionalism are succinctly expressed by Tononi and Edelman (1998): “Consciousness, as William James pointed out, is not a thing, but a process or stream that is changing on a time scale of fractions of seconds (James 1890).” Since the mantra of functionalists is “consciousness is a process, not a thing”, this group of workers are not very interested in the specific neural correlates of consciousness, preferring to study the abstract processes that underpin mental functions. Generalisation is always dangerous, but the main scientific group who take this

approach tend to be psychologists. Artificial intelligence (AI) aficionados and to a certain extent connectionists also appreciate the possibility promised by functionalism of producing consciousness by replicating functions using hardware instead of wetware.

3. The third major idea about the nature of consciousness that has the potential to drive a distinct experimental paradigm is *the electromagnetic (EM) field theory of consciousness* (Pockett 1999, 2000, 2002, 2007, 2011). This theory proposes that conscious experiences are identical with certain spatial EM patterns generated by neural activity in the brains of conscious subjects. While the EM field theory is an identity theory, it differs radically from the psychoneural identity theory in that (like functionalism) it predicts the possibility of producing consciousness without neurons. According to the EM field theory, putatively conscious EM fields could in principle be generated using hardware instead of wetware. There are major differences between the EM field theory and either functionalism or connectionism with regard to the methodology for generating such non-biological consciousness: while the approach of the EM field theorist would be to measure the 3-D shape of the putatively conscious fields produced by the brain and reproduce these fields artificially, the approach of connectionists and present-day AI workers would be to model the functions performed by the brain and hope that any model or instantiation which reproduces the function will reproduce whatever conscious experience goes with the function. However, there is no intrinsic incompatibility or argument between EM field theorists and functionalists. The EM field theory essentially provides a means of reifying functionalism, by removing the reason for the latter's prohibition of "things" as the basis of conscious experiences. Electromagnetic fields are like things, but unlike material things they can and do change on a time scale of fractions of seconds. The current experimental program that best fits the EM field theory of consciousness involves recording scalp or intracranial EEG, (although most scientists who use those techniques at present either don't know about the EM field theory of consciousness or actively repudiate it). The hypothesis put forward in the main body of this paper points the way to a distinctly new experimental paradigm, which promises to reveal the 3-D shape of conscious EM fields.

Three useful objections to the EM field theory of consciousness

As with any novel theory, a number of objections to the EM field theory of consciousness have been raised. Six of the most common ones were answered in the original statement of the theory (Pockett 2000). However, over the last eleven years three more objections have arisen which are not answered by Pockett (2000). There is no doubt that objections to a theory can be extremely useful: the answer to the second of these objections has recently allowed an answer to the third, and the answer to the third is here expanded into the hypothesis outlined in the present paper. To take them one by one, the three objections and their answers are as follows.

Objection 1

The first objection is that it is not intuitively obvious why – or in more extreme versions of the objection 'remotely plausible' that – any particular spatial electromagnetic pattern should be identical with a particular conscious experience. What can it be, the objector asks, about possessing this specific spatial pattern that gives an EM field the characteristic features of conscious experiences: qualia, subjectivity, privileged access, whatever?

Answer to Objection 1

Aside from the privileged access part, which is easy (see Objection 2), this question is exactly analogous to asking a physicist to explain what it is about the arrangement of mass/energy into a particular spatial pattern of atoms and molecules that gives it the characteristic features of matter. This is a question that is unlikely to be asked. If it were, the physicist's response would probably be bemused incomprehension.

The issue here is that to those of us who were educated in the 'developed' world in the latter half of the 20th century, it seems completely unremarkable that matter should be composed of molecules, atoms, electrons, protons and an ever-expanding zoo of smaller particles, and that different forms of matter should exist as a result of different arrangements of these entities. It does not seem necessary to ask *why* this should be so – we simply accept that this is the way matter is. But if these ideas seem in any way inherently or intuitively plausible to us (as opposed to plausible because they have been experimentally proven over the course of several centuries) it is only because we are so familiar with them. Were we living in, say, China during the 14th century, we would almost certainly greet the same ideas with undisguised scepticism and a polite request that it should be explained to us why any sane person should even entertain the thought that an obviously solid rock is actually composed of tiny, invisible bits of buzzing energy. (Where on earth does THAT idea come from? we might have asked – to which our 14th century atomist might have responded with a long peroration about the philosophical origins of atomist ideas in both ancient Greece and ancient India¹ – but that's beside the point).

The point is that intuition can be trained. When it comes to mind, which has traditionally been set in opposition to matter, most of us are not – yet, perhaps – used to the idea that consciousness is composed of spatial electromagnetic patterns. So that idea does not – yet, perhaps – seem “remotely plausible”. But should that idea eventually be shown to withstand experimental scrutiny as robustly as the idea of atoms did, we will no doubt again stop asking why things should be so and accept that this is just the way consciousness is. That time may yet be some way off: my estimate is that we are presently at about the same stage with regard to proving the existence of conscious EM fields as Newton, Boyle, Huygens, Leeuwenhoek and Halley were with regard to proving the existence of material atoms in the latter half of the 17th century. (But on the question of where this not-yet-intuitive idea about consciousness came from, yes, what could be seen as a field theory of consciousness was also put forward in both ancient India and ancient Greece (Pockett 2000)).

Objection 2

The second major objection to the EM field theory of consciousness that was not answered by Pockett (2000) pertains to one of the features of the idea that was originally touted as a major point in its favour. Electromagnetic fields are well documented to be capable of causing neurons to fire. This, it was suggested at some length in Chapter 7 of Pockett (2000), provided a potential physical mechanism by which consciousness could cause behaviour. But the objection to that idea was not long in coming – and this time the objector was the author of the original theory herself (Pockett 2002).

¹ Leucippus and Democritus taught atomism in Greece around 450 BC. Kanada wrote the explicitly atomistic Vaisesika Sutras in India around 200 BC. See Pockett (2000).

The objection hinges on the fact that the sorts of EM patterns proposed by the theory as being conscious are extremely local. They fall off with distance according to not merely an inverse square law, but an inverse cube law (Pockett 2011). This means that they exist at all only within a few millimetres of the neurons that generate them. Such extreme localisedness is reflected in the name of the individual EM waveforms that make up each putatively conscious pattern – *local* field potentials, aka LFPs. It means that these patterns (i) can not be shared with other conscious entities (which explains the privileged access part of Objection 1); and more importantly (ii) are not even accessible to the neurons within the same nervous system that directly cause behaviour. The neurons that most directly cause behaviour are motor neurons in the spinal cord. These are largely driven by neurons in the primary motor cortex, which in turn are driven by neurons in the premotor and supplementary motor areas of the cortex, with a good deal of interplay from subcortical structures. Simple physics dictates that the putatively conscious EM patterns generated by most other areas of brain (with the possible exception of primary somatosensory cortex, although there the orientation of the pattern poses a problem) are too far away to be accessible to any of these neurons. So Objection 2 is that putatively conscious EM field patterns can not directly cause the firing of motor neurons. They can not be the direct cause of behaviour.

For a while, this objection seemed fatal to the theory. If, as we all intuitively believe, voluntary behaviour is directly caused by consciousness; and if behaviour can not be directly caused by the EM patterns this theory talks about; then consciousness can not be the EM patterns this theory talks about.

Answer to Objection 2

The answer to this objection lies in the assumption that voluntary behaviour is directly caused by consciousness. It seems that in this respect, intuition has let us down again. Consciousness does not directly cause voluntary behaviour (Pockett 2004, 2011; Pockett et al 2006; 2009). Observations leading to this conclusion include the following:

- (1) The conscious experience of willing or causing a movement is neither necessary nor sufficient for the performance of voluntary actions. Wegner (2002) discusses a wide variety of circumstances in which subjects either perform apparently volitional actions without consciously willing them (conscious will is not necessary), consciously will volitional actions that they do not objectively perform (conscious will is not sufficient), or feel after the event that they have willed actions which were actually forced or even made by the experimenter (conscious will can be wrongly inferred, even when it logically can not have existed).
- (2) The subjective experience of agency or ownership of an action is dissociable from objective agency. Lesions in the right parietal cortex can produce syndromes in which the patient perceives their hand to be under the control of someone else (Leiguardia et al 1993; Bundick & Spinella 2000) or their limbs as not belonging to them at all (Critchley 1953; Nightingale 1982; Daprati et al 2000).
- (3) Libet's famous experiments (Libet et al 1982, 1983), show that the brain activity coupled to a spontaneous action (i.e. the readiness potential or RP) starts of the order of 350 ms before the subject reports having consciously willed the action. For many years this highly repeatable and methodologically robust result was taken to mean that voluntary acts are initiated pre-consciously. Recently Pockett and Purdy (2010) showed that when the same action is made not

spontaneously but as the result of a specific decision, the RP preceding the action shortens so that the RP starts at about the same time as the reported willing of the action – which on the face of it restores the possibility that consciousness does directly cause actions. But by the time this experiment hit the presses, experiments by others had shown that the time at which the subject reports having willed an action is affected both by events that take place after the action (Lau et al 2007) and by manipulation of feedback to the subject about the time at which the action occurs (Banks and Isham 2009). For example, if the subject is led to believe that their individual actions happen progressively later than they actually did, the time at which these acts were willed is also reported as being progressively later. This latter group of experiments and others described in Section 5.1 strongly suggest that the *initiation* of voluntary actions is not consciously experienced at all. The subject simply infers after the event that they must have initiated their movement shortly before they made it.

