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ON THE BORDERS OF CONSCIOUSNESS

**an evaluation of the delineation between the neural substrates of conscious and
unconscious cognition.**

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Abstract

The neural mechanism by which the brain creates conscious awareness remains unknown. The present thesis employs electroencephalography to investigate these neural substrates of conscious awareness through an investigation of the distinctions between neural activity associated with conscious awareness and neural activity which is not accompanied by conscious awareness. The temporal dynamics and the complexity of content during the unconscious processing of information are assessed in the first two chapters using the masked presentation of word stimuli. Results reveal that abstract information is extracted from unconsciously presented stimuli more rapidly than is usually associated with the neural indices of the conscious representation of information. It is also shown that the delay between the processing of different elements of word stimuli is such that some form of stable reentrancy is likely established during unconscious neural activity. The third experiment investigate the oscillatory event related beta desynchrony (ERD) preceding movement with and without awareness of the impending movement. The results show that beta ERD, unlike the evoked EEG response, reflects the awareness of the intention to move. It is argued that beta ERD allows the establishment of reverberating neural assemblies that are thought to be necessary for conscious representation. The final experiment uses a binocular rivalry paradigm to investigate the role of synchronous oscillations in determining the contents of consciousness. It is argued on the basis of this chapter that synchrony reflects the reorganisation and coordination of neural activity but is not, in itself, a mechanism for the binding of neural assemblies. The results are discussed in relationship to the distinction between conscious and unconscious cognition existing across a spectrum rather than representing qualitatively different neural states.

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Abbreviations

AC Anterior Cingulate
Ag Silver
BOLD Blood Oxygen Level Dependent
Cl Chlorine
CS+ Conditioned Stimulus Paired with a US
EEG Electroencephalography
EI Effective Information
ERD Event Related Desynchronisation
ERP Event Related Potential
FFA Fusiform Face Area
FFS Feed Forward Sweep (model)
fMRI Functional Magnetic Resonance
GFP Global Field Power
GWT Global Workspace Theory
IFG Inferior Frontal Gyrus
IIT Information Integration Theory
ISI Inter-Stimulus Interval
IT Inferior Temporal Cortex
LGN Lateral Geniculate Nucleus
LIP Lateral intra-parietal area
M1 Primary Motor Cortex
MEG Magnetoencephalography
N1/N170 Negative visual evoked response occurring with a latency of approximately 170ms
N400 Negative scalp deflection with a latency of 400 milliseconds
NCC Neural Correlates of Consciousness
P400 Positive intracranial potential with a latency of 400 milliseconds
PET Positron Emission Tomography
PFC Prefrontal cortex
PPA Parahippocampal Place Area
REM the stage of sleep characterised by Rapid Eye Movement
RP Readiness Potential
RPM Recurrent Processing Model
RS Repetition Suppression
SMA Supplementary Motor Cortex
SOA Stimulus Onset Asynchrony
STS Superior Temporal Sulcus
US Unconditioned Stimulus
V1 The primary visual/striate cortex, Brodmann area 17
V2 Area of the visual cortex the receives input from V1, Brodmann area 18
VWFA Visual Word Form Area

Chapter 1 Introduction

Perhaps the last bastion left standing in the wake of the cognitive revolution of the 1970s, the study of consciousness is *in statu nascendi*. The writings of Vygotsky in the early part of the last century opined that the “psychological nature of consciousness is persistently and deliberately avoided” (Vygotsky, 1925). Though the cognitive revolution re-opened the door to the study of the internal function of the brain, the internal representation of cognitions, conscious awareness, remained outside mainstream psychology inquiry (Crick & Koch, 1990).

With the rise of functional imaging as an alternative to introspection, the empirical study of internal states became tenable. However the scientific study of consciousness still lies in infancy and, as yet, there are no clear distinctions that delineate conscious neural activity. The current paradigm focuses on the Neural Correlates of Consciousness (NCC) (Crick & Koch, 2003; Frith, Perry, & Lumer, 1999; Rees, Kreiman, & Koch, 2002) defined as the bare minimum of neural activity required to manifest a conscious representation (Chalmers, 2000).

In this thesis I shall attempt to test empirically some aspects of the neural substrates of consciousness. Empirical testing of the substrates of consciousness is a difficult area and several approaches are used within this thesis. The first two chapters will use the scientifically unassailable logic to test the causal role a particular form of neural activity in consciousness (i.e. if *a* then *b*). The premise is that if you observe *a* (type of neural activity) in the absence of *b* (conscious awareness), then a theory of consciousness that postulates that *a* is the mechanism for consciousness is invalid. In

the third experimental chapter attempts are made to keep all aspects of the experiment equivalent, except for the presence of conscious awareness. This will not shed the same direct causal light on the substrates of consciousness but it is hoped that it will identify neural processes that are related to the formation of conscious awareness. In the final experimental chapter the strength of the relationship between a particular form of neural activity and conscious awareness will be tested. The form of neural activity underlying consciousness should not only be found to co-occur with conscious awareness but also to vary with variations in the consciousness. This relationship will be assessed by comparing experimental and control conditions to investigate whether this neural correlate of awareness co-varies with variations of the conscious experience during binocular rivalry transfer.

Theories that address the neural substrates of consciousness will be discussed. As can be expected with theories relating to such a new and complex area of research, these theories are of a conceptual nature and are, in general, not the sort of theories that make differing empirical predictions. Attempts, however, have been made to explore the differences between these theories and consider some of the differing predictions that they may make.

Identification of the minimal neural requisites for consciousness, the NCC, does not distinguish neural activity that contributes to conscious awareness from the neural activity that plays a supporting role. For example, conscious awareness of a visual percept requires the activity of retinal ganglion cells, but these neurons are not thought to contribute to the neural ensemble that creates the conscious representation of the visual scene (Crick & Koch, 2003; Edelman & Tononi, 2000).

Some theorists use the subjective characteristics of consciousness to make predictions about the type of neural activity that will reflect consciousness. These theorists note that consciousness is an integrated and differentiated experience, and state that the neural activity reflecting this process should share these characteristics (Tononi & Edelman, 1998). To this subjective bounding box I would add a consideration of the functional role of consciousness as a tool to make predictions about the properties of its neural carriage.

In addition to the consideration of introspective reports, another avenue for making predictions over what may be the neural substrates of consciousness is to consider the functional role of conscious awareness. The primary function of the brain is to flexibly govern interaction with the environment. To do so it must integrate current sensory input with stored knowledge and select an appropriate motor response. At some point in evolution it became expedient not only to form this integration but to form an internal representation of this process, one that is evident to the organism.

This representation for the organism, the user interface of the mind, is what we commonly refer to as conscious awareness. It is the metaphorical representation of the computations performed in the brain, in the form of perception, planning, language, movement and more. Consciousness has been likened to the CEO of a company (Edelman & Tononi, 2000). It sits atop the hive of cognition occurring in the brain and makes high level integrative judgments for this cognitive corporation. However, like any CEO, or decent user interface, it deals with only a simple summary of the end

result, not the mundane actions formed by every minion. Like any good CEO, the conscious self seamlessly attributes the actions of its underlings to itself, and the acts it performs as the most complex. Viewing consciousness in this light makes the prediction that the information carried in consciousness will be an iconographic representation of the exponentially more complex operations that this conscious icon represents. But this model makes predications only about the complexity of information.

A useful distinction when approaching the problem of consciousness is to distinguish between those mechanisms that determine the *level* of consciousness and those that determine the *contents* of consciousness (Frith et al., 1999). The *level* of consciousness refers to the current level of arousal (Frith et al., 1999) and is influenced by activity of the reticular activating system of the pons and its influence on the thalamus (Siegel, 2001). The level of consciousness distinguishes between states such as sleep and coma, where no conscious awareness is presumed to be experienced, and states of wakefulness and dreaming, which are associated with subjective conscious experience. Examining differences between these levels of consciousness may shed light on mechanisms by which conscious awareness arises.

The *contents* of consciousness refer to the elements which make up a particular subjective conscious moment. This refers to the phenomenology, or the qualia, of this conscious moment. The contents of the quale can be incredibly rich. A given conscious moment can integrate information from the sensory systems, information retrieved from memory and information about future goals and plans to attain them.

Qualia arise and change rapidly but continue stably during their experience which can span several hundreds of milliseconds.

Neuronal models attempting to account for the contents of consciousness must be able to explain at least two important features of consciousness. Conscious representations have the vast potential for both the *differentiation* of separate qualia and the mandatory *integration* of different elements into a unified quale (Tononi & Edelman, 1998).

These features could be achieved through reentrant connections amongst thalamocortical neurons binding the neuronal assemblies involved in a given quale. Such reentrant connections have the capacity to rapidly integrate distributed populations of neurons into a common neural process. Differentiation is achieved by the potential of a diverse range of neurons to contribute to the dynamic core, a term for the neural ensemble contributing to the current conscious moment (which will be discussed further shortly). This endows the potential for the vast array of experiences that can comprise conscious awareness. Integration is achieved through the formation of dominant coalitions, quieting rivals, and gaining a monopoly over the reverberant brain (Crick & Koch, 2003).

Neural assemblies, first proposed by Donald Hebb (1949), have been defined as distributed networks of neurons transiently linked by reciprocal dynamic connections (Varela, Lachaux, Rodriguez, & Martinerie, 2001). Neural assemblies are generated through the mechanisms of association envisaged in Hebb's precocious neuronal doctrine. Elements of a neural assembly are formed when events co-occur and strengthen reciprocal links between neurons. After a neural assembly has formed, activation of one element of the population will ignite the entire neural assembly.

When activated, units within such assemblies, such as cortical columns, coordinate and strengthen their activity through reciprocal connectivity. Larger functional units connected by long distance cortical connections allow the recruitment to the neural assembly of more distal parts of the cortex. A feature of such reciprocally connected assemblies is that activation can be sustained in the absence of external input; excitation can reverberate through the assembly sustaining the encoded information across time. As Hebb noted, the interval between thought and action lasts beyond the duration of mere sensory input (Hebb, 1949). Such reverberant, self-renewing, activity has been most convincingly observed in the cortex of the monkey during delayed response tasks (Fuster & Alexander, 1971). Within the cortex, long distance connections are almost always bi-directional (Felleman & Van Essen, 1991). Such reentrant neural assemblies meet the trinity of demands needed for a conscious moment. They can incorporate vast arrays of information within hundreds of milliseconds, access almost all information stored in the cortex, and rapidly recombine into an almost infinite variety of states.

Contemporary Theories of the Neural Substrates of Consciousness

Contemporary theories of consciousness have coalesced on concepts such as ‘Dynamic Cores’ (Tononi & Edelman, 1998) or ‘Global Workspaces’ (Baars, 1997; Dehaene & Naccache, 2001) or ‘coalitions’ of neurons (Crick & Koch, 2003). Under these theories a form of neural Darwinism is occurring. Before a moment enters consciousness, neural assemblies are competing amongst each other, forming alliances with those of similar alignment and inhibiting others outside their coalition. Eventually consciousness forms as the dominant amalgam of many competing neural assemblies. This amalgam dominates the cortex and provides the unified conscious experience of the moment. The information in the individual coalition members, sometimes called

nodes (Crick & Koch, 2003), can be shared and integrated with the conscious moment allowing the rich differentiation apparent in conscious cognition. The four major theories of the neural underpinnings of consciousness are presented in Table 1-1.

These theories share much in common and differ only subtly. All three theories hold that:

- Consciousness is an emergent property of the neural activity of the thalamo-cortical system and does not reside in one particular cortical region.
- Neural populations are either inside or outside of the Workspace/Core/Coalition and therefore contribute or do not contribute to the conscious experience.
- The neural mechanism of conscious awareness must be able to share and integrate information flexibly over multiple parts of the cortex.

Of the three, Crick and Koch's 'coalition' model is probably the most metaphorical in nature, stemming from a political election simile and, like the Dynamic Core model, is left intentionally vague on the specific neural mechanisms by which these coalitions may form. This vagueness reflects the limited knowledge of such mechanisms at the present time, though it is asserted strongly that the thalamo-cortical system certainly has the requisite ingredients to work in this fashion (in the form of excitation, inhibition and reentrant connections). Global Workspace Theory (GWT) contains perhaps the most specific assertions. At least as argued by Dehaene (2001), Workspace theory incorporates aspects of Jerry Fodor's (1983) influential modular view of the brain. The modular view of the brain views the mind as a series of parallel, specialised, modules which function largely independently and are opaque to awareness. According to GWT,

Table 1-1 Summary of the four main theories of the neural substrates of consciousness

Global	
Workspace Theory	<ul style="list-style-type: none">• Proposed by Baars. More recently promoted by Stanislas Dehaene• Consciousness is determined by the broadcasting of information to the ‘Global Workspace’ which includes frontal regions• Unconscious processing occurs when information is not broadcast to the Global Workspace but remains confined outside the Workspace
<hr/>	
‘Coalition Theory’	<ul style="list-style-type: none">• Proposed by Francis Crick and Christof Koch• Consciousness arises from dominant coalition formed through the processes of mutual excitation and the inhibition of rivals, populations of neurons inhibit or co-opt other neuronal populations in a winner takes all manner.• Neuronal populations that lack sufficient connections to the rest of the cortex will not be able to directly contribute to conscious awareness (e.g. V1).• Unconscious processing takes place outside of the dominant neural population, either as independent supplicant neuronal populations or through the stimulation of neurons on the periphery of the dominant coalition.
<hr/>	
Information	
Integration Theory of Consciousness	<ul style="list-style-type: none">• Proposed by Giulio Tononi and Gerald Edelman.• This model emphasises the importance of information integration in the formation of consciousness and presents a method for determining the <i>complex</i> (i.e. neuronal population) within which information is more tightly integrated than with neuronal populations outside this complex• Complexity is determined by the number of possible states (differentiation) of a neural population while integration measures the degree to which elements of a complex can effect changes in other elements within the complex.• Consciousness is an emergent property of the integration of complex information and is likened to a fundamental property of nature, such as mass or gravity.• Neuronal activity that is not integrated with the main complex or is highly integrated but does not have a large number of potential states (low differentiation) will not form a conscious representation.
<hr/>	
Victor Lamme’s	
recurrent processing	<ul style="list-style-type: none">• Neural activity is characterised by a feed-forward sweep of activation (unconscious cognition) which is succeeded by the formation of recurrent connections (conscious cognition).• Local recurrent processing within the visual cortex will place a neurons activity in the wide visual context of neuronal activity (binding) and result in <i>phenomenological awareness</i>.• As recurrent activation incorporate temporal, parietal and frontal regions the visual information will be placed in the context of the current goals and history of the system, creating <i>access awareness</i>.

modular processes which amalgamate with the Global Workspace contribute to the conscious experience. This seems like a subtle distinction from the other two theories but the connotations of this modular approach will be discussed later with respect to unconscious cognitive processes. A second specification present in the Global Workspace Theory is that it places specific anatomical locations (namely the prefrontal cortex) above others in the formation of consciousness. This shall be discussed alongside some criticisms of this approach made by Victor Lamme and colleagues (2000). Tononi and Edelman's Dynamic Core model emphasises the high degree of mutual information inside the core, which is distinct from the information contained outside of the core. This theory has been termed the Information Integration Theory (IIT) of consciousness (Tononi, 2004) and is consistent with the other two theories

Tononi and Edelman's Dynamic Core model offers an operational definition of the core. As information integration is the key element of the dynamic core then the core can be defined as the population which has a high number of informational states within itself, which cannot be subdivided into smaller subunits, and does not contain greater informational integration with any elements outside of the set. To date, it has not been possible to test this model *in vivo*, however it provides a useful theoretical framework for the specification of what a 'dominant coalition' may be.

The level of information within a complex can be reflected in terms of Effective Information (EI) (Tononi, 2004). EI can be determined by dividing a system into two complementary elements, A and B. The EI is determined as the sum of the possible states which alterations in the state of A can induce in B and the possible number of states alterations in B and produce in A. This relationship can be quantified by

perturbing sub-complex A in every possible way (by inserting noise into each element of A, which is to say by maximising entropy within the sub-complex) and monitoring the effect of this upon sub-complex B. If A is integrated with B then the number of alterations in A will be large. If, for example, A and B were only lightly interconnected, then although there may be a great number of states available to A and to B, then number of states that A can change in B will be small and the EI of the A-B complex will be low. To establish some index of the level of EI within a complex one can find the minimal EI between all possible subdivisions of the A/B complex. When the EI of each of these new variants of the A-B sub-complexes are normalising to the maximum number of states available within the separate A and B components, a measure of integration can be established. The lowest of these values (the dividing of the complex with the least EI) represents the closest complex A-B comes to being divisible into two separate complexes A and B. With this information the whole system can be examined. Considering every possible combination of subsets of the system ranging from subsets of two elements to a subset containing the total number of elements within the system, *complexes* are then determined (with the stipulation that a complex cannot be contained within a larger complex containing more effective information). A complex is a functional cluster, where the participating neural populations are more strongly integrated amongst themselves than with other complexes (Tononi & Edelman, 1998). The complex containing the most information is known as the *main* complex (Tononi, 2004). The theory predicts that the neural activity contributing to conscious awareness will be that with the most highly complex and integrated nature, which is to say the main complex (Tononi, 2004), or the dynamic core (Tononi & Edelman, 1998). The main complex may be functionally re-sculpted

by attentional mechanisms, probably through the alteration of functional connectivity within the complex, endowing the main complex a dynamic nature (Tononi, 2004).

Tononi (2004) postulates the intriguing possibility that the system's capacity to integrate information is one and the same as subjective experience and that as information integration increases so does subjective experience. Experience is not determined just by the current active state of the dynamic core but also all the states *in which it is not presently*. This is to say that the experience of seeing blue is enriched by our ability to see red and the knowledge that we are not presently seeing red. As the information about what the state which the dynamic core is presently in is shared across the complex the subjective experience of being in this state is formed.

A further model which warrants discussion is Lamme's recurrent processing model (RPM) of consciousness. The RPM is distinct from the three previously discussed models in that it does not accentuate dynamic cores as such. The RPM asserts that recurrent activation is necessary and sufficient for awareness. This model has an aspect similar to the dynamic core type models in that reentrant connections to the attentional system are necessary for *access* awareness but is distinct from other theories in that it proposes that reentrant activity outside of attentional networks (e.g. limited to striate and extra-striate regions) will result in *phenomenological* awareness (Lamme, 2004). The attentional system acts as a 'bottle neck', limiting the scope of access awareness that is processed at any one time. The terms 'access' and 'phenomenological' awareness are borrowed from Ned Block (1996; 2005). The distinction made is that some aspects of consciousness can be reported (access awareness) while other aspects

present only a brief phenomenological experience which cannot enter working memory (phenomenological awareness; such as the cup in the periphery of one's vision, of which one is phenomenological aware but could not be reported until attention is directed to it). Under Lamme's proposed theory all recurrent activation results in awareness and only that which forms connections with the attentional system will result in reportable awareness (in a way this is similar to dynamic core type models). This theory is particularly useful in that it provides a clear and distinct role for attention in conscious awareness and that it explains, in part, the various degrees to which we (subjectively) can be conscious of particular stimuli.

Exactly how the dynamic core/GWT/coalition theories distinguish between Lamme's phenomenological and access awareness is unsure. That is to say, would IIT's main complex comprise of the subset of reentrant activity that contains attentional networks, the awareness which we have access to? or does the main complex include both phenomenological and access components of awareness?

Lamme argues that during the initial neural response neurons respond to particular features of a stimulus but that later components of a neurons discharge depend on contextual influences. For example, in the visual cortex a neuron's response is initially determined by input within its classical receptive field (e.g. tuning to a particular orientation), however later aspects of firing of the same neuron are influenced by context (whether the neuron's receptive field is part of the figure or ground of the stimulus) (Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999). Likewise, within neurons of the motor cortex, the neural discharge of a particular cell that initially reflects sensory events will later reflect motor commands (Zhang, Riehle, Requin, &

Kornblum, 1997). The information it encodes varies within the context of the neural assembly within which it is currently contained. In this way the formation of reentrant connections provides an enriched representation of the information contained in the single 'receptive field' placing it within its broader context.

The theories discussed do not, in general, make separable testable predictions. The exception to this would be that Lamme's RPM predicts that reentrant cortical activity will result in conscious awareness and should not occur during unconscious cognition. The other theories, which emphasise the dynamic core, allow the possibility that reentrancy can exist during unconscious processing.

The basic medium by which the Coalitions/Cores/Workspaces are thought to form is through the immensely interconnected medium of the thalamo-cortical system. The term reentrant (synonymous with recurrent) connections refers to a series of neural connections that can feed back onto itself, these may be reciprocal in nature (where neural populations are directly coupled i.e. $A \leftrightarrow B$) or can occur with intermediary connections ($A \rightarrow B \rightarrow C \rightarrow A \rightarrow \dots$). Reentrant connections can occur at several levels within the brain. Reciprocal cortico-cortico connections link distal parts of the cortex and have the capacity to modulate long distance neural assemblies (Edelman & Tononi, 2000). In particular, heavy fibre tracts such as those between the prefrontal and posterior parietal lobules or the arcuate fasciculus connecting Brodmann's regions 44/45 to 22, may play an important role (Wang, 2001). Thalamocortical connections, particularly those routed through the intra laminar non specific nuclei, are also thought to play an important role in rapidly establishing widespread reentrant assemblies (Crick & Koch, 2003; Llinas, Ribary, Contreras, & Pedroarena, 1998; Tononi & Edelman,

1998). Further, reciprocal interactions occur within neighbouring pyramidal cells or between neighbouring cortical columns. These connections provide reentrancy great flexibility in uniting regions of the cortex.

The discussed models require that information is flexibly and dynamically integrated across the thalamo-cortical system and that the neural activity inside the core is distinct from the neural activity outside of the core. One postulated mechanism of this distinction is the synchrony of neural activity.

Coherence, Phase Synchrony and the Binding of Neural Activity

Several models of consciousness focus on phenomenological awareness through avenues similar to those trod by theorists struggling with the binding problem. Namely how can such a diverse, flexible array of disparate cortical regions choose to, and communicate their, participation in a conscious percept. And then moments later a separate population of cortical regions reconvene to form a separate conscious percept, potentially with overlapping elements. The Binding Problem refers not only to perceptual binding of an object's form, colour, motion and location, but also to a more 'cognitive' binding (Roskies, 1999), a binding of the properties of a semantic concept; the colour, taste, feel, the edibility of the apple, as well as its more esoteric properties, such as its disreputable role in the biblical eviction from Eden. Though the binding problem does not directly attempt to explain consciousness (theoretically, binding does not necessarily create a conscious representation) it does address the issues of integration and diversity, the central problem for theorists who attempt to discern the neural mechanisms of consciousness.