The conclusion forced by this confluence of evidence is that voluntary actions are not initiated by consciousness. We infer that our conscious thoughts directly cause our actions, but they actually don't. Returning to Objection 2, if consciousness does not cause behaviour, there is no need to postulate that putatively conscious fields cause behaviour. The conclusion that consciousness does not initiate or directly cause behaviour relieves putatively conscious EM fields of any requirement to cause the firing of behaviour-initiating neurons. Fortuitously, it also allows development of an answer to Objection 3.

Objection 3

The third objection is that the EM field theory of consciousness as it stands consists of little more than a bare statement of the idea that consciousness is some kind of electromagnetic pattern generated by brains. The idea has not been developed or elaborated enough even to specify what distinguishes conscious EM fields from unconscious EM fields, let alone what distinguishes the fields of cognitive thoughts from those of the various sensory modalities like hearing, touch or vision, what makes one modality of sensory experience different from another, or what separates the plethora of different experiences within one sensory modality. Without at least an attempt at such specification, the EM field theory fails to rise above the vagueness that characterises both psychoneural identity theory and functionalism.

Answer to Objection 3

The answer to Objection 2 now provides a lever with which to prise open the question of what distinguishes the brain-generated EM fields that do underpin conscious experiences from those that do not. The answer to Objection 2 tells us that brain activity underpinning the initiation of movements is not associated with conscious experiences. It is clear *a priori* that spatial patterns of local field potentials are critically dependent on neuroanatomy, specifically cytoarchitectonics. So all we need do is ask what is different about the cytoarchitectonics of areas that subserve the initiation of movements. Surprisingly, the answer is clearcut and stunningly simple. Unlike almost all other areas of neocortex, motor areas lack a layer 4. The next section explains how this creates a particular 3-D pattern of LFPs, which may now be postulated to be necessary (though clearly not sufficient) for conscious experience.

2. GENERATION OF LOCAL FIELD POTENTIALS AND EFFECT OF MISSING LAYER 4

In order to appreciate the hypothesis proposed in this paper, it is necessary first to understand the mechanism by which the fields referred to in the EM field theory of consciousness are generated by the brain. Importantly, these fields are different from the hypothetical 'figure currents' whose existence was proposed by Köhler (1920, 1929, 1938, 1940) and experimentally disproved by Lashley (Lashley and Semmes 1951) and Sperry (Sperry et al 1955) sixty years ago. Rather, the electromagnetic patterns of the modern EM field theory of consciousness are nothing more exotic than spatial patterns of local field potentials (LFPs).

LFPs are easily measured extracellular electrical events that are generated by the synchronous activity of a large number of chemical synapses on cortical pyramidal neurons. The main factor permitting LFP generation is the spatial alignment of pyramidal cell apical dendrites. In the neocortex of mammalian brains, the cell body of each pyramidal cell is located in one of 6 histologically distinguishable layers which stack on top of one another from the inside of the cortex (layer 6) to the outside (layer 1). The long apical dendrite of each pyramidal cell extends radially in a more or less straight line from the cell body towards the surface of the brain, in most cases ending in a tuft in layer 1, just below the pia mater. In layer 1, both cortico-cortical axons from other regions of the cortex and thalamo-cortical axons from M-type cells in thalamus (Jones 2007; Rubio-Garrido et al 2009) make excitatory chemical synapses on the pyramidal cell apical dendrites. Figure 1 shows diagrammatically how the activation of such synapses produces LFPs.

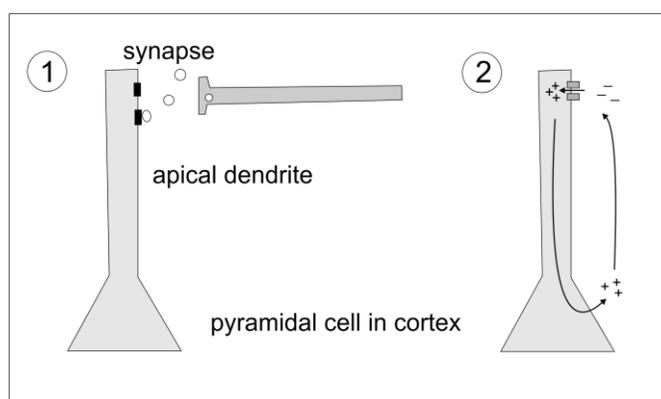


Figure 1: Diagrammatic representation of the generation of LFPs (local field potentials).

In step 1, vesicles of chemical neurotransmitter are released from the presynaptic axon terminal into the synaptic cleft and bind to receptors on the apical dendrite of the pyramidal cell. In step 2, ion channels open and positive ions flow into the dendrite. The influx of positive ions leaves a transient negativity in the extracellular fluid outside the dendrite. If enough synapses on enough neighbouring dendrites fire synchronously, this transient extracellular negativity achieves an amplitude of anything up to tens of mV, and is called a population epp (Figure 2). In neocortical layer 1, where the synapses in question are located, the population epp is negative-going (upper part of step 2 Figure 1; Figure 2). However, the associated intra-cellular positivity in the dendrite essentially has to go somewhere, so to complete the circuit, positive ions more or less simultaneously flow out of the pyramidal cell in the region of the pyramidal cell body, producing a positive-going population epp at that level (lower part of step 2 Figure 1; Figure 2). If the associated intracellular epps are large enough to trigger action potentials at

the initial segment of enough pyramidal cell axons, a relatively small and brief population spike appears in the middle of the population epsps (Figure 2).

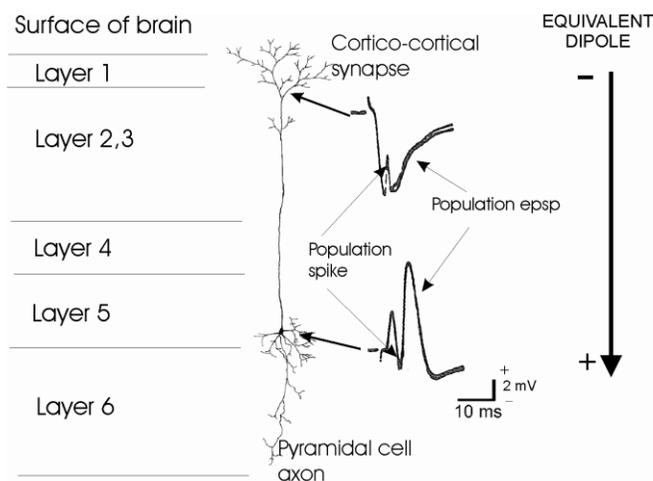


Figure 2: LFPs in neocortex.

This general mechanism of LFP production was worked out for hippocampal LFPs about 40 years ago (e.g. Bliss and Lømo 1973) and is well enough accepted to have entered various neuroscience textbooks (e.g. Bindman and Lippold 1981; Kandel et al 1991).

Figures 1 and 2 illustrate two important facts about LFPs:

- (1) LFPs are largely synaptic potentials, generated by the action of excitatory chemical synapses. Action potentials have little effect on the shape of LFPs. This latter fact has been noted since the earliest studies (Bremer 1938; 1949; Eccles 1951) and may well be explained (Bédard et al 2004) by the strong low-pass filtering properties of cortical tissue, which are probably due to significantly non-homogeneous extracellular resistance (see Section 5.5.1).
- (2) LFPs always come in pairs: one negative-going transient around the synapses and one positive-going transient outside another region of the cell. These positive-negative pairs are conveniently modelled as dipoles (right hand side of Figure 2).

The EM field theory of consciousness proposes that conscious fields are distinguished from different conscious fields on the one hand – and from completely non-conscious fields on the other – by the 3-dimensional patterns in which these dipoles are arranged.

One anatomical fact which is especially important in the context of the hypothesis presented here is that in neocortical layer 4, there are virtually no pyramidal cell bodies. Layer 4 consists mainly of stellate cells, which receive input from C-type cells in the thalamus (Jones 2007). Since the dendrites of stellate cells are not spatially aligned but extend from the cell body in all directions, the dipole charges generated by synaptic activity on stellate dendrites tend to cancel each other out. Therefore, activity in layer 4 is very likely (although this question has not yet been investigated experimentally) not to generate any measurable LFPs (see Figure 3).

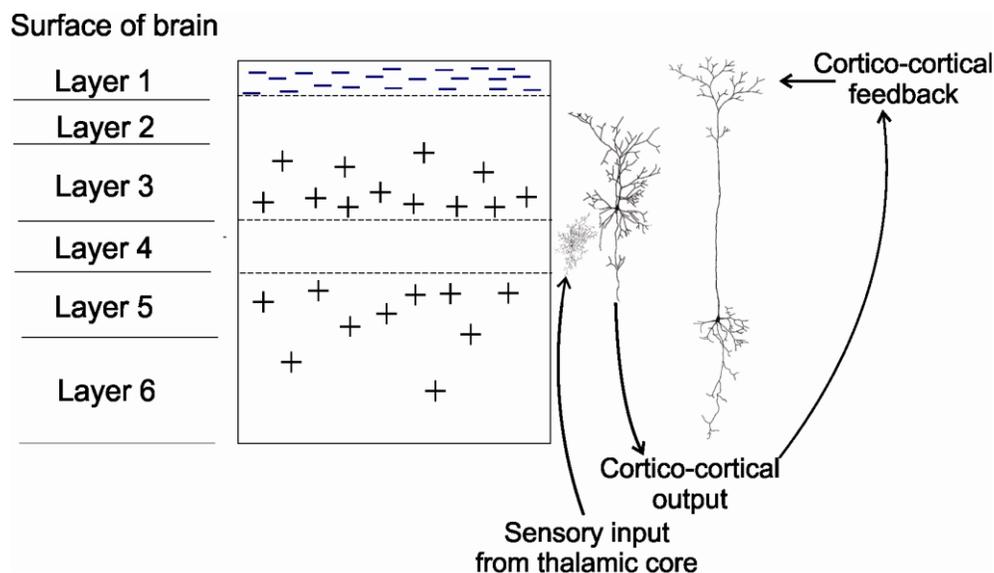


Figure 3: Sensory input to layer 4 does not generate measurable LFPs

3. THE HYPOTHESIS: A SPATIAL FEATURE DIAGNOSTIC OF CONSCIOUS EM FIELDS

The hypothesis proposed here is that one necessary (albeit clearly not sufficient) characteristic of conscious as opposed to non-conscious EM fields or patterns of charge is a spatial structure something like that shown in Figure 3. The essence of the proposal is that in the radial direction (perpendicular to the surface of the cortex) conscious fields will have a surface layer of negative charge above two deeper layers of positive charge, separated by a distinct neutral layer. A 3-D model of such fields is shown in Figure 4.

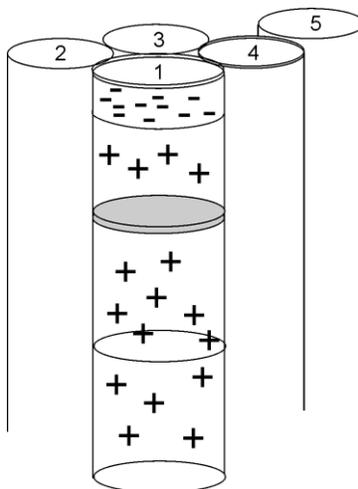


Figure 4: 3-D model of conscious field. Gray layer in middle of column 1 is neutral.

According to this hypothesis, the main distinguishing feature of conscious fields is the neutral layer in the middle of the field pattern (Figure 4 and Figure 5A). Many brain-generated EM fields that are not conscious will be similar, except that they will lack the neutral layer (Figure 5B).

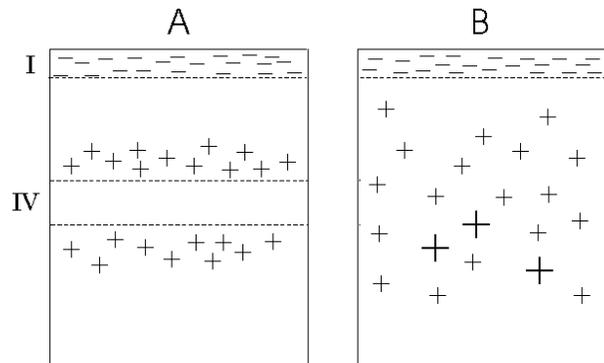


Figure 5: Hypothesized distribution of electric charge in brain-generated fields that are (A) conscious and (B) non-conscious (one example from many possibilities). Roman numerals to left indicate cortical layers.

At this point, two secondary hypotheses can also be foreshadowed regarding the characteristics distinguishing (a) different modalities of conscious experience and (b) different experiences within any given modality:

- (a) On the axis radial or perpendicular to the surface of the cortex, the putatively conscious patterns are most affected by the laminal locations of contributing pyramidal cell bodies, as described in Section 2. In humans, the overall thickness of the cerebral cortex varies between 1mm and 4.5 mm and there are large regional differences in the relative thickness of each of the six cytoarchitectonic layers (Campbell 1905; Brodman 1909; Fischl and Dale 2000). In line with the well-accepted association of various cytoarchitectonically defined areas with particular sensory and cognitive functions (Campbell 1905; Brodman 1909) it is likely that variations in the radial structure of LFP patterns will distinguish different kinds or modalities of conscious experience.
- (b) On the axes tangential to the surface of the cortex, some consciousness-related EM patterns exist with spatial frequencies in the 1 – 3 mm range (Pockett et al 2007). This spatial frequency suggests that the patterns are underpinned by variations in the activity of neighboring cortical columns (Mountcastle 1957, 1997; Hubel and Wiesel 1963; Abeles and Goldstein 1970; Swindale 1990; Horton and Adams 2005; Innocenti and Vercelli 2010). It is likely that differences in these tangential patterns – i.e. differences in the degrees of positivity/negativity between columns 1,2,3,4 and 5 in Figure 4 – will distinguish different individual experiences within a given modality.

These two secondary hypotheses will not be developed further in the present paper, which will concentrate on the main hypothesis.

4. PREDICTIONS OF THE MAIN HYPOTHESIS

The main hypothesis proposed here gives rise to a number of testable predictions.

1. Any area of brain that can generate EM fields with the hypothesized structure might or might not produce conscious experiences. Any area of brain that can not generate EM fields with the hypothesized structure will not produce conscious experiences.
2. Conscious sensory experiences will not be generated during the first, feed-forward pass of peripheral activity through primary sensory cortex. Recurrent or feed-back activity to the primary sensory cortex from other regions of cortex will be required.
3. One manifestation of this requirement for feed-back activity will be a correlation of consciousness with the firing of action potentials by particular cells in regions down-stream from the primary sensory areas.
4. Another manifestation of the requirement for feed-back activity will be synchronization during the feedback of activity in these down-stream areas and activity in the primary sensory cortex.
5. Imposition of external EM fields which may or may not vary temporally, but spatially are unpatterned, will have no effect on conscious experiences. In the terminology of physics, there will be no coupling between biological and external fields. The biologically generated spatial pattern defining the conscious experience will simply ride on top of the spatially homogeneous external field, like a boat on an ocean.
6. Imposition of external EM fields that *are* spatially patterned (in such a way that they do couple with the biologically generated fields) will affect consciousness. Specifically, imposition of an external field that is inversely patterned – one positive surface layer and two deeper negative layers, each with a strength perfectly matched to that of the biologically generated inverse pattern – will cancel the biological field and thereby obliterate the relevant conscious experience.
7. Prevention of the occurrence of LFPs in the relevant areas *without disruption of the underlying synaptic activity* will prevent the relevant conscious experiences.

Existing neurophysiological evidence relating to these predictions and proposals for testing of predictions that are not currently supported by any existing evidence are given in Section 5.

5. EXISTING EVIDENCE AND PROPOSED TESTS

5.1 Any area of brain that can generate EM fields with the hypothesized structure might or might not produce conscious experiences. Any area of brain that can not generate EM fields with the hypothesized structure will not produce conscious experiences.

Evidence relating to this prediction can be studied in two parts.

5.1.1 Any area of brain that can generate EM fields with the hypothesized structure might or might not produce conscious experiences.

At this stage, the idea that *any* area of brain gives rise to the hypothesized EM pattern is yet to be tested. The fact that LFPs are negative-going around excitatory synapses and positive-going around the corresponding cell bodies has been experimentally validated for hippocampal pyramidal cells (e.g. Bliss and Lømo 1973) and diagrams depicting a similar situation as occurring in 6-layered neocortex certainly appear in neuroscience texts (e.g. Bindman and Lippold 1981; Kandel et al 1991). But the hypothesis here suggests that EM fields with the structure shown in Figures 3, 4 and 5 might appear only in the brains of conscious subjects. It is certainly possible to measure LFPs in waking animals (e.g. Bliss and Gardner-Medwin 1973; Wiest and Nicoletti 2003; Dejean et al 2007; Eliades and Wang 2008; Roš et al 2009; Rolston et al 2009) and chronic intracortical recording is standard even in humans (e.g. Pockett and Holmes 2009). But to date, no such measurements have been done in a way that is specifically motivated by the present hypothesis. Thus, to my knowledge there are presently no reports on the simultaneous measurement of peripherally-induced LFPs at a series of depths in the 6-layered neocortex of waking mammals. While technically challenging, it should be relatively straightforward in principle to make such recordings and thereby see whether the hypothesized EM pattern does appear in the brains of waking mammals, and whether it degrades or disappears when the subject is anaesthetised or otherwise loses consciousness. Microelectrodes would have to be positioned in cortical layers 1, 2/3, 4 and 5/6; probably in small animal subjects initially, so that dye spots could be deposited after recording to confirm electrode location. The pick-up range of an electrode is reported to depend on its size (Bindman and Lippold 1981), so in order on the one hand to avoid missing the neutral layer (by contaminating records taken in putatively neutral layer 4 with pickup from the adjacent putatively negative layers 3 and 5) and on the other hand to record LFPs at all (see Section 5.5.1) it would be necessary to use microelectrodes of a size commensurate with a pick-up range of the order of 50 -100 μm . This requirement could be fulfilled by the positioning of multitrodes consisting of 10-12 glass microelectrodes, each of whose shafts was bent so that the tips were in the same axis, with tips spaced $\sim 200 \mu\text{m}$ apart, each tip with a diameter of $\sim 5 \mu\text{m}$ and an impedance of 0.5 – 3 M Ω . Alternatively a multicontact metal electrode with similar characteristics could be used.