The largest conceptual difference between the Binding Problem and the Consciousness Problem is that binding can occur largely in parallel whereas consciousness experience is mandatorily experienced as an amalgam. When presented with a scene comprising of a bird and a ball, perceptual binding requires that the colour, form and motion of a ball are bound to the ball while simultaneously the colour, form and motion of bird are ascribed to the bird. These features must be bound simultaneously yet kept distinct to bird and ball, with a distinct neural code encoding each bound object. Consciousness, according to some theorists (Tononi & Edelman, 1998), requires that the conscious experience must be interpreted as a whole. This distinction is nicely encapsulated in the Ruben-Vase illusion. Binding will allow the separation of figure from ground, but consciousness selects which will be figure and which ground.

In the same article as the Binding Problem emerged as a debutant, so emerged a solution (von der Malsburg, 1981), which went on to gain much support (Singer, 1999). The Temporal Binding Hypothesis holds that the combination of cortically disperse elements can achieve their commonality through the synchronisation of spikes across neurons involved in a common percept. Such a mechanism's appeal lies in its endowment of a given cell with the potential to contribute to a large number of states through its flexible participation in separate assemblies at different points in time, while retaining the ability for a given assembly to recruit from almost all knowledge stored in the cortex to represent a given percept.

Empirical support for the Temporal Binding Hypothesis comes from the finding that oscillatory bursts observed within cortical columns of the cat primary visual cortex (Gray & Singer, 1989) can demonstrate synchrony across columns separated by up to

7mm (Gray, Konig, Engel, & Singer, 1989). When two receptive fields are stimulated by separate bars of light their respective neurons in V1 both increase their firing rate. If the bars are moving in the same direction this discharge rate becomes correlated. If the two bars are connected, creating a single continuous bar, an even greater correlation is observed. The importance of such a correlation is that information encoded in the firing rate is insufficient to encode whether the activity of two neurons reflects isolated activations of their respective receptive fields or stimulation of the receptive fields by a single object. This information was encoded in the phase synchrony between these two neurons. This type of synchrony does not reflect local processes, calculated at a particular receptive field, but the integration of form and motion calculated across non-overlapping receptive fields.

Here the term 'Synchrony' is used to denote the tendency of one action potential to be followed or preceded by another as a function of distance in time, rather than the simultaneous discharge of action potential across the network. Neurons partaking in a synchronous assembly have an increased probability of firing an action potential on the peak of each oscillatory period. Individual neurons fire largely stochastically. However when observing the activity of many neurons, by for example, measuring Local Field Potentials, these stochastic action potentials are pooled and the oscillatory nature of the assembly becomes apparent. Synchrony in the cat cortex can be measured through either autocorrelation within a single unit or cross-correlation when two units are compared. Gray and Singer (1989) found that within cortical columns, peaks in autocorrelation fell approximately 25ms apart creating an oscillation at 40Hz, the so called gamma band (in fact these oscillation centred around $50\text{Hz} \pm 6\text{Hz}$ in this experiment but 40Hz has become the exemplar frequency of gamma). It was the

synchronicity of this oscillation that was noted during the fused activation of the spatially separate column of Gray and colleagues (1989). This phase synchrony in the gamma range (between 30-70Hz) is the candidate mechanism of the Temporal Binding Hypothesis.

Gamma is ubiquitous in the brain. It was first observed in the olfactory bulb of the hedgehog as a transient synchrony induced by olfactory stimulation (Adrian, 1942). It is found piggybacking upon the back of hippocampal theta in maze running rats (Chrobak & Buzsaki, 1998), in primitive brain stem regions, such as the superior colliculus (Brecht, Singer, & Engel, 1999) and in the visual, auditory (Galambos, Makeig, & Talmachoff, 1981) and somatosensory (Meador, Ray, Echauz, Loring, & Vachtsevanos, 2002) cortices.

In the cat, synchronous gamma oscillations have been found across cortical divisions: between neurons in striate and extra striate cortices (Engel, Konig, Kreiter, & Singer, 1991) and between left and right hemispheres (Engel, Kreiter, Konig, & Singer, 1991). In fact, as distance between neuronal populations increase, so too does the ratio of oscillatory to non-oscillatory correlations increases (Konig, Engel, & Singer, 1995). Synchronous gamma oscillations have been observed between visual and parietal and parietal and motor cortices indicating that this mechanism has the potential to not only bind perceptions, but also to bind perception to actions (Roelfsema, Engel, Konig, & Singer, 1997).

In human measures, Electroencephalography (EEG), Magnetoencephalography (MEG) and, to a lesser extent, intracranial electrocorticography (iEEG), can reveal pooled

synchronous activity amongst large neural populations. These techniques have revealed locally synchronous gamma activity associated with perception (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1997; Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996), motor tasks (Pfurtscheller, Flotzinger, & Neuper, 1994) and in higher cognitive tasks (Spydell & Sheer, 1982). Gamma synchrony has also been shown to be modulated by attention (Fries, Reynolds, Rorie, & Desimone, 2001).

The mechanism which produces gamma oscillations is still uncertain and may differ between different parts of the brain. Most evidence from computational models suggests that oscillations are derived from synaptic dynamics. One model posits that the discharge of the 80% of excitatory pyramidal cells is modulated by the 20% of inhibitory interneurons in the cortex (Wang, 2003). Another suggests that there is a feedback inhibition with both excitatory and inhibitory neurons playing a role in the neurogenesis of gamma (Jefferys, Traub, & Whittington, 1996; Wang, 2003). Both of these models are realisable on biologically realistic computational simulations and have received support from *in vitro* studies. A further putative mechanism for the generation of oscillatory synchrony is that there exist mechanisms intrinsic to the membranes of some cells, such as the hyperpolarisation induced calcium conduction observed to underlie the rhythmic self generation of action potentials in the thalamus (Llinas, 1988; Llinas, Grace, & Yarom, 1991). Neurons in the cat visual cortex have been found to exhibit intrinsic oscillatory activity and this has been proffered as a candidate mechanism for cortical gamma neurogenesis (Gray & McCormick, 1996). Such ‘chattering’ cells are created through interplay between inwards sodium leak-type currents and voltage sensitive potassium channels. It is possible that interplay between these synaptic and membrane dynamics may underlie the generation of gamma, with

membrane properties of some neurons responding preferentially to certain input frequencies, acting as resonators (Llinas, 1988).

Although synchronous gamma oscillations are presently the leading contender for the binding process it is not certain whether the same mechanism can account for consciousness. Despite this there is a vast consensus amongst theorists that gamma synchrony is necessary both for large scale cortical integration (Varela et al., 2001) and for conscious awareness (Crick & Koch, 2003; Dehaene & Naccache, 2001; Edelman, 2003; Llinas et al., 1998; Tononi & Edelman, 1998; Ward, 2003).

Local synchronous gamma observed at single or neighbouring sites at the scalp (Tallon-Baudry et al., 1997) or between proximal single unit recording sites (Gray & Singer, 1989) are the most commonly reported. A clear distinction between perceptual binding and the binding of conscious quale predicted by these models is that conscious representations should involve widely distributed regions of synchrony. A conscious moment must be able to coordinate information of sight, of sound, of meaning and action, across many cortical regions. If the same mechanism of integration that underlies local binding underlies consciousness, then such synchronous neural activity should be present at distal cortical sights. Fewer studies have observed such synchrony at a distance. In animals, synchrony has been observed between the visual and parietal cortex and between the parietal and motor cortex during a visuo-motor integration task (Roelfsema et al., 1997). In the human, ambiguous figures in the form of Mooney faces, have been shown to elicit wide spread gamma range synchrony when they are consciously perceived, but not when they remain unperceived (due to inversion) (Rodriguez et al., 1999). Intracranial EEG recordings have shown transient phase

synchrony between the fusiform face area (FFA) and a wide spread group of cortical regions during a delayed face recognition task (Klopp, Marinkovic, Chauvel, Nenov, & Halgren, 2000). The regions involved consisted of the temporal pole, hippocampus, rhinal cortex, middle temporal gyrus, ventrolateral prefrontal cortex, cingulate gyrus, supramarginal gyrus and the gyrus rectus, in fact all regions sampled from demonstrated phase synchrony with the FFA but not with each other. Synchrony was not limited to the gamma range, and was reported in the alpha band as well. Phase lag existed between recording sites and this lag increased monotonically with distance from the FFA. These findings demonstrate that the capacity for wide spread, high frequency synchrony exists in the human cortex and that it occurs in situations associated with conscious awareness. The findings do not, however, demonstrate that this coherence generates conscious experience.

A challenge which remains to these theories is to demonstrate that synchrony has the ability to integrate information across the brain. In itself, predicting that there will be synchronous activity during tasks that have a high 'consciousness-demand' is not risky. These tasks are pre-selected for cognition that involves diverse brain regions focussed upon a common task. In such a demand-environment it would not be unreasonable to expect different parts of the brain to be sharing information, and because of the need to share information, to observe correlated activity. But this does not necessitate that it is the synchronous activity that is the root cause, and not an epiphenomenon, of consciousness.

The problem of finding appropriate referent states is a crucial issue in the study of consciousness. Inverted Mooney faces look like meaningless blobs. A comparison of

exposure to meaningless blobs versus faces contains too many dissimilarities to attribute observed differences to conscious representation. This difficulty was handled skilfully by Tononi and colleagues (Srinivasan, Russell, Edelman, & Tononi, 1999; Tononi, Srinivasan, Russell, & Edelman, 1998). Binocular rivalry occurs when two incompatible stimuli are presented to each eye. Instead of perceiving a fused image the reported conscious experience is of alternatively seeing one or the other image (Blake, 2001). Tononi and colleagues employed a binocular rivalry task and presented two different visual stimuli at two different driving frequencies (Tononi, Srinivasan et al., 1998). This allowed the assessment of the neural activity induced by two stimuli where the sole difference was that one of the stimuli was consciously perceived while the other was not. The driving frequencies varied between 7.41, 8.33, 9.5 and 11.12 Hertz, creating the so called steady state response at these frequencies. The use of the driving frequency as a tag allowed the direct comparison of coherence when perception was accompanied by conscious awareness and when it was not. Measures of cortical coherence (through MEG) demonstrated a widespread increase at the driving frequency of the consciously perceived stimulus (Srinivasan et al., 1999).