5.1.2 Any area of brain that can not generate EM fields with the hypothesized structure will not produce conscious experiences

Of course, it is not a logical requirement of this hypothesis that the postulated EM pattern will fail to appear in unconscious subjects. The pattern in question is proposed to be necessary but not sufficient for consciousness, so if it did appear in unconscious brains one could always argue that consciousness depends on some additional, yet-unrecognised factor that is not present in unconscious brains. However, the claim that the proposed structure is necessary for consciousness does make the very strong prediction that brain areas which can not generate this spatial EM pattern will not be able to produce consciousness. In order to produce the EM field structure hypothesized here as being conscious, essentially a 6-layered architectonic structure is necessary. So the second half of Prediction 1 boils down to a prediction that areas which do not have 6-layered architectonics will not have the capacity to generate consciousness experiences. Is this supported by available evidence?

Most areas of neocortex do exhibit the necessary 6-layered structure. According to Fatterpekar et al (2002), only Brodman Areas 4, 6, 8, part of 11, 24, 25, 26, 28, 29, 30 and 33 were classified by Economo (1925, 1927) as “agranular”, which means they do not have a layer 4. These agranular areas are all

concerned with motor function (Porter and Lemon 1993; Shipp 2005). Outside the neocortex, the putatively more ancient allocortex – i.e. hippocampus and one region of what is loosely termed olfactory cortex (Mesulam and Mufson 1982) – has only 3 layers. The cerebellum is highly structured, but does not have pyramidal cells like those in the cortex at all (Eccles et al 1967). Sub-cortical structures such as thalamus, basal ganglia and amygdala do not show any layering comparable with that of cortex. So basically, the present hypothesis predicts that most areas of neocortex might or might not be capable of producing conscious experiences. The only areas in the brain that are predicted to be definitely incapable of producing conscious experiences are BA4, BA6 and BA8 (the primary motor and premotor cortices), several medial areas also concerned with motor function, the cerebellum, the hippocampus, one part of the general area including olfactory cortex, and all sub-cortical structures.

These are very specific predictions. Are they supported by the available evidence? With regard to primary motor and premotor cortex, the answer is clearly yes. When Desmurget et al (2009) directly stimulated the cortex of awake patients undergoing brain surgery, stimulation of parietal regions elicited subjective reports of a conscious intention or desire to move the relevant part of the body, which escalated with stronger stimuli to a belief that a movement had actually been made, even though no electromyographic activity was detectable. However, stimulation of the region incorporating BA4, BA6 and BA8 elicited no reports of any conscious experience and in fact firm denials that any bodily movement had taken place, even when the stimuli were so strong that movement of the relevant body part was clearly observed by the experimenters. Parietal regions are thought to generate conscious intentions to move at some time in the near future, while pre-motor cortex and its associated subcortical structures are thought to underpin movement initiation (Pockett 2006). Hence, the physiological results reported by Desmurget et al (2009) are reinforced by a wide range of psychological results showing that people are not consciously aware of the initiation of their own voluntary movements (Wegner 2002; Pockett 2004; Aarts et al 2005; Pockett et al 2006; Lau et al. 2007; Banks and Isham 2009; Kühn and Brass 2009, Rigoni et al 2010). So the prediction of the present hypothesis that precentral motor areas should not generate conscious experiences appears to be well supported by available evidence.

The present hypothesis also predicts that a number of other brain areas will be incapable of generating conscious experiences. These areas include cerebellum, hippocampus, olfactory cortex and all sub-cortical structures. To take these in turn, cerebellum is widely understood to underpin unconscious control of movements (e.g. Jeannerod 2006). Hippocampus certainly has something to do with the laying down of potentially conscious long-term declarative memories, but it is not the site where such memories are stored (Scoville and Milner 1957; Stefanacci et al 2000; Corkin 2002). The idea that hippocampus may represent a cognitive map (O'Keefe and Nadel 1978) suggests that it may subservise some form of spatial consciousness, but initial formulations of this cognitive map theory have recently been repudiated (Hardt and Nadel 2009); so at this stage there is no evidence suggesting that the hippocampus generates conscious experiences. With regard to olfaction, it is not yet clear exactly where conscious olfactory sensations (or indeed any conscious sensations) are generated, but Mesulam and Mufson (1982) show that many parts of the general region labelled olfactory cortex do have 6 layered architectonics. The neural correlates of emotion have in the past been studied primarily in the context of the neurotransmitters involved and their effects on various sub-cortical structures (Panksepp 1998; Nestler and Malenka 2004). However, 6-layered cortex does participate in the networks that incorporate these sub-cortical structures and there is evidence for the involvement of frontal and temporal grey matter in the primary emotional sensation of cocaine-induced euphoria, for example (Hitri et al 1994; Bartzokis et al 2004; Dong et al 2005).

So to summarise, the available evidence fails to disprove the current hypothesis with regard to any of the brain areas predicted to be unable to generate conscious experiences.

5.2 Conscious sensory experiences will not be generated during the first, feed-forward pass of peripheral activity through primary sensory cortex. Recurrent or feed-back activity to the primary sensory cortex from other regions of cortex will be required.

This prediction arises because feed-forward thalamic input from the peripheral sense organs initially reaches the cortex by way of the stellate cells of layer 4 (e.g. Salami et al 2003), which generate only very small LFPs because there is no anatomical alignment of multiple stellate cell dendrites (see Figure 3). As explained above, LFPs of any significant size are generated only by the activity of feed-back circuits, which synapse largely in layer 1 and generate LFP dipoles extending between layer 1 and layers 2/3 or 5/6 in neocortex.

So does existing evidence suggest that feed-back or recurrent activity is necessary for consciousness? At least with regard to the visual system, the answer is now a definitive 'yes'. After some initial controversy about whether or not V1 activity is a neural correlate of visual consciousness at all (Crick and Koch 1995a,b; Pollen 1995), evidence has steadily accumulated that consciousness does not correlate with the first, feed-forward passage of activity through V1, but does correlate with feedback to V1/V2 from 'higher' visual areas, 100 – 200 ms after the external visual stimulus (Lamme et al 1998; Lee et al 1998; Pollen 1999; Lamme and Roelfsema 2000; Pascual-Leone and Walsh 2001; Supèr et al 2001; Juan and Walsh 2003; Pollen 2003; Ro et al 2003; Juan et al 2004; Lamme 2004; Silvanto et al 2005; Fahrenfort et al 2007; Pollen 2008; Koivisto et al 2010; Thielscher et al 2010). Most of this evidence comes from experiments in which various areas of brain are temporarily inactivated using TMS (Transcranial Magnetic Stimulation) at various times after an external stimulus. For example, Boyer et al (2005) show that blindsight can be induced by brief inactivation of V1 at 100 ms post-stimulus and Silvanto et al (2005) report that consciousness of motion can be ablated by TMS delivered to any of (i) V1 at 40-60 ms (ii) V5/MT at 60-80 ms or (iii) V1 at 80-100 ms post-stimulus.

5.3 One manifestation of this requirement for feed-back activity will be a correlation of consciousness with the firing of action potentials by particular cells in regions down-stream of the primary sensory areas

Figure 2 shows that the firing of action potentials by the pyramidal cells that directly generate our putatively conscious EM fields has little effect on those fields. Population spikes may sculpt LFP patterns somewhat, but the firing of individual cells in these regions does not have much to do with the patterns we are interested in. However, in order to generate the feedback activity that produces the LFP patterns of interest, neurons must certainly fire in regions where the feedback originates. Some of the feedback in question will come from M-type cells in the thalamus, but much of it will arise in various far-flung regions of the cortex. So Prediction 3 boils down to the suggestion that recording the firing of individual cortical cells will not necessarily show correlations between consciousness and firing in regions where consciousness arises. Rather, it will show correlations between consciousness and regions where the *feedback* necessary to generate a hypothetically conscious LFP pattern arises.