The steady state responses in the 40Hz range are not thought to reflect representational binding (Tallon-Baudry & Bertrand, 1999). However, the finding of Srinivasan and colleagues (1999) has been construed as reflecting the presences of high frequency synchrony associated with consciousness (Dehaene & Naccache, 2001; Ward, 2003). However in the study of Srinivasan and colleagues the difference in coherence was a reflection of the driving frequency, evoked by stimulus presentation frequency, rather than the endogenously driven high frequency synchronous oscillations that are the putative mechanism of conscious awareness. These studies show that conscious

awareness gates coherence of the steady-state response but do not show that this coherence was a manifestation of conscious processing. Widespread coherence in the range of 7 to 11 Hertz is typically associated with decreases rather than increases in conscious awareness (Pfurtscheller & da Silva, 1999). Although Srinivasan and colleagues argue that disparities between the steady state power change and coherence changes suggest that a greater amount of information is being explained than could be explained by changes in passive responses to the driving frequency, it could not be said that this form of coherence is a reflection of the internal binding of a conscious moment. Although the type of coherence measure used here records coherence between electrode sites that is *not* synchronised to the input stimulus, the reported oscillatory coherence is in the alpha range. The direct comparison of this to natural endogenous gamma oscillations, a purported mechanism of conscious binding, is possibly premature.

Lessons from Binding

Questions exist over whether synchronous activity is a refined enough vehicle to communicate belonging to a conscious coalition. When Von der Malsberg (1981) originally proposed the Temporal Binding Hypothesis he speculated that for temporal binding to occur action potentials must arrive within a 3 ms window. Theories of oscillatory synchrony have moved a long way from this 3 ms window, yet no attempt has been made to assess whether this system has the combinatorial degrees of freedom necessary to bind (Shadlen & Movshon, 1999). If the firing of one neuron in a correlogram can be taken to be indicative of the inputs from the contributing neuronal assembly across the oscillatory cycle and if a cosine function is used to model oscillatory relationships, then in a wave with a period of 25ms, 48% of spikes will fall

within a 3ms window. However, reported cross-correlelograms also contain significant background firing with discharge in the trough of the oscillation being in the order of 40 to 60% of the peak oscillatory response (Gray et al., 1989; Kreiter & Singer, 1996). Under such conditions only approximately 18% of action potential spikes will fall within a 3ms window. Some argue (Shadlen & Movshon, 1999) that cortical neurons possess no mechanism to detect coincidence with such a high background rate or over a broad time range. These authors argue that, without vast numbers of synchronous inputs from cells, the ratio of synchronous-signal to asynchronous-noise would be impossible to detect. However, stating that there is a need for coincidence detection per se, underestimates the effects of recurrent connectivity in gradually sculpting, and in turn being sculpted, by fellow neurons. It has been shown computationally that populations of neurons can speed or slow their firing rate to coincide with the input (Jefferys et al., 1996; Sporns, Gally, Reeke, & Edelman, 1989). When this connection becomes recurrent, stable oscillatory activity can be reached in moments.

Klopp and colleagues (2000) found that the phase lag between distant brain regions increased monotonically with distance. Time lags are typically built into measures of phase synchrony (Varela et al., 2001). If the lag between two sections of an assembly is anything but half the resonant frequency then closure of reentrant loops becomes untenable. For example, if phase in the FFA is 5ms ahead of phase in the anterior cingulate (AC) the return signal from the AC to the FFA will be 10ms apart, arriving near the trough of FFA activity. Time lags create a plausible delay from communication of information from one region to another but make no allowances for the return trip. Although local information could be integrated using synchrony, if such phase lag is typical of large scale neural assemblies then phase synchrony becomes an

untenable mechanism for encoding membership in the conscious coalition of the moment. Klopp and colleagues reported synchrony between the FFA and other cortical regions but did not find synchrony amongst the other cortical regions. If synchrony was the mechanism by which these brain regions form a dynamic core then there would be coherence between them. The study of Klopp and colleagues suggests that coherence plays a role in the distribution of a signal across brain regions involved in a quale but that the integration between brain regions is achieved through some other mechanism than synchrony.

Employing synchrony as a mechanism for cortical integration limits the way in which temporal and spatial information must be used within the assembly. Spatial information encodes meaning and temporal information encodes integration. For example; in the monkey, during delayed response tasks tactile neurons show a parametric analogue representation of the vibrating frequency of the stimulus that is maintained for the duration of the retention period (Romo, Brody, Hernandez, & Lemus, 1999). It is hard to see how such a network would interact with a process that encoded integration through temporal mechanisms. In the perception of an object, form and colour may be bound in through the preservation of retinotopic information in areas like V2 and V4. Likewise at association levels the role of the lateral intra-parietal area (LIP) in binding has recently been re-asserted in the hierarchical binding of features to actions (Shadlen & Movshon, 1999).

Relationships between synchronous populations have not just been observed within frequency bands but between them. Phase locking ratios of 1:2 and 1:3 have been observed (Varela et al., 2001). This suggests that there are many more levels of

complexity to the dynamics of thalamo-cortical synchrony. Different parts of a neural assembly can be active at different harmonic frequencies and still have correlated activity.

The possibility exists that the synchronous activity recorded in the experiments discussed is merely a symptom of the neural processes underlying consciousness, a symptom of vastly more complicated processes induced by first, second and higher order phase synchronies across temporally *and* spatially encoded neural assemblies. The correlation in firing and concomitant synchrony may be an emergent property of complex neural integration, an epiphenomenon, rather than the cause of consciousness. These properties emerge during conscious processing, more so than other cognitive states, because comparatively it is such a complex integrative computation.

Lamme's RPM in particular (Lamme et al., 2000), excludes any special role for synchrony in the form of modulations in firing rate. As noted earlier, later alterations of a neuron's firing rate reflect successive stages of information encoding depending on the neural context of the neuron (Lamme & Roelfsema, 2000). It is possible that the inclusion of a particular neuron inside or outside of the dynamic core is determined by the neuron's present context of neural activity (i.e. which *complex* it is part of) without the need of some particular code to communicate belonging to the core.

Anatomical Considerations in the Study of Consciousness

There is consensus that the thalamo-cortical system underlies conscious experience (Crick & Koch, 1998; Dehaene & Naccache, 2001; Tononi & Edelman, 1998). If consciousness is produced by large scale reentrant neural assemblies then it must take part in areas of the brain that have sufficient capacity for these assemblies to form.

Purely input regions such as the retina are thought not to partake in the conscious amalgam, in that the activity of the retina cannot be influenced by the neural activity of the dynamic core (Crick & Koch, 2003; Edelman & Tononi, 2000). Other regions, such as the pathways of the medial superior olive which detect inter-aural delays, are not thought to contribute directly to the dynamic core because the information about inter-aural delays is not available to awareness and is only evidenced by the ability to spatially locate sound (Dehaene & Naccache, 2001). Two types of connections are thought to have the capability to form and stabilise conscious co-allied neural assemblies: long distance cortico-cortico fibres and thalamo-cortical reentrant loops. Although both mechanisms have their adherents some argue a special importance for the thalamus.

Thalamic neurons, particularly those in the intra-laminar non-specific nuclei, are the prime candidates for such a wide-spread binding mechanism (Crick & Koch, 2003; Llinas et al., 1998). Such a candidacy is based on the ability of thalamic neurons to demonstrate resonance with cortical neurons (Llinas, 1990) and that this mechanism can plausibly create synchrony within 200-400 (Wang, 2001). Llinas (1998) argues that intrinsic membrane properties, namely a voltage sensitive calcium channel, create an endogenous gamma oscillation responsible for generating cortical gamma, though similar 'chattering' neurons have been found in the cerebrum (Gray & McCormick, 1996).

The thalamus appears to play a distinct role in the *level* of consciousness. During dreamless sleep, when consciousness is absent, due to a lack of acetylcholine and norepinephrine and other neuromodulatory inputs the membrane potentials in the

thalamus enter bursting modes creating the slow wave oscillations typical of this state (Wang, 2003). In situations where consciousness is present, REM sleep and wakefulness, thalamic nuclei are sufficiently depolarised that the calcium channel mediated ~40Hz oscillatory character is present (Wang, 2003). The fact that the absence of consciousness is associated with the extinction of high frequency reverberant thalamic activation has been proffered as evidence of the thalamus's central role in state, and possibly content, of consciousness (Llinas et al., 1998). Under this model thalamocortical afferents enhance and modulate oscillatory activity in the cortex. In a wakeful state, reciprocal connections between the cortex and the intralaminar nuclei of the thalamus cohere the dominant sensory or cognitive processes. Such a model is distinct from dynamic core style models in that it endows the thalamus a kind of pacemaker role in the generation of consciousness. Llinas has proposed that the intrinsic activity of the thalamus creates an oneiric-like role in the contents of consciousness, whereby the ebbing and flowing of thalamic activation governs the contents of the conscious. In endowing wakeful conscious states as a sensory-modulated version of dream states, Llinas suggests that during dreaming the same process occurs but disregards input from sensory afferents. Indeed, during REM sleep, when measured by MEG, gamma oscillations are present but are not reset by external sensory stimuli, despite effects on the sensory evoked potential (Llinas & Ribary, 1993).

A sub population of thalamic intra-laminar neurons have been found that project widely across cortical regions projecting into layer I where they have access to the dendrites of neurons in all layers. These neurons possess the potential to synchronize disparate cortical regions into coherent activation (Jones, 2001). Such findings show that the

thalamus may possess the necessary means to coordinate, or even determine, the conscious moment but they do not exclude the role of cortico-cortico connections.

Although models of reentrant neural assemblies stress the importance of dynamic functional connectivity over anatomically distinct centres of consciousness, it is doubtful that the entire cortex plays an equal role. A prediction of GWT is that regions underlying the five elements of cognition that partake in the workspace; high level perception, motor, long-term memory, evaluative and attentional circuits, will have strong reciprocal connections. Dehaene and Naccache (2001) propose that these elements of cognition are subserved by the strong connections between the prefrontal cortex (PFC) and premotor, superior temporal, inferior parietal, anterior and posterior cingulate cortices and through links to the parahippocampal gyrus, the neostriatum and the thalamus which have been observed in the monkey (Goldman-Rakic, 1988). Cortico-cortico fibres are most common in layers 2 and 3 of the cortex. It has been suggested that layers 2 and 3 should be thickest in regions that are most often associated with conscious awareness (Dehaene & Naccache, 2001). Layers 2 and 3 are thickest in the inferior parietal cortex and dorsolateral PFC.

GWT holds the PFC as particularly important in conscious awareness noting that many early neuroimaging studies focussing on complex or effortful tasks found PFC activation. Tasks that involve the executive control: planning, working out new rules, retaining information or internally driven mental activities, all activate the PFC. GWT suggests that the PFC play the role as attentional ombudsmen, modulating the contents of sensory consciousness through selectively amplifying information in the sensory

association areas and permitting them to gain enough momentum to form the long distance reentrant connections necessary for entry into the global workspace.

It is unclear whether all of these regions could be said to be part of the conscious moment as the five elements of consciousness identified by GWT seem to include elements of executive control and explicit learning. GWT applies more to areas linked to conscious awareness rather than the embodiment of awareness in itself. The PFC and AC were previously implicated in many forms of cognition because of the association of these regions with attention and task performance. The implication of conscious awareness in certain parts of the brain may be a more subtle manifestation of the same attribution error. Conscious awareness is required for the formation of explicit memories, yet there is no sense of 'this is what it is like to form a memory'. However the perirhinal cortex is included in the GWT's collections of brain regions involved in consciousness because of its importance in memory formation. The anatomical distinctions emphasised by GWT may reflect brain regions which interplay heavily with conscious awareness but this does not necessitate that these regions are involved in the formation of conscious awareness.

Studies have investigated the relationship between neural activity in different parts of the cerebrum and states of consciousness. Binocular rivalry was used in the rhesus monkey to investigate how conscious perception affected the pattern of firing within the cortex. It was found that neurons in the primary visual cortex responded to their preferred stimulus which was only moderated slightly (changes of between 7 and 11

percent) by the conscious perception of the image (Leopold & Logothetis, 1996). In higher areas of the inferior temporal area (IT) and the superior temporal sulcus (STS) 90% of neurons firing depended on which stimuli was reported as being perceived (Shenbergl & Logothetis, 1997). These findings suggest that higher association areas are more important in determining the contents of consciousness than lower order sensory areas.

In contrast, V1/V2 neurons responding to the dominant eye in strabismic cats were found to demonstrate a 141% increase, not in firing rate, but in synchrony, when stimuli moved from monocular to binocular presentation (Fries, Roelfsema, Engel, Konig, & Singer, 1997). During the same transition synchrony between neurons that responded to stimuli from the non-dominant eye decreased to 44% of baseline levels. These experimenters made use of the fact that, in early stage strabismus, during binocular rivalry the image presented to the dominant eye is the one that is consciously perceived. This provides the means to be certain of what percept the animal consciously perceives but must be cautiously interpreted as a reflection of non-pathological inter-ocular rivalry.

The work of Fries and colleagues' (1997) study suggests that firing rate may not be the critical factor in determining which neural activity enters conscious awareness.

However, firing rate does appear to reflect consciousness in IT and STS, and the presence and importance of synchrony in these higher order association areas has not been assessed. Indeed it has been noted that, in the alert behaving monkey, gamma oscillations are largely absent in high-order cortical areas (Bair, Koch, Newsome, & Britten, 1994; Young, Tanaka, & Yamane, 1992). This leaves open the possibility that

anatomically separate brain regions may have different neurophysiological determinants of what activity will enter consciousness. In lower sensory cortices synchrony may play a role in determining what neural activity is passed into conscious awareness while in higher cortical areas, where oscillatory activity has not been observed, conscious information representation is influenced by the firing rate within neurons partaking in the conscious moment. Unfortunately, in none of these studies was synchrony between distant brain areas, such as V1 and STS investigated. This would be the critical test of the role of synchrony in determining conscious awareness as this would test whether the synchrony between cortical regions was contingent on awareness of the stimuli.

The study correlating ocular dominance to visual association areas has been replicated with humans demonstrating increased activity of higher association areas, the FFA and the Parahippocampal Place Area (PPA), when their preferred stimulus is consciously perceived (Lumer, Friston, & Rees, 1998; Tong, Nakayama, Vaughan, & Kanwisher, 1998). The primary visual cortex is sensitive to differences in contrast between the dominant monocular images (Polonsky, Blake, Braun, & Heeger, 2000). This contradicts the observations during single unit recordings in animals suggesting that activity in the primary visual cortex reflects the conscious perception.

It may be that neurons in V1 can be functionally disconnected from the dynamic core and continue to be active. Participation in the conscious amalgam is not thought to be rate dependent, and the studies above have measured, either directly or indirectly, the magnitude, rather than the pattern, of neuronal activity. Dehaene and Crick both place special emphasis on the connections between frontal regions and higher perceptual

areas rather than primary sensory regions (Crick & Koch, 1998; Dehaene & Naccache, 2001).

Debate exists as to whether the activity of V1 is necessary or sufficient for visual awareness (Crick & Koch, 1995a; Lamme et al., 2000). It has been proposed that the primary visual cortex does not possess the interconnectivity required for participation in wide scale neural assemblies, lacking direct connections to any area of the frontal cortex or to the non-specific nuclei of the thalamus (Crick & Koch, 1995a). However, the need for direct projections to the frontal lobe is speculative and since participation in an active conscious neuronal assembly could be coordinated through intermediary (i.e. extastriate) areas, this remains hypothetical. It has been argued that since we are not aware of some information that is only available to V1, we are therefore not conscious of any information only in V1 (Crick & Koch, 1995a). Very fine gratings, which only V1 possesses receptive fields with enough acuity to detect, remain invisible to conscious experience, their effects only being observed in the form of a tilt aftereffect (He & MacLeod, 2001). Flicker fused black and white stimuli presented at 50Hz are not seen to vary in luminance, however changes in the evoked response *have* been recorded from primary visual region (Wollman & Palmer, 1995). However taking evidence that we are unaware of some of the information in V1 as evidence that we are unaware of all information in V1 is a logical non-sequitur.

Lamme cautions against such approaches (Lamme et al., 2000), which he terms Localisationist. *Localisationist* approaches explore the importance of sub-populations of neurons in the development of awareness, in contrast to *Global* approaches which postulate that it is the pattern of activation (such as synchrony) that determines whether

they contribute to conscious awareness. Localisationist approaches seek ‘awareness dedicated’ neurons both in particular regions of the cortex (e.g. V1) or in particular classes of neurons (e.g. layer 2 and 3). Lamme argues for such an approach to be fruitful the activity of these awareness dedicated neurons must by *necessary* and *sufficient* for conscious awareness. The afore mentioned studies of flicker-fusion and very fine gratings which suggest that the activity of V1 is not sufficient for consciousness are supported by the observation that lesions to both parietal elements of the dorsal stream and temporal lobe elements of the ventral stream (Goodale, Jakobson, & Keillor, 1994) prevent visual awareness. This suggests that the activity of V1 may not be involved in the neural substrates that manifest consciousness. However as Lamme notes, the same criteria exclude the involvement of all areas of the visual system from conscious representation.

The finding that damage to either the dorsal or ventral streams can both independently prevent the formation of visual awareness suggests that the activity of neither area is sufficient for conscious awareness. Likewise, evidence from neuroimaging studies provides evidence that the activity of almost all cortical areas is insufficient for visual awareness. When two stimuli of opposing colours are rapidly (~ 100ms) presented to each eye, the two colours fuse and the conscious percept is that of a uniform square or the combined wavelengths. Stimuli could take the form of a red house on a green background (to one eye) and a green house on a red background (to the other eye). Within the conscious perception, these colours fuse and the percept is that of a single yellow square, indistinguishable from the presentation of a veridical yellow square to both eyes. Moutoussis & Zeki (2002) used such stimuli to show that in the absence of awareness both dorsal and ventral streams are activated. In particular, regions of the

temporal cortex that responded preferentially to either houses or faces when stimuli were rendered visible, were seen to preferentially activate even in the absence of any visual awareness of the stimuli. So the evidence from both neuroimaging and lesion studies would, as in the case of V1, preclude higher visual areas of the dorsal and ventral streams from a special role in consciousness.

Although the concerns raised are confined to aspects of the visual system Moustousses and Zeki (2002) also observed activation in regions of the prefrontal cortex. Suggesting even activation at the site of the 'highest' level of processes is insufficient for the formation of a conscious representation.

Although some differences may exist in the probability of certain anatomical regions contributing to the conscious experience, there is no evidence for a qualitative distinction based on anatomical structures within the thalamo-cortical system.

Considerations on the Neural Correlates of Consciousness

Research to date aiming towards a neural understanding of consciousness can best be summarised as a search for the Neural Correlates of Consciousness (Crick & Koch, 2003; Frith et al., 1999; Rees et al., 2002; Tononi, Srinivasan et al., 1998). With this emphasis on events that co-occur with subjective awareness, causality and understanding of the neural patterns that related to conscious awareness suffered.

Perhaps the assertion that began the search for the NCC was that oscillatory activity was sufficient for the emergence of a conscious representation (Crick & Koch, 1990).

Such a view has now largely been rejected (Crick & Koch, 1998b; Tononi & Edelman,

1998) because although oscillatory activity was correlated with consciousness, it was also present during events that did not include consciousness. The same problem underlies the role of widespread synchrony, although it is correlated with consciousness there is little to suggest that it is causally related to it and not a symptomatic manifestation of a more complex process.

Short term memory has been defined as the process by which neural activity persists after stroboscopic stimulation (Rolls & Tovee, 1994), the persistent neural activity that lasts for a few hundred milliseconds after stimulus presentation. This model is so close to models of consciousness that it serves to accentuate another problem with the NCC approach. It is often a struggle to disentangle consciousness from other higher cognitive function. The appropriate referent state in comparisons of the conscious and unconscious conditions is often elusive. Events that are used to monitor the correlates of consciousness often involve delayed responses and the focusing of attention, whereas the referent state does not. As pointed out by Baars (1989) the best way to gain insight into the neural substrates of consciousness is to employ tasks where the only difference in conditions is the presence or absence of awareness. The correlates observed under this approach may simply be the Neural Correlates of Working Memory, or the Neural Correlates of Attention. If consciousness is to be seen as a phenomenon separable from such processes as attention and working memory then attempts must be made to balance these in the referent condition, striving for *ceteris paribus*, with the bare minimum of confounding task-elements. Further, it is vital that studies of the neural correlates of consciousness seek not neural events that co-occur with consciousness, but those that distinguish it.

What Separates Conscious from Unconscious Processing – on the Borders of Consciousness

A potentially fruitful approach may be to focus on what lies at the juncture of conscious and unconscious cognition. There is a vast array of evidence to show that these two states are qualitatively different in nature. A thesis I propose as an alternative to the search for the NCC is that, to gain an understanding of the neural mechanisms that underlie consciousness, it is useful to investigate the neural mechanisms that distinguish an unconscious neural assembly from a conscious one.

Unconscious Processing

Aside from the accompaniment of subjective awareness, conscious and unconscious processing differ qualitatively in several ways. Unconscious cognition cannot be maintained in short term memory (Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Goodale et al., 1994). Although contention exists over laboratory measures of unconscious (often referred to as implicit) learning (Cleeremans, Destrebecqz, & Boyer, 1998; Dienes & Berry, 1997) it can be agreed that unconscious learning does not occur on single trials, taking many trials to learn in a probabilistic, rather than hypothesis driven form (Dienes & Berry, 1997). Explicit memory formation is contingent on the hippocampus (Milner, 1968), whereas implicit learning does not share this dependency (Milner, 1972). Lastly, it has been shown that conscious and unconscious strategies can exist concurrently in direct opposition to each other (Debnar & Jacoby, 1994).

Unconscious cognition can be broadly grouped into cognition where the observer is aware of neither the initiating stimulus nor the end result, such as masked priming or divided attention scenarios, and into cognition where the individual is aware of the cogent stimuli but not the results of the elicited cognition, such as procedural learning.

The first grouping usually occurs when the stimulus is presented in such a form that it does not have sufficient transduced momentum to initiate the activation of its associated neural pathway. The second grouping occurs when stimuli are apparent but the computations governing behaviour are opaque to awareness. This suggests that the network associated with these forms of cognition is not conducive to consciousness, regardless of the strength of the stimulus, as these networks exist outside of the main complex. These forms of cognition can be associated with early perceptual processes, such as the perception of objects within a visual scene; with fine motor control (the knowledge required to stay vertical on a bicycle); or with knowledge or rules and relations, such as grammar and sequence learning. In all these cases an individual's explicit beliefs about the nature of the underlying computations can exist contrary to those evidenced through direct observation of the behaviour.

Integration of Unconscious Processing with Neural Theories of Consciousness

Both the Dynamic Core Hypothesis (Tononi & Edelman, 1998) and Global Workspace Theory (Dehaene & Naccache, 2001) propose that unconscious processes are the manifestation of those neural assemblies that do not join the dynamic core. Events that produce a weak, brief activation will fail to reach the necessary threshold for the closure of longer reentrant routes, thus preventing their entry to the dynamic core.