This prediction is perhaps supported by a number of reports that conscious events correlate best with the firing of individual neurons in regions well outside the primary and secondary sensory areas. For example, various specific visual percepts have been correlated with the firing of single cells in the medial and inferior temporal cortices and around the superior temporal sulcus (Logothetis and Schall 1989; Leopold and Logothetis 1996; Scheinberg and Logothetis 1997; Krieman et al 2000; Quian Quiroga et al 2005). The most convincing of these experiments concerns binocular rivalry, a paradigm in which the information presented to each eye of the subject is different enough so that it cannot be fused into one binocular image but is seen as two competing images alternately, one percept replacing the other spontaneously every few seconds. Logothetis and colleagues arranged for this situation to occur in waking monkeys and correlated the firing of single cells in various regions of brain with which of the two figures the monkey reported seeing. In areas V1/2, V4 and V5, between 60% and 80% of cells depending on the area continued to respond to their preferred stimulus regardless of whether it was perceived or not. However, in areas IT (inferior temporal cortex) and STS (upper and lower banks of superior temporal sulcus) about 90% of cells reliably predicted the perceptual state of the animal, by firing only when their preferred stimulus was perceived. Because the exact moment at which the percept switched was not accessible, these experiments did not distinguish between early and late firing in V1/2. In the context of the present hypothesis, the results could be interpreted as indicating that most of the firing in early visual areas subserves early feedforward transmission (which does not correlate with perception), while firing in IT and STS initiates the feedback that is necessary for perception.

5.4 Another manifestation of the requirement for feed-back activity will be a transient synchronization during the feedback of activity in these down-stream areas and activity in the primary sensory cortex.

Coherence or synchrony has been observed as a necessary (though not sufficient) correlate of consciousness for many years now, but so far this observation has not been transparently explained in terms of its being a necessary part of any specific theory of consciousness. The present hypothesis is that certain LFP patterns are identical with consciousness. There are at least two distinct ways in which synchrony is important in the generation of LFPs.

5.4.1 Synchronous firing of many synapses required for production of LFPs

First, the synchronous firing of many cortico-cortical or thalamocortical axons is necessary to produce measurable LFPs at all. Electrophysiological potentials are measured as the voltage drop across a particular resistance. With intracellular recording, the relevant resistance is that of the cell membrane. With extracellular recording, it is the resistance of the extracellular fluid, which in most locations is very low compared with the resistance of the cell membrane. By Ohm's Law, a given current flow will produce a smaller voltage across a smaller resistance, so the amplitude of an extracellular epp is much smaller than that of an intracellular epp: extracellular epps due to activation of a single pyramidal cell are (probably) unmeasurably small. In order to produce a measurable LFP, many individual extracellular epps have to occur close to each other in both space and time. In fact the extracellular resistance in neocortex is probably not uniform, but acts to impose a low-pass filter on the electromagnetic products of neural activity (Bédard et al 2004). This means that the relatively low-frequency fluctuations of epps are measurable at much greater distances from their sites of generation than is the case for the faster action potentials, which allows spatial summation of epps over a relatively wide area.

The upshot of all this is that synchronous feedback onto the apical dendrites of a number of adjacent pyramidal cells results in more summation and thus larger LFPs. The hypothesis presented in the present paper predicts that a certain minimum amplitude of LFPs is necessary for conscious experience. This prediction is supported by the fact that perception during binocular rivalry is clearly correlated with more intense spatiotemporal electromagnetic patterns (Tononi et al 1998). Thus synchronous feedback onto many adjacent pyramidal dendrites is a necessary correlate of consciousness according to our hypothesis.

5.4.2 Long-range synchrony as an indicator of feedback activity

A second way in which synchrony is important for the generation of LFPs is that synchronous neural activity between far-flung regions of cortex serves an indicator of the presence of active feedback.

Some difficulty arises with regard to the best method of measuring feedback-related synchrony. As pointed out above, single cell technologies certainly pick up action potentials in the regions where feedback originates, but it is far from clear that the cells receiving the feedback – the cells of interest to the present hypothesis – will necessarily fire as a result of feedback to them. Reverberatory activity has to stop sometime, and perhaps the appearance in ‘early’ sensory areas of [conscious] feedback-generated LFP patterns is the normal endpoint of sensory input. On this reasoning it is possible that single cell recording techniques are better suited to the measurement of feedforward-related synchrony (Roelfsema et al 1997; Singer et al 1997) than they are to the measurement of feedback-related synchrony.

However, EEG-based phase synchrony measurements (which examine the accumulated signature of multiple LFPs rather than that of action potentials *per se*) do come with their own set of pitfalls. A major one is related to the inevitable use of a recording reference that is itself active to some varying degree (Fein et al 1988; Pockett et al 2009). Such problems can easily lead to erroneous conclusions: for example, one widely cited early report that long-distance synchrony correlated with face perception (Rodriguez et al 1999) was later shown to be repeatable only if recordings were made against a nose reference contaminated with microsaccades (Trujillo et al 2005). However, *pace* such difficulties, long-distance phase synchrony does seem to be necessary (Lutz et al 2002; Melloni et al 2007; Gaillard et al 2009; Tallon-Baudry 2009), albeit not sufficient (Pockett and Holmes 2009; Luo et al 2009), for conscious perception.

In summary, prediction 4 of the current hypothesis does appear to be supported by what relatively little evidence is available.

5.5 Imposition of external EM fields that may or may not vary temporally, but spatially are unpatterned, will have no effect on conscious experiences.

Life in the 21st century involves constant exposure to external electromagnetic fields. Microwave ovens, wireless LAN networks, radio and TV broadcasts, cell phones and a host of other sources bath us continuously in EM oscillations in the GHz and MHz ranges. In a frequency range more relevant to the oscillations generated by brains, not only high voltage electricity transmission lines but also such common appliances as hair-dryers routinely supply respectable levels of 50 or 60 Hz electromagnetism.

MRI machines generate enormous magnetic fields. And apart from the occasional visual scintillation caused by stimulation of the visual cortex in MRI magnets, none of it has any effect on consciousness.

This is entirely as predicted by the EM field theory of consciousness. According to this theory, the defining feature of fields that are conscious is not the frequency with which they wax and wane, but their 3-D spatial pattern. All of the aforementioned environmental EM fields are spatially unpatterned. One result of their spatial homogeneity is that these environmental fields have no effect on the spatial EM patterns involved in the present theory. In the terminology of physics, there is no coupling between external and biological fields. The biologically generated spatial pattern defining the conscious experience simply rides on top of the spatially homogeneous external field, like a boat on an ocean.

Another, perhaps less fortunate, result of the spatial homogeneity of common EM fields is that so far there has been no technology-driven incentive to develop signal processing techniques that would allow the mathematical description and manipulation of spatial EM patterns. Development of such techniques will be essential to the advancement of the EM field theory of consciousness.

5.6 Imposition of external EM fields that are spatially patterned, in such a way that they do couple with the biologically generated fields, will affect consciousness.

One specific example of this prediction is that imposition of an inversely patterned external field – one surface positive layer and two deeper negative layers, each with a strength perfectly tuned to that of the biologically generated pattern – will cancel the relevant biological field and thereby obliterate the relevant conscious experience. This prediction is certainly testable in principle, but at present not enough is known either about the precise patterns underlying any given conscious experience or practical means of generating such patterns using hardware to make it testable in practice.

5.7 Prevention of the occurrence of LFPs in the relevant areas *without disruption of the underlying synaptic activity* will prevent the relevant conscious experiences.

However, Prediction 7 – that disruption of the LFPs underpinning a putatively conscious em field pattern should disrupt the conscious experience in question – certainly is testable. If the means by which the LFPs were disrupted simply involved preventing the synaptic activity that generated the LFPs, the experiment would fail to distinguish between the neural identity hypothesis and the electromagnetic field hypothesis. In order to test the electromagnetic field hypothesis, it would be necessary to disrupt LFPs without disrupting the underlying synaptic activity. The most straightforward way of achieving this would be to voltage clamp the LFPs.

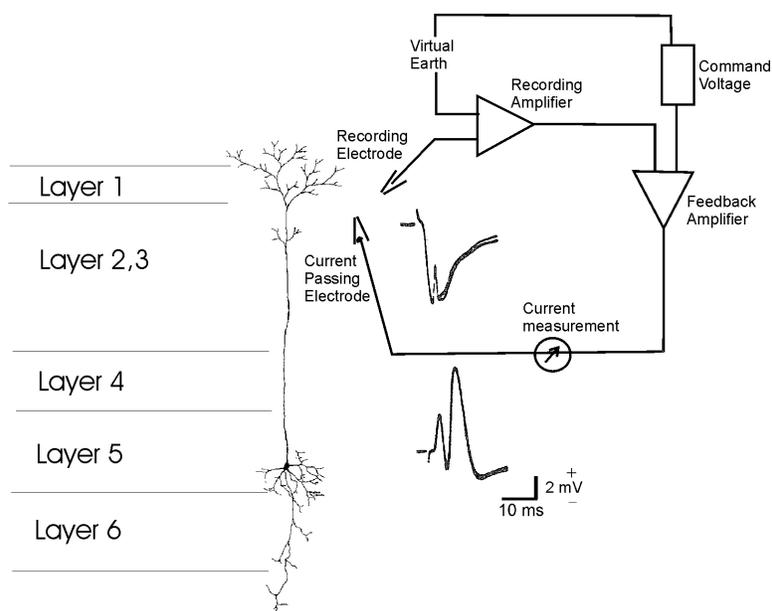


Figure 6: Schematic showing principles involved in voltage clamping LFPs

A schematic showing the principle of how a two-electrode voltage clamp might be used to clamp a negative-going population epsp in Layer 1 of the neocortex is shown in Figure 6. The recording amplifier measures the difference between electrical events at the recording electrode and a virtual earth – the result is shown as the negative-going population epsp (with its associated population spike). The feedback amplifier then makes a real-time comparison between this waveform and a command voltage, which in the present case is set to the virtual earth. Finally current is fed to the current passing electrode in such a way that the population epsp is neutralised as it occurs. In practice, the whole sequence of events would probably be best accomplished using a single microelectrode which alternates between measuring and passing current – the discontinuous single electrode voltage clamp technique popularised by Finkel and Redman (1984). It would obviously be impossible to achieve much of a space clamp in such an experiment – only the region immediately around the current passing electrode would be clamped – but this could actually be an advantage rather than a limitation because it would allow precise dissection of the region of most importance in the extracellular electric field pattern. Optimally at least two independent clamps would be applied, to control the extracellular voltages in limited regions of both layer 2/3 and layer 5/6; but according to the present hypothesis clamping even one of these areas should disrupt the overall pattern enough to disrupt the conscious experience.