Cognition that is opaque to awareness does not possess the necessary hardware; connectivity with the global workspace or main complex or within its own neural assemblies, to enter the conscious moment regardless of stimulus strength.

A study supporting this view, and the role of gamma oscillations in conscious awareness was conducted on six epileptic patients using intracranial EEG. Near-threshold somatosensory stimulation produced gamma oscillations in detected trials but no similar oscillations during undetected trials (Meador et al., 2002). The disparity in oscillatory behaviour was dissociated from the raw evoked potential where no significant difference was observed (although the style of analysis was particularly conservative). This finding suggests that the failure to establish local synchrony prevented entry into the dynamic core.

If a briefly presented priming stimulus is followed in quick succession by a masking pattern, the priming stimulus will be rendered, at least consciously, invisible. During this backwards masking it is thought that the mask interrupts the activity associated with the masked stimuli (Rolls & Tovee, 1994) which may prevent the closure of reentrant connections (Dehaene & Naccache, 2001). Despite this lack of conscious awareness, masked primes have been shown to have an effect on judgements made to later target stimuli. Almost identical findings have been observed during divided attention tasks (Merikle & Joordens, 1997). Under current theories of consciousness, this effect occurs because the eclipsing of the stimulus by the mask provides insufficient time to develop reentrant connections. Under the global workspace model the failure of prime stimuli to reach conscious awareness during divided attention tasks results from the lack of attention-directed amplification of the prime stimulus (Dehaene

& Naccache, 2001). Results on divided attention tasks could be explained in terms of a coalition monopoly, whereby the distracter task has formed a dominant coalition and the enterprise of the peripheral task is doomed to neural bankruptcy. In blindsight, when early visual pathways are damaged, individuals show a similar pattern of behaviour to masking and divided attention studies, with long stimulus durations (Sahraie, Weiskrantz, Barbur, Simmons, & Williams, 1997).

In the case of cognition that is incapable of a manifestation of a conscious representation, the answer may lie in the circuitry. It has been suggested that this incapacity results from an inability of the underlying circuits to mobilise into reverberant assemblies, or, in situations where mobilised assemblies are tenable, a lack of bidirectional connectivity between the neural elements underlying these forms of cognition and those involved in the dynamic core (Dehaene & Naccache, 2001). The lack of connectivity excludes the formation of reverberatory loops preventing these systems from entering into the conscious workspace. One such circuit involves the basal ganglia, which are thought to be involved in automatic unconscious tasks (Poldrack et al., 2001; Rauch et al., 1997). One would expect such a circuit to either be largely disconnected from cortical neurons, which it is not, or to possess some property that precludes coordination with the conscious neural assembly. It has been noted that the circuitry in the basal ganglia differs to the thalamo-cortical system in that it is largely parallel, with very little cross talk (Edelman & Tononi, 2000). Interestingly, there is a conspicuous absence of the ubiquitous gamma range oscillations in the basal ganglia, which demonstrates oscillations below 30Hz and above 60Hz but with no reported oscillations in between these frequencies (Brown, 2003)

Many cognitive events, such as skilled reading, occur with automaticity. When a task is first learned it is often effortful and involves conscious processing but as skill increases these tasks can be achieved with no, or minimal, conscious input. Crick and Koch (2003) refer to such automatic states that routinely exist outside of the conscious moment as zombie states, cortical reflexes of stereotyped responses that do not require conscious intervention. Goodale and Milner (1999) have proposed that some information in the dorsal stream remains outside of conscious awareness without the need for development of automaticity. Evidence supporting this stance comes from findings that zombie states can exist in contradiction to awareness. For example, D.F., who suffered damage to the ventral stream, can still interact with objects despite an inability to perceive them (Goodale et al., 1994). In neurotypical subjects, illusions such as the muller-lyer illusion affect conscious perception of stimuli (in terms of estimates of the size) but produce much smaller effects on hand grip size when reaching for the object (in terms of accuracy of the grip) (Gentilucci et al., 1996). This dissociation between conscious experience and behaviour led Goodale and Milner (1999) to suggest the existence of an automatic perception to action systems that does not enter conscious awareness. They have proposed that, when visual information reliably requires a specific action, conscious mediation is not required, and that those elements of the dorsal stream, that involve the visual guidance of actions, exist outside of the workspace of consciousness. As the strong reciprocal connections thought to be indicative of entry into the global workspace are abundantly present between posterior parietal and premotor regions, the mechanisms which distinguish these circuits from those that do reach consciousness are elusive.

Crick and Koch (2003) also suggest the existence of the penumbra. This is a sort of halo of neurons around the neural assembly which are facilitated by the activity of the neural assembly but are not part of its reverberant activity. They state that this may be the site of automatic priming but do not speculate further into the form of activity in the penumbra.

Complex tasks such as word reading combine conscious and zombie states. Word reading is usually accompanied by awareness but, at least on the lexical arm of the dual route of reading (discussed shortly), only the end result is conscious, not of the process that lead to the result. There have been repeated examples of word reading occurring in the absence of awareness (Cheesman & Merikle, 1986; Greenwald, Draine, & Abrams, 1996). This raises the interesting question of how a widely distributed network can integrate information across a wide variety of functional and anatomical divisions without invoking the neural mechanisms responsible for consciousness. Further, what differentiates the neural activity associated with reading that is accompanied with awareness and that which is not?

Conscious Capable Circuits Behaving Unconsciously

During masked priming an effect can be found even if the only relation between prime and target is of a semantic nature (Cheesman & Merikle, 1986; Greenwald & Draine, 1998; Greenwald et al., 1996). Criticism has been made of the veracity of these studies, suggesting that non-reported conscious processing could account for the effects, which are typically small (Holender, 1986). However studies tightly controlling for conscious influences (Greenwald & Draine, 1998; Greenwald et al., 1996) and those that place such influences in opposition to the experimental effect (Cheesman & Merikle, 1986)

have transcended these criticisms. The approach of Cheesman and Merikle (1986) is particularly convincing. Here the experimental paradigm is contrived in such a way that the effect of a conscious representation of the stimulus will *reduce* any observed influences of unconscious processing. In contrast the meticulous approach of Greenwald and colleagues has received criticism (Merikle & Reingold, 1998). The most substantial criticism is that the d' regression used does not actually measure all aspects of awareness and that this is merely another of a number of studies that show indirect effects of stimuli which the observer could not report (e.g. Marcel, 1983). d' is a measure of sensitivity that counters response bias; however it cannot counter a non-directional response bias. If a subject chose (for whatever reason) to respond randomly on occasional trials then a d' set threshold would be too high. The same would be true if a subject were not accessing and employing all the information which they had awareness of. Notwithstanding these criticisms, these studies do seem to show differential effects (i.e. unconscious priming has a very brief lifespan) and the work of Greenwald and colleagues are presently the most influential representatives of the class of studies that attempt to demonstrate unconscious processing through indirect stimulus effects in the absence of direct conscious awareness of the stimuli.

Investigations of the effect of backwards masking on neuronal discharge have been performed in the monkey (Rolls & Tovee, 1994). The discharge of neurons in the STS, which respond to particular face stimuli, can persist for approximately 500ms and are interrupted by the occurrence of the masked stimuli, suggesting that the effect of backward masking may be mediated through the inhibition of this continuous firing. However, although SOAs shorter than 40ms have been claimed to result in no

awareness of the stimuli in an identical paradigm using humans, subjects performed at 50% accuracy (corrected for chance) at the 20ms SOA. This casts into doubt whether the burst of firing in face cells of the STS can occur in unconscious face processing. It is clear that the masking stimulus interrupts stimulus induced neural activity; however the study would have ideally collected awareness reports from the animal at the same time as neural recordings (awareness reports could be attained through forced choice detection or some similar measure as is commonly used in humans). This would allow the comparison of presentations that were and were not accompanied by awareness.

In humans, presentation of masked emotional faces has been shown to elicit different activation of the amygdala than emotionally neutral faces (Whalen et al., 1998). Morris and colleagues (1998) paired a noxious UC with an angry face and compared activation between the masked and visible presentation of the CS+. These researchers found that the effect of the CS+ pairings manifest in the differential activation of the right amygdala.

It has been suggested that emotionally valenced stimuli, including faces, may be processed automatically through direct thalamo-amygdaloid connections and not reflect conscious processing (Ledoux, 1996). Although this is not certain, the existence of such a network in the processing of such a primitive system is plausible. The type of circuits involved in conscious and unconscious representation of conditioned responses to faces were shown to depend on whether or not the subjects were aware of the stimuli (Morris et al., 1998). Masked CS+ activated the right amygdaloid complex, but only when subjects were not consciously aware of the CS+. When the subjects were aware of the CS+, the left amygdala was preferentially activated. This suggests that, at least

in the case of unconscious emotional learning, separate pathways may exist for conscious and unconscious components.

During masked word reading information must be integrated across multiple levels of orthographic, lexical and semantic processing but conscious awareness is not required for this to occur. Although word reading can proceed along the lexical arm of the dual route of reading without awareness, semantic information, as measured by priming studies, is thought to have the potential to be processed in automatic or in conscious forms (Neely, Keefe, & Ross, 1989). Without building in infeasible redundancy, parsimony suggests that the same neural substrates underlie both conscious and unconscious cognition during semantic priming. The differences between unconscious and conscious word reading, particularly the activation of semantic information, may shed light on the dynamics of conscious representations of information.

Lamme (Lamme, 2004; Lamme & Roelfsema, 2000) postulates what he terms a Feed Forward Sweep (FFS) hypothesis to explain the effects observed during masked processing, which can be employed to account for the effects observed during masked word reading. Lamme's RPM of consciousness stipulates that recurrent processing is sufficient for consciousness. Under the FFS model activity sweeps through the system, as has been discussed in the work of Rolls and Tovee, but then fails to form an enduring neural representation due to the inability to form reentrant connections with visual areas (where processing is now monopolised by the masking stimulus).

Global Workspace Theory, in particular, would suggest that active neuronal population, be they recurrent or no, will remain outside of conscious awareness if they fail to form

into the global workspace. This is an implication of the modular nature of the theory. GWT does not insist that purely modular process do form recurrent connections, only allows the possibility. Here GWT and Lamme's recurrent processing theory of consciousness make differing predictions. GWT holds that modular process will remain outside of consciousness if they do not form into the global workspace and *may* be recurrent (or reverberant) in nature. While Lamme's RPM holds that if activity attains reentrancy in any form then it will enter into at least into 'phenomenological' awareness.

Because of the need for recurrent connections to sustain neural activity, the FFS model posits that unconscious activity will persist for a very limited period of time. The exact maximum duration of this persistence of purely feed forward activity is uncertain but is limited to the duration of the feed forward sweep. Transmission times in the macaques have led to estimates in the order of 60ms (Lamme & Roelfsema, 2000).

Chapter Two of this thesis presents an investigation of both the temporal dynamics and extent of information extraction during the unconscious processing of word stimuli.

Chapter Three investigates the neural response evoked by purely semantic elements of unconscious processing. The processing of levels of information contained within words is usually spread over time. A modular model of unconscious processing allows that this pattern may persist during unconscious processing; the FFS model predicts that it will not. In this way the first two experimental chapters will use unconscious processing to test a model about the neural substrates of conscious awareness.

Integration into the Conscious Moment

Models of consciousness focus on competing assemblies of cells vying for dominance until one attains it. Instead of monitoring the neural correlates of consciousness, the key to understanding consciousness may require focusing on how these nascent conscious assemblies differ from those that have entered conscious awareness.

Consciousness emerges not only from sensory information but also from within, in the form of volition.

When a soon-to-be-conscious thought is still in its pre-conscious stage, when the neural assembly underlying pre-conscious cognitions are forming coalitions and competing amongst themselves, many potential cognitions are represented in the neural activity of the cortex, cognitions of which we have no awareness. Introspectively, by definition, we possess no insight into the capacity or sophistication of these nascent conscious thoughts. The ability of these pre-conscious thoughts to exist outside of the conscious amalgam, to function independently and to display a pseudo-sentience such as in alien hand syndrome, is one of the more interesting questions in the study of consciousness.

Experimentally, one way to gain insight into cognition that is occurring below or outside of conscious awareness that may or may not develop into a coalition member of a conscious moment is through studies of capricious voluntary movement.

Electroencephalographic investigations of the spontaneous generation of movement have found that measurable neural activity occurs before the moment when the neural network underlying the preconscious violation gains enough momentum to amalgamate into a conscious moment (Haggard, 2005; Haggard & Eimer, 1999; Libet, Gleason, Wright, & Pearl, 1983). A comparison between the neural activity during spontaneous

movements, where the urge to move is in a preconscious form, to those where the subject is cued to the future time of movement and possesses a conscious representation of the impending movement, will be made in Chapter Four. In this way the third chapter will be the only chapter in this thesis to compare directly conscious and unconscious forms of the same cognition. It is hoped that, as the motor task remains unchanged, that awareness is the only substantial difference between these conditions and that differences in the recorded neural activity will reflect differences in the character of conscious and unconscious neural representation of the same cognitive process.

Specifically the role of beta range (18-24 Hz) oscillation over the motor cortex shall be investigated. Beta oscillations, along with alpha oscillations (8-12Hz), belong to a class of naturally occurring oscillations within the brain that are thought to reflect 'idling' processes of the cortex (Pfurtscheller & da Silva, 1999). It is hypothesised that the persistence of beta oscillations during unconscious movement preparation may predict whether movement preparation remains outside of consciousness. In terms of the IIT, tonic inhibition in the form of beta oscillations may reduce the effective connectivity of the widespread neural system underlying volition. Alterations in connectivity have been observed during non-REM stages of sleep (Massimini et al., 2005) and idling cortical oscillations may play a similar role during the waking state.

The fifth chapter shall instigate the postulated neural code thought by some to coordinate the neural activity presently contributing to conscious awareness, in an attempt to determine whether gamma synchrony lies at the border of conscious

awareness. Although gamma has been found to co-occur with binding and conscious awareness, the interdependence between binding, consciousness and induced gamma-band activity has remained largely unexplored. The fifth chapter shall aim to systematically explore this relationship. During binocular rivalry transition, both the subjective experience of binding and the spread of neural activity responsive to a bound percept are known to be smeared across time, providing an opportunity to assess whether modulations of perceptual and neural binding are accompanied by modulations of induced gamma. The fifth chapter of this thesis shall use a time locked induction of the rivalry change to investigate the change in natural oscillatory dynamics associated with rivalry transfer.

Chapter 2 Temporal Dynamics of Unconscious Word

Reading

Introduction

Current models of the neural substrates of conscious awareness centre on phenomenological awareness resulting from the formation of Hebbian reverberant, reentrant neural assemblies into a dynamic core (Crick & Koch, 1998b; Dehaene & Naccache, 2001; Tononi & Edelman, 1998). Under such models the backwards masking of a stimulus interrupts neural activity associated with the stimulus (Rolls & Tovee, 1994) and prevents the establishment of reentrant connections, sustained activity, and the concomitant access to the dynamic core. The result is that the stimulus is not consciously perceived, though paradoxically, its influence on later behaviour and neural activity has often been documented (Cheesman & Merikle, 1986; Debner & Jacoby, 1994; Dehaene et al., 2001; Dehaene et al., 1998; Draine & Greenwald, 1998; Greenwald et al., 1996).

The Neural Mechanism of Backward Masking – a failure of reentrancy

During visual backward masking the aligning phase of oscillatory gamma activity in V1/V2 (Gray et al., 1989) may be scattered by the onset of the mask. During binocular rivalry, neurons in the visual cortex have been shown to continue to discharge even when their output is not part of the conscious percept (Fries et al., 1997; Leopold & Logothetis, 1996). However, although the rate of firing does not change, an increase in the synchrony of neurons receiving input from the dominant eye occurs with the introduction of a rivalrous stimulus in strabismic cats (Fries et al., 1997), suggesting

that it is synchrony of firing, not the rate of firing, that is important in determining what stimuli will be available for conscious processing.

This suggests that the mechanism for the effect of backwards masking may be the interruption of local reverberatory oscillations in the primary sensory cortices necessary for the closure of reentrant connections with the dynamic core. Indeed, investigation of the activity of the human somatosensory cortex in response to near threshold tactile stimulation revealed that local oscillations in the gamma range (40-60Hz) occurred when stimulation was accompanied by awareness but was not present when the stimulus was not consciously perceived (Meador et al., 2002).

The role of gamma in conscious awareness of auditory stimuli also lends support to this hypothesis. Discriminations of two auditory clicks separated by 1-2ms can be made in the form of tonal distinctions. For the conscious perception of two discrete tones ISI of 15-20ms are required (Joliot, Ribary, & Llinas, 1994). Joliot and colleagues (1994) found that the point of subjective discrimination corresponded to the point at which a second gamma oscillatory phase was evoked by the stimulus. This finding suggests that the chronometry of conscious discrimination may be contingent on the temporal dynamics of oscillatory neural activity, although information can be discerned unconsciously (tonal distinction) at briefer time courses.

Insight from Word Reading

Word reading as a form of cognition provides unique insight into how conscious and unconscious processes differ across a learned cognition that forms across non-

specialised neural circuits. Word reading involves a distributed neural network that includes stages of visual, orthographic and lexical processing as well as semantic access. Masking a word with a non-orthographic pattern interrupts activity in the early visual cortex, yet processing has been shown to proceed to the semantic level (Greenwald et al., 1996). Theories of consciousness that emphasise a dynamic core leave uncertain the dynamics associated with the passage of neural activity along the required pathways in the absence of the formation of long distance reentrant connections with the widely dispersed cortical regions associated with reading.

Beyond the primary sensory cortices, a study which investigated the relation of gamma oscillations to awareness of word stimuli found significantly greater gamma range power over temporal sites when consciously perceived words were compared to word presentation accompanied by the absence of awareness (Summerfield, Jack, & Burgess, 2002). However this study unevenly collapsed several presentation durations into the two levels of subjective awareness, allowing the possibility that the presence of gamma was a reflection of stimulus intensity. The gamma activation was observed over right temporal regions and persisted for only 6ms. Further, because the aware condition was paired with a particular response set, the changes in gamma observed may have been due to task related factors. Gamma was found to positively increase with the level of subjective awareness reported even during incorrect trials when no stimulus was present, suggesting the possibility of a response, rather than stimulus, driven effect. Lastly, this study did not assess whether gamma was absent, in comparison to baseline, in situations where the subject was unaware of the stimulus, allowing no conjecture on the necessity of gamma for stimuli-awareness.

A Competing Model for the Distinction between Conscious and Unconscious Processing

Work on the monkey cortex has shown that neurons respond to their preferred face stimulus with high frequency bursts of firing which occurs in the STS within 75ms after stimulus presentation. This activation is then sustained for some 200-300ms after a 16ms stimulus presentation. If a masking pattern is introduced in immediate succession of the face stimuli, firing is extinguished 20-30ms after its initiation (Rolls & Tovee, 1994). However, within this 20-30ms period approximately 65% of the information present in a 400ms pattern of sustained activity can be encoded (Tovee, Rolls, Treves, & Bellis, 1993). It should be noted that these findings may not reflect true unconscious processing, as under similar stimulus conditions humans correctly performed 50 percent above chance (Rolls, Tovee, Purcell, Stewart, & Azzopardi, 1994). However, these studies show definitively that masking exerts its influence through stopping the sustained information-impoverished firing but does not interfere with the initial high-information burst.

Evidence from the effects of backward masking in the monkey suggests an interesting possibility. The possibility is that cognition following stimulus driven neuronal activation sweeps through a neural assembly, reaching the Hebbian threshold of ignition, spreading unconscious automatic cognisance and gaining access to all elements of the assembly. Then, if the stimulus is not eclipsed by masking stimuli, the network reaches a threshold for reverberation, recurrent connections are formed (Lamme & Roelfsema, 2000) and sustained activity persists across the same network in a style amenable to conscious representation. Under such a sweep and sustain model, complex complete processing of the stimuli occurs during the rapid sweep phase. This

is followed by a sustained representation. Rolls et al. (1994) speculate that the high information capacity of the initial burst leaves little need for the encoding of information through synchrony. It may be that reverberant activity is not required for its capacity for information processing, but to create a sustainable representation, the complex stage of processing has already been performed unconsciously. The reverberant stage is consistent with a sustained iconographic representation of information amenable for conscious awareness. If the stimulus is present *and* reentrant connections are not formed, there is nothing to sustain neural activity and it will rapidly disappear. This theory provides a working model for distinctions between conscious and unconscious processing in relation to masked stimuli, explaining both the sustained neural activity required for consciousness and the wealth of information associated with unconscious processing.

This sweep and sustain model has been presented earlier under the name of the feed forwards sweep (FFS) model (Lamme & Roelfsema, 2000). This model predicts that, during word priming, activity will initially sweep through the network of neurons associated with reading, and then as reverberant assemblies build, will travel through consciously in a manner consistent with wave transfer. During masked word priming reentrant connections will not form and only the initial burst of activity will propagate through the network. As this sweep of activity can not form stable, renewing patterns of firing once the stimulus is removed the longevity of this sweep is limited to that of transmission delays across the cortex. Such a model predicts an early, punctuated activation of a widely distributed neural population during unconscious word processing and a slower multistage progression during conscious word processing.

Word Reading in the Brain

The sequence of neural events associated with reading are particularly sensitive to the nuances of experiments used to study them (Demonet, Thierry, & Cardebat, 2005).

This has rendered the picture of the brain events accompanying skilled reading a tentative one.

According to Coltheart's dual route theory, reading can occur along both the graphophonological or lexicosemantic route (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). The phonological route is associated with the grapheme to phoneme conversion that allows access to the stored auditory representation of the words, and through this, access to lexical and semantic information. The lexical route involves direct lexical processing of the word form which allows direct access to stored semantic and phonetic information.

The first stage of reading that extends beyond the physical features of the stimulus probably involves a region in the middle of the left fusiform gyrus that responds more to words or pseudowords than to illegal non-word strings (Cohen & Dehaene, 2004; Cohen et al., 2000; Cohen et al., 2002; Cohen et al., 2003; Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002; Price & Devlin, 2003). This region, as it responds to repetitions of strings regardless of case, is invariant of hemifield location but responds indistinguishably to words and pseudowords and is thought to be involved in pre-lexical processing. This area has been dubbed the Visual Word Form Area (VWFA).