At present it is far from clear exactly where in the brain the neural correlates of any given sensory experience are to be found, but the evidence cited in Section 5.2 suggests that the primary sensory area related to the sensation evoked by any given external stimulus would be a good place to start. Since most of the ion channels linked to neurotransmitter receptors are not voltage sensitive, controlling the external voltage in this region should produce relatively little effect on the synaptic action that normally generates the LFPs being controlled – in other words, the synapses should largely continue to work normally. Whether or not this expectation was fulfilled could in any case be measured directly, by measuring the current that has to be passed in order to clamp the extracellular voltage.

Experimental support for the prediction that disruption of conscious experiences can be achieved by disrupting LFP patterns without affecting the underlying synaptic activity that produces those patterns would provide (a) confirmatory evidence for the present hypothesis (b) strong support for the wider EM field theory of consciousness and (c) a potentially useful clinical method of controlling unwanted conscious experiences like chronic pain. This latter outcome would provide ethical justification for performing the voltage clamping experiment in human subjects, who could report verbally (rather than *via* pre-trained behavioral actions) on the presence or absence of particular conscious experiences. However, preliminary results from animal experiments would probably be necessary to establish both the technical details and the viability of the test as a whole.

6. DISCUSSION

The hypothesis outlined here has four important features.

First, as a hypothesis it sits squarely within a larger theory, the electromagnetic field theory of consciousness.

The only theories of the nature of consciousness that compete for the same intellectual ground as the electromagnetic field theory are (a) psychoneural identity theory (b) functionalism and (c) various theories that invoke quantum mechanical formalisms. With regard to (a) and (b), it is difficult to find any very specific statement of the modern version of the psychoneural identity theory, but its name implies the basic tenet that psyche is identical with neurons – or neural activity, or some types of neural activity. Probably the most succinct published statement of the idea is Crick's famous paraphrase of Alice in Wonderland: "You're nothing but a pack of neurons" : or, slightly more precisely "[You are] no more than the behavior of a vast assembly of nerve cells and their associated molecules." (Crick 1994). Already the insertion of the phrase "the behavior of" into this latter definition seems to make The Astonishing Hypothesis (and, inasmuch as the two can be equated, psychoneural identity theory) uncomfortably similar to the dogma of functionalism, which says "consciousness is a process, not a thing". The electromagnetic field theory of consciousness blurs this apparent distinction even further, by proposing that consciousness is not a brain process *per se*, but an electromagnetic product of a subset of brain processes – thereby reifying or providing a physical basis for functionalism's abstract "process", while at the same time removing the intuitive difficulties associated with equating functioning neurons *per se* with consciousness, as psychoneural identity theory apparently does. With regard to (c), the relationship between the electromagnetic field theory and quantum mechanical or quantum field theories of consciousness is presently moot. Several advantages enjoyed by EM field theory, which QM theories are presently hard pressed to match, are enumerated below.

The second important feature of the present hypothesis is that it draws together and provides a coherent explanation for a variety of empirical observations that otherwise appear unconnected. These observations include (i) the long-recognized regional variations in cytoarchitectonics; (ii) the fact that consciousness takes time to develop; (iii) the fact that recurrent activity is necessary for consciousness; (iv) the importance to consciousness of various kinds of synchrony; (v) the fact that spatially unpatterned external EM fields do not affect consciousness; and last but not least, (vi) the recently recognised inability of humans to perceive the initiation of their own voluntary actions.

A third feature of the present hypothesis is that it provides a transparent predictor of the circumstances under which consciousness is possible. Basically, the present hypothesis predicts that nervous systems

(or parts of nervous systems) that do not exhibit 6-layered cytoarchitectonics will not be capable of generating consciousness. This provides a basis for answering in principle the vexed question of whether or not any given animal species is consciousness-capable.

The fourth and arguably most important feature of the present hypothesis is that it is directly testable. Experimental requirements for performing the critical tests are outlined in Sections 5.1.2, 5.6 and 5.7. In particular the prediction of the hypothesis that is tested by the experiment proposed in Section 5.7 – that alteration of the field *and only the field* which goes with a particular conscious experience will alter the experience – converts the main hypothesis described in this paper from a merely correlative to a completely mechanistic construct. If this prediction is supported by the proposed experiment, the simplest explanation will be that the field *is* the conscious experience.

Of course if the experiment in Section 5.7 did produce the predicted result, it would remain logically possible that the EM field was only a correlate of something else, something completely unknown – perhaps a dualist phenomenon, inaccessible to science and ultimately unknowable. But science basically works by means of Occam's razor – the simplest explanation is generally accepted, at least for the time being, as the right one. The argument that something more complicated is the real truth could be made about absolutely anything that is presently accepted as scientific fact. Perhaps things are not as they seem. Perhaps there is a completely different explanation, about which we don't have a clue. Well yes, perhaps. But it is also possible that the desire to follow this logically impeccable but scientifically untenable line of reasoning may be at least a partial explanation for why philosophers have been hammering away at the mind-body problem for the last 2,000-odd years with so little success.

REFERENCES

- Aarts, H., Custers, R., and Wegner, D. M. (2005). On the inference of personal authorship: enhancing experienced agency by priming effect information. *Consciousness and Cognition* 14, 439–458.
- Abeles, M., and Goldstein, M.H.Jr (1970) Functional architecture in cat primary auditory cortex: columnar organization and organization according to depth. *J. Neurophysiol.* 33, 172-187.
- Banks, W. P., and Isham, E. A. (2009) We infer rather than perceive the moment we decided to act. *Psychological Science* 20, 17–21.
- Bartzokis, G., Beckson, M., Lu, P.H., Edwards N., Rapoport, R., Bridge, P., and Mintz, J. (2004) Cortical gray matter volumes are associated with subjective responses to cocaine infusion. *American Journal on Addictions* 13, 64-73.
- Bédard, C., Kröger, H. and Destexhe, A. (2004) Modelling extracellular field potentials and the frequency-filtering properties of extracellular space. *Biophysical Journal* 86(3): 1829-1842.
- Bindman, L. and Lippold, O.C.J. (1981) *The neurophysiology of the cerebral cortex*. Edward Arnold, London. 495pp.
- Bliss, T.V.P., and Gardner-Medwin A.R. (1973) Long-lasting potentiation of synaptic transmission in the dentate area of the unanaesthetized rabbit following stimulation of the perforant path. *J. Physiol.* 232, 357-374.
- Bliss, T.V.P., and Lømo, T. (1973) Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path. *J. Physiol.* 232, 331-356.
- Bremer, F. (1938) L'activité électrique de l'écorce cérébrale. *Actualités Scientifiques et Industrielles* 658: 3-46.
- Bremer, F. (1949) Considérations sur l'origine et la nature des "ondes" cérébrales. *Electroenceph. Clin. Neurophysiol.* 1: 177-193.
- Brodman K. (1909) *Vergleichende Lokalisationslehre der Grosshirnrinde: in ihren Prinzipien dargestellt auf Grund des Zellenbaues* Verlag von Johannes Barth, Leipzig. (*Brodman's localisation in the cerebral cortex: the principles of comparative localisation in the cerebral cortex based on cytoarchitectonics*. Trans J.L.Garey, Springer 1994).
- Bundick, T. Jr. and Spinella, M. (2000) Subjective experience, involuntary movement and the posterior alien hand syndrome. *Journal of Neurology, Neurosurgery and Psychiatry* 68, 83-85.
- Campbell A.W. (1905) *Histological studies on the localization of cerebral function*. Cambridge University Press.
- Corkin, S. (2002) What's new with the amnesic patient H.M.? *Nature Rev Neurosci* 3, 153- 160.
- Crick F (1994) *The astonishing hypothesis: the scientific search for the soul*. Simon & Schuster, New York, London, Toronto. p.3.
- Crick, F. and Koch, C. (1995a) Are we aware of neural activity in primary visual cortex? *Nature* 375, 121-123.
- Crick, F. and Koch, C. (1995b) Cortical areas in visual awareness: reply. *Nature* 377, 294-295.
- Critchley, M. (1953) *The Parietal Lobes*. Hafner Press, New York.
- Daprati, E., Sirigu, A., Pradat-Diehl, P., Franck, N. and Jeannerod, M. (2000) Recognition of self-produced movement in the case of severe neglect. *Neurocase* 6, 477-486.
- Dejean, C., Gross, C.E., Bioulac, B., and Boraud, T. (2007) Synchronous high-voltage spindles in the cortex-basal ganglia network of awake and unrestrained rats. *European J. Neurosci.* 25, 772-784.
- Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C and Sirigu A (2009) Movement intention after parietal cortex stimulation in humans. *Science* 324, 811- 813.

- Dong, Y., Nasif, F.J., Tsui, J.J., Ju, W.Y., Cooper, D.C., Hu, X.T., Malenka, R.C., and White, F.J. (2005) Cocaine-induced plasticity of intrinsic membrane properties in prefrontal cortex pyramidal neurons: adaptations in potassium currents. *J. Neurosci* 25(4), 936-40.
- Eccles, J.C. (1951) Interpretation of action potentials evoked in the cerebral cortex. *J. Neurophysiol.* 3: 449-464.
- Eccles J.C., Ito M. and Szentagothai J. (1967) *The cerebellum as a neuronal machine*. Springer 335pp.
- Economo C.V.von (1925) Die fünf Bautypen der Grosshirnrinde. *Schweiz Arch Neurol Psychiatri (Zürich)* 16, 266-269.
- Economo C. von (1927) *Zellaufbau der Grosshirnrinde des Menschen*. Aehn Vorlesungen. Verlag von Julius Springer.
- Eliades, S.J. and Wang, X. (2008) Chronic multi-electrode neural recording in free-roaming monkeys. *Journal of Neuroscience Methods* 172, 201-214.
- Fahrenfort, J.J., Scholte, H.S. and Lamme, V.A.F. (2007) Masking disrupts reentrant processing in human visual cortex. *J. Cog. Neurosci.* 19, 1488-1497.
- Fatterpekar, G.M., Naidich, T.P., Delman, B.N., Aguinaldo, J.G., Gultekin, S.H., Sherwood, C.C., Hof, P.R., Drayer, B.P., and Fayad, Z.A. (2002) Cytoarchitecture of the human cerebral cortex: MR microscopy of excised specimens at 9.4 Tesla. *Am J Neuroradiol* 23, 1313-1321.
- Feigl H (1958) The 'mental' and the 'physical'. *Minnesota Studies in the Philosophy of Science* Vol 2. Ed H. Feigl, G. Maxwell and M. Scriven. Minneapolis: University of Minnesota Press.
- Fein, G., Raz, J., Brown, F.F. and Merrin, E.L. (1988) Common reference coherence data are confounded by power and phase effects. *Electroenceph Clin Neurophys.* 69, 581-584.
- Finkel, A.S. and Redman, S. (1984) Theory and operation of a single microelectrode voltage clamp. *Journal of Neuroscience Methods* 11(2), 101-127.
- Fischl, B., and Dale, A.M. (2000) Measuring the thickness of the human cerebral cortex from magnetic resonance images. *Proc Natl Acad Sci USA* 97, 11050-11055.
- Gaillard, R., Dehaene, S., Adam, C., Clémenceau, S., Hasboun, D., Baulac, M., Cohen, L. and Naccache, L. (2009) Converging intracranial markers of conscious access. *PLoS Biol* 7(3): e1000061. doi:10.1371/journal.pbio.1000061
- Hardt, O., and Nadel, L. (2009) Cognitive maps and attention. *Prog. Brain Res.* 176, 181-194.
- Hitri, A., Casanova, M.F., Kleinman, J.E., and Wyatt, R.J. (1994) Fewer dopamine transporter receptors in the prefrontal cortex of cocaine users. *American Journal of Psychiatry* 151, 1074-1076.
- Horton, J.C. and Adams, D.L. (2005) The cortical column: a structure without a function. *Phil Trans R Soc B* 360, 837-862.
- Hubel, D.H., and Wiesel, T.N. (1963) Shape and arrangement of columns in cat's striate cortex. *J. Physiol.* 165, 559-568.
- Innocenti GM and Vercelli A (2010) Dendritic bundles, minicolumns, columns, and cortical output bundles. *Front Neuroanat.* 4:11. doi 10.3389/neuro.05.011.2010
- James W (1890) *The principles of psychology*. Holt, New York.
- Jeannerod M (2006) Consciousness of action as an embodied consciousness. In *Does consciousness cause behavior?* eds S. Pockett, W Banks and S Gallagher, MIT Press; Cambridge Mass; p. 25-38.
- Jones, E.G. (2007) *The thalamus*. 2nd ed. Cambridge University Press, New York.
- Juan, C.-H., and Walsh, V. (2003) Feedback to V1: a reverse hierarchy in vision. *Exp. Brain Res.* 150, 259-263.
- Juan, C.-H., Campana, G., and Walsh, V. (2004) Cortical interactions in vision and awareness: hierarchies in reverse. *Prog. Brain Res.* 144, 117-130.
- Kandel, E.R., Schwartz, J.H. and Jessell, T.M. (1991) *Principles of neural science*. 3rd Ed. Appleton and Lange, London. 1135pp.

- Koivisto, M., Mäntylä, T., and Silvanto, J. (2010) The role of early visual cortex (V1/V2) in conscious and unconscious visual perception. *Neuroimage* 51, 828-834.
- Köhler, W. (1920). *Die psychischen Gestalten in Ruhe und im stationären Zustand*. Braunschweig: Vieweg und Sohn.
- Köhler, W. (1929). *Gestalt psychology*. New York: Liveright.
- Köhler, W. (1938). *The place of value in a world of fact*. New York: Liveright.
- Köhler, W. (1940). *Dynamics in psychology*. New York: Liveright.
- Kreiman, G., Koch, C., and Fried, I. (2000) Category-specific visual responses of single neurons in the human medial temporal lobe. *Nature Neuroscience* 3, 946-953.
- Kühn, S., and Brass, M. (2009). Retrospective construction of the judgment of free choice. *Consciousness and Cognition* 18, 12–21.
- Lamme, V.A.F. (2004) Separate neural definitions of visual consciousness and visual attention; a case for phenomenal awareness. *Neural Networks* 17, 861-872.
- Lamme, V.A.F., Supèr, H. and Spekreijse, H. (1998) Feedforward, horizontal and feedback processing in the visual cortex. *Curr. Opin. Neurobiol* 8, 529-535.
- Lamme, V.A.F. and Roelfsema, P. (2000) The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* 23, 571-579.
- Lashley, K.S., & Semmes, K.L.C.a.J. (1951). An examination of the electric field theory of cerebral integration. *Psychological Review*, 58, 123-136.
- Lau, H. C., Rogers, R. D., and Passingham, R. E. (2007). Manipulating the experienced onset of intention after action execution. *Journal of Cognitive Neuroscience* 19, 81–90.
- Leiguardia, R., Starkstein, S., Nogues, M., Berthier, M. and Arbeláiz, R. (1993) Paroxysmal alien hand syndrom. *Journal of Neurology, Neurosurgery and Psychiatry* 56, 788-792.
- Lee, T.S., Mumford, D., Romero, R., and Lamme, V.A.F. (1998) The role of primary visual cortex in higher level vision. *Vision Research* 38, 2429-2454.
- Leopold, D.A. and Logothetis, N.K. (1996) Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* 379, 549-553.
- Libet, B., Wright, E.W. Jr, Feinstein, B. and Pearl, D.K. (1982) Readiness potentials preceding unrestricted 'spontaneous' vs pre-planned voluntary acts. *Electroencephalography and Clinical Neurophysiology* 54, 322-335.
- Libet, B., Gleason, C.A., Wright, E.W. and Pearl, D.K. (1983) Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). *Brain* 106, 623-642.
- Logothetis, N.K., and Schall, J.D. (1989) Neuronal correlates of subjective visual perception. *Science* 245, 761-763.
- Luo, Q., Mitchell, D., Cheng, X., Mondillo, K., Mccaffrey, D., Holroyd, T., Carver, F, Coppola, R. and Blair, J. (2009) Visual awareness, emotion and gamma band synchronization. *Cerebral Cortex* 19, 1896-1904.
- Lutz A, Lachaux J-P, Martineres J, Varela FJ. (2002) Guiding the study of brain dynamics by using first-person data: synchrony patterns correlate with ongoing conscious states during a simple visual task. *Proc Nat Acad Sci USA* 2002;99:1586–91.
- Melloni, L., Molina, C., Pena, M., Torres, D., Singer, W. and Rodriguez, E. (2007) Synchronization of neural activity across cortical areas correlates with conscious perception. *J. Neurosci.* 27(11), 2858-2856.
- Mesulam, M.-M., and Mufson, E.J. (1982) Insula of the old world monkey. I. Architectonics in the insulo-orbito-temporal component of the paralimbic brain. *J. Comp. Neurol* 212, 1-22.

- Mountcastle, V.B. (1957) Modality and topographic properties of single neurons of cat's somatosensory cortex. I. Neurophysiol. 20, 408-434.
- Mountcastle, V.B. (1997) The columnar organization of the neocortex. *Brain* 120, 701-722.
- Nestler, E.J., and Malenka, R.C. (2004) The addicted brain. *Scientific American* 290(3) 78-85.
- Nightingale, S. (1982) Somatoparaphrenia: a case report. *Cortex* 18, 436-467.
- O'Keefe, J., and Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Clarendon Press.
- Panksepp, J. (1998) *Affective neuroscience: the foundations of human and animal emotions*. Oxford University Press; Oxford, New York, 466pp.
- Pascual-Leone, A., and Walsh, V. (2001) Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science* 292, 510-512.
- Place, U. T. (1956) Is consciousness a brain process? *British Journal of Psychology*, 47: 44-50.
- Pockett S (1999) Anesthesia and the electrophysiology of auditory consciousness. *Consciousness and Cognition* 8: 45-61.
- Pockett, S. (2000) *The nature of consciousness: a hypothesis*. iUniverse; Lincoln Nebraska, Shanghai. 212 pp. <http://www.psych.auckland.ac.nz/webdav/site/psych/shared/about/our-people/documents/sue-pockett/TheNatureofConsciousnessAHypothesis.pdf>
- Pockett, S (2002) Difficulties with the electromagnetic field theory of consciousness. *J. Consc. Stud.* 9, 51-56.
- Pockett, S (2004) Does consciousness cause behaviour? *Journal of Consciousness Studies*, 11 (2) 23-40.
- Pockett S (2006) The neuroscience of movement. In *Does consciousness cause behavior?* eds S. Pockett, W. Banks and S. Gallagher, MIT Press, Cambridge Mass p. 9-24.
- Pockett, S. (2007) Difficulties with the electromagnetic field theory of consciousness: an update. *Neuroquantology* 3, 271-275.
- Pockett, S. (2011) Initiation of intentional actions and the electromagnetic field theory of consciousness. *Humana.Mente* 15, 159-175.
- Pockett S, Banks W and Gallagher S (2006, reprinted 2009) *Does consciousness cause behavior?* MIT Press ; Cambridge Mass 364 pp.
- Pockett S and Purdy SC (2010) Are voluntary movements initiated preconsciously? The relationships between readiness potentials, urges and decisions. In: W Sinnott-Armstrong and L Nadel (Eds) *Conscious Will and Responsibility: A Tribute to Benjamin Libet*. pp34-46. New York; OUP.
- Pockett S, Zhou ZZ, Brennan BJ and Bold GEJ (2007) Spatial resolution and the neural correlates of sensory experience. *Brain Topog.* 20: 1-6.
- Pockett, S., and Holmes, M.D. (2009) Intracranial EEG power spectra and phase synchrony during consciousness and unconsciousness. *Consciousness and Cognition* 18, 1049-1055.
- Pockett, S., Bold, G.E.J. and Freeman, W.J. (2009) EEG synchrony during a perceptual-cognitive task: widespread phase synchrony at all frequencies. *Clin Neurophys* 120, 695-708.
- Pollen, D. (1995) Cortical areas in visual awareness. *Nature* 377, 293 - 377.
- Pollen, D. (1999) On the neural correlates of visual perception. *Cerebral Cortex* 9, 4-19.
- Pollen, D. (2003) Explicit neural representations, recursive neural networks and conscious visual perception. *Cerebral Cortex* 13, 807-814.
- Pollen, D. (2008) Fundamental requirements for primary visual perception. *Cerebral Cortex* 18, 1991-1998.
- Porter, R. and Lemon, R. (1993) *Corticospinal function and voluntary movement*. Monographs of the Physiological Society 45. Oxford University Press. 428 pp.
- Quian Quiroga, R., Reddy, L., Kreiman, G., Koch C., and Fried, I. (2005) Invariant visual representation by single neurons in the human brain. *Nature* 435, 1102-1107.

- Rigoni D, Brass M and Sartori G (2010) Post-action determinants of the reported time of conscious intentions. *Frontiers in Human Neuroscience* 4, 38. doi: 10.3389/fnhum.2010.00038
- Ro, T., Breitmeyer, B., Burton, P., Singhai, N.S. and Lane, D. (2003) Feedback contributions to visual awareness in human occipital cortex. *Current Biology* 14, 1038-1041.
- Rodriguez E, George N, Lachaux J-P, Martinerie J, Renault B, Varela FJ. (1999) Perception's shadow: long-distance synchronization of human brain activity. *Nature* 379, 430-3.
- Roelfsema, P.R., Engel, A.K., König, P., and Singer, W. (1997) Visuomotor integration is associated with zero time-lag synchronization among cortical areas. *Nature* 385, 157-161.
- Rolston, J.D., Gross R.E. and Potter, S.M. (2009) A low-cost multielectrode system for data acquisition enabling real-time closed-loop processing with rapid recovery from stimulation artifacts. *Frontiers in Neuroengineering* doi: 10.3389/neuro.16.012.2009
- Roš, H., Sachdev, R.N.S., Yu, Y., Šestan, N., and McCormick, D.A. (2009) Neocortical networks entrain neuronal circuits in cerebellar cortex. *Journal of Neuroscience* 29(33) 10309-10320.
- Rubio-Garrido, P., Pérez-de-Manzo, F., Porrero, C., Galazo, M.J., and Clascá, F. (2009) Thalamic input to distal apical dendrites in neocortical layer 1 is massive and highly convergent. *Cerebral Cortex* 19, 2380-2395.
- Salami, M., Itami, C., Tsumoto, T., and Kimura, F. (2003) Change of conduction velocity by regional myelination yields constant latency irrespective of distance between thalamus and cortex. *Proc Nat Acad Sci USA* 100 (10) 6174-6179.
- Searle, J.R. (1993) The problem of consciousness. In G.R. Brock and J. Marsh (eds) *Experimental and theoretical studies of consciousness* Vol 174 pp61-80. Chichester: John Wiley & Sons.
- Scoville, W. B. & Milner, B. (1957) Loss of recent memory after bilateral hippocampal lesions. *J. Neurol. Neurosurg. Psychiatry* 20, 11-21.
- Sheinberg, D.L., and Logothetis, N.K. (1997) The role of temporal cortical areas in perceptual organization. *Proc. Nat. Acad. Sci. USA* 94, 3408-3413.
- Shipp, S. (2005) The importance of being agranular: a comparative account of visual and motor cortex. *Phil Trans R Soc B* 360, 797-814.
- Silvanto, J., Lavie, N., and Walsh, V. (2005) Double dissociation of V1 and V5.MT activity in visual awareness. *Cerebral Cortex* 15, 1736-1741.
- Singer, W., Engel, A.K., Kreiter, A.K., Munk, M.H.J., Neuenschwander, S., and Roelfsema, P.R. (1997) Neuronal assemblies: necessity, signature and detectability. *Trends in Cognitive Sciences* 1(7) , 252-261.
- Smart, J.J.C. (1959) Sensations and brain processes. *Philosophical Review* 68, 141-156.
- Sperry, R.W., Miner, N., and Myers, R.E. (1955) Visual pattern perception following subpial slicing and tantalum wire implantations in the visual cortex. *Journal of Comparative and Physiological Psychology* 48, 50-58.
- Stefanacci, L., Buffalo, E.A., Schmolck, H., and Squire L.R. (2000) Profound amnesia after damage to the medial temporal lobe: neuroanatomical and neuropsychological profile of patient E.P. *J. Neurosci.* 20(18) 7024-7036.
- Supèr, H., Spekreijse, H. and Lamme, V.A.F. (2001) Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neurosci.* 4(3) 304-310.
- Swindale, N.V. (1990) Is the cerebral cortex modular? *Trends in Neurosci.* 13(12) 487- 492.
- Tallon-Baudry, C. (2009) The roles of gamma-band oscillatory synchrony in human visual cognition. *Frontiers in Bioscience* 14, 321-332.
- Thielscher, A., Reichenback, A., Uğurbil, K., and Uludağ, K. (2010) The cortical site of visual suppression by transcranial magnetic stimulation. *Cerebral Cortex* 20, 328-338.
- Tononi, G., and Edelman, G.M. (1998) Consciousness and complexity. *Science* 282, 1846-1851.

- Tononi, G., Srinivasan, R., Russell, D.P., and Edelman, G.M. (1998) Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proc Nat Acad Sci USA* 95, 3198-3203.
- Trujillo, L.T., Peterson, M.A., Kaszniak, A.W., and Allen, J.J.B. (2005) EEG phase synchrony differences across visual perception conditions may depend on recording and analysis methods. *Clin Neurophysiol.* 116:172–89.
- Wegner, D.M. (2002) *The Illusion of Conscious Will*. MIT Press, Cambridge Mass.
- Wiest, M.C. and Nicolelis, M.A. (2003) Behavioral detection of tactile stimuli during 7-12 Hz cortical oscillations in awake rats. *Nature Neuroscience* 6(9), 913-914.