The location of the networks involved in lexical encoding remains elusive. Exploration is frustrated, in part, by the fact that the test stimulus which is lexical but contains no

semantic information, novel pseudowords, reliably activates both semantic and lexical processes to a greater extent than words (Price, 2000). This may be due to an increased duration of the cognitive search, as all possible words must be excluded before a word can be recognised as a non-word.

Beyond processing of the visual word form, brain regions activated during word reading depend on the task. Tasks that involve grapheme to phoneme conversion activate the posterior superior temporal gyrus and the supramarginal gyrus and the opercular part of the inferior frontal gyrus IFG (Jobard, Crivello, & Tzourio-Mazoyer, 2003; Price, 2000) and have also been implicated in semantic generation tasks (Abdullaev & Posner, 1997; Snyder, Abdullaev, Posner, & Raichle, 1995).

The silent, skilled reading of common words that is the focus of this study is thought to rely on the lexicosemantic route. Such tasks activate the basal inferior temporal cortex, the posterior middle temporal cortex and the triangular part of the IFG (Jobard et al., 2003). Frontal regions shown to be active during reading tasks that require semantic access such as the left posterior IFG (Gabrieli et al., 1996; Petersen, Fox, Posner, Mintun, & Raichle, 1988) have been shown to activate during passive silent reading (Petersen, Fox, Snyder, & Raichle, 1990) and may reflect direct lexical semantic access (Jobard et al., 2003).

Incongruencies exist over the time course of the passage of information through this system. Activity of the VWFA has been linked to a late (180-200ms), left lateralised period of the garden variety N1 visual component (Cohen et al., 2000). However it has been suggested the posterior left IFG responds to words as early as 160ms (Abdullaev

& Posner, 1997; Posner & Pavese, 1998), suggesting semantic information is accessed before the word form is processed. This interpretation must be taken with caution as estimates of the onset of this component have varied (Snyder et al., 1995). In addition, these tests relied on the instructions to either read aloud, or to semantically match the upcoming word list, the resulting measured activations may be better characterised as reflecting preparatory cognition and it is possible that the frontal activation in these studies is a response to the task demand rather than the rapid processing of the word stimulus. This interpretation is supported by the early (100ms) increase in activation of anterior cingulate regions during the use-generation task (where a use must be generated for a noun, Abdullaev & Posner, 1997).

Following the N1 component by ~200ms is a central negativity, the N400 which has been implicated in semantic processing. However as noted by Posner and Pavese (1998), this component is too late to explain that the saccade length can be influenced by the semantic nature of the presently fixated word because, for a skilled reader, word fixation persists for only approximately 300ms (Sereno, Pacht, & Rayner, 1992). This suggests that earlier semantic processing is occurring.

MEG analysis of the time course of word reading in the temporal lobe found that recruitment of the IFG precedes activation in the VWFA and that VWFA activation coincides with the recruitment of anterior middle temporal sites (Pammer et al., 2004). This suggests a distributed parallel process rather than the sequential processing of increasingly complex elements may be occurring during word reading.

Although the end product of reading is associated with awareness, as with any perceptual process, knowledge of the end product does not imply awareness of all stages of the cognitive process (Edelman & Tononi, 2000). Introspectively one is furnished only with the visual features, the meaning and the sound of the word, but the process by which orthography was converted into sound and meaning is outside conscious awareness. The activation of regions implicated in lexicosemantic processing prior to the overt extraction of word form in the VWFA may reflect unconscious steps in the skilled perception of words. Skilled reading may not simply reflect a spreading of consciousness generating neural activity across the circuits involved, rather, the process may begin and end with a conscious representation but intermediary steps may be processed unconsciously. It is presently unknown which of the above mentioned brain regions may be accessible to conscious awareness, and which may not.

Unconscious Word Reading

Functional magnetic resonance imaging (fMRI) and electroencephalographic (EEG) imaging of the processes that accompany unconscious word perception yielded a diminished and delayed form of the neural activity associated with conscious word perception (Dehaene et al., 2001). These findings are consistent with a model of unconscious processing where neural activity forms self sustaining local reentrant assemblies successively along the neural pathways associated with reading and which distinguish themselves from conscious neural activity by remaining isolated from each other. A delayed and reduced pattern mobilising similar neural populations suggests that unconscious processing is a low end variant of a unitary process occurring in both conscious and unconscious word reading. This is in stark contrast to findings that

conscious word reading evokes opposing behaviour responses to masked word reading (Cheesman & Merikle, 1986; Debner & Jacoby, 1994; Merikle & Joordens, 1997). If unconscious neural activity proceeds in a delayed, low amplitude fashion then the unconscious neural events would be occurring in the tail end of this distribution of neural firing observed in the monkey cortex during backward masking (Rolls & Tovee, 1994), after, not before, neural activity has been interrupted by masking. The findings of Dehaene and colleagues (2001) of a slower time-course argue against a model which holds the formations of self-sustaining reentrant connections as the distinction between conscious and unconscious processing. This would suggest that unconscious processing follows conscious processing.

Behavioural studies of unconscious semantic priming also argue against unconscious processing being an attenuated, delayed version of conscious processing. Masked semantic priming occurs with a maximal efficacy after a 60ms SOA and has no discernable effect after 100ms suggesting a rapid, not delayed, neuronal lifespan (Greenwald et al., 1996).

Part of the reason for the findings of Dehaene and colleagues may be that they searched for unconscious homologues of conscious evoked responses. Electrodes of interest were predominantly selected from differences observed during the condition where participants were consciously aware of the stimulus. This may preferentially focus on similarities to conscious processing and is an approach vulnerable to confounding influences from occasional non-reported conscious trials.

Traditional approaches to sub-threshold priming have examined the effect of a masked prime through an indirect measure, usually the behavioural response to a subsequently presented target stimulus. Neuroimaging removes the need for an indirect measure as it provides direct insight into the processing occurring during masked stimulus presentation. It is possible to compare the neural response elicited by two classes of stimuli and to determine if differing forms of cognition, evidenced by different neural responses, are occurring. A benefit of this method is that tightly controlled comparisons between stimulus classes are possible allowing, the application of a metaphorical scalpel to the type of cognition contributing to observed neural responses. A further advantage of this method is, unlike the traditional method, it affords the opportunity to examine the events occurring during unconscious word processing and not solely the repercussions.

The goal of the present experiment is to investigate the temporal dynamics associated with masked unconscious word reading. The sweep hypothesis of unconscious processing postulates that a wide range of processing (encompassing the brain regions involved in word reading) should occur with close temporal proximity. Under this feed forward model activity cannot persist after the removal of the stimulus (as there is nothing to drive it) and the degree of temporal proximity in this model is constrained by the transmission times across the areas of the cortex comprising the word reading network. The specific duration of this feed forwards sweep is uncertain, though estimates from the macaque brain provide a *rough* estimate in the order of 60ms from V1 across the cortex.

In an attempt to isolate abstract processes specifically related to reading, words will be compared to word-like stimuli. Previous techniques have measured the level of processing achieved unconsciously through performance on an indirect measure, such as reaction time or repetition suppression. This study shall directly compare two masked stimuli of differing complexities. If a difference is observed in the evoked response then this must be due to the processing of the differing complexity.

Methods

SUBJECTS

18 right handed subjects (9 female) participated. The mean age was 27, ages ranged from 19-45 years. All subjects had normal or corrected to normal vision and no history of neurological impairment. All procedures were approved by the University of Auckland Human Subjects Ethics Committee.



Figure 2 1 Experimental paradigm. Masking stimuli present for 67ms flank the experimental ‘masked’ stimuli (left). Visible stimuli were flanked by a 67ms blank which was the same color and contrast as the background (right). Shown is the Word condition. The same sequence was presented in the non-word and blank conditions.

STIMULI

Three classes of stimuli were utilised: words, orthographically-illegal non-words and ‘blanks’ (where no stimulus was presented). 320 word stimuli, 160 nouns, 160 verbs between three and eight letters in length (mean length 5.53) were presented. The 320 illegal non-words were matched for string length (mean 5.54). Stimuli presentation was controlled by a PC compatible computer. Stimuli were presented on a LCD screen. A masking pattern of overlapping triangles and squares was presented so that it subtended 2.5° by 1° degrees of visual angle, fully covering the letter stimuli (2x0.8°). Black (10 Lumen) stimuli were presented on a white (135 Lumen) background.

PROCEDURE

Subjects were presented with a continuous stream of masking patterns interspersed with the experimental stimuli. Individual masks were presented for 67ms, experimental stimuli for 27ms. In the visible condition, the experimental stimuli were flanked by a 67ms blank. In the masked condition stimuli were flanked by masks but each flanking mask was preceded or succeeded by a 67ms blanks (see figure 1) as per the method of Dehaene et al. (2001). Between 11 and 15 masking patterns separated each stimulus presentation, each trial lasting between 764ms and 1032ms. The veracity of internal time audits was verified via an external photosensitive diode.

To ensure the subjects attended to the stimuli they were instructed to press the space key when they viewed a series of seven uppercase 'x's. A total of forty such targets were present.

The experiment consisted of 1000 trials, 320 in each experimental condition and 40 target stimuli. Stimuli presentation was ordered randomly. Subjects received a break period every two minutes.

Behavioural Measures

Following the main experiment subjects participated in two forced choice tests and an identification test. Each test consisted of 40 trials. Behavioural measures were taken immediately after the main experiment. All properties of mask, stimulus and ambient variables (lighting, presence of the electrode net) were kept the same. Stimuli were preceded by between 6 and 9 alternating masking patterns and succeeded by 5 masking patterns. In the first test, subjects indicated by pressing the '1' or '2' key whether the word stimuli occurred before or after a briefly presented tone (two trials were joined together, one containing a word the other containing a 'blank'). In the second test

subjects discriminated between illegal non-words and blanks by pressing the '1' or '2' key. For the third test subjects reported the presented word using a keyboard to enter in the observed word. Words were selected randomly from the 320 words used in the imaging study.

Electrophysiological Recordings

Recordings were made in an electrically shielded, sound-attenuated room, using a 128 channel Electrical Geodesic amplifier (200M Ω input impedance) with Ag/AgCl electrodes (Tucker, 1993). EEG was recorded continuously with a sampling rate of 500Hz and referenced to the vertex channel. Impedances were set below 40 k Ω which is within acceptable parameters for this system. During recording the data were band-passed filtered between 0.1 to 100 Hz.

Following data acquisition EEG recordings were averaged across trials within conditions. Trial epochs consisted of a 250ms prestimulus baseline and a 700ms post stimulus time period. The resulting event related potentials (ERPs) were corrected for baseline over the 250ms pre-stimulus interval, re-referenced to the algebraic average of all the channels (the average reference) and band-pass filtered (0.1-20Hz).

Automated artefact rejection algorithms were employed to remove trials contaminated by eye blinks or other artefacts.

Results

Behavioural Results

Subjects performance did not differ significantly from chance for either the forced choice detection (52%, $t_{(17)}=0.626$, $p=.539$) or forced choice word versus non word discrimination (51%, $t_{(17)}=0.643$, $p=.529$). 96% of words could be named in the visible condition.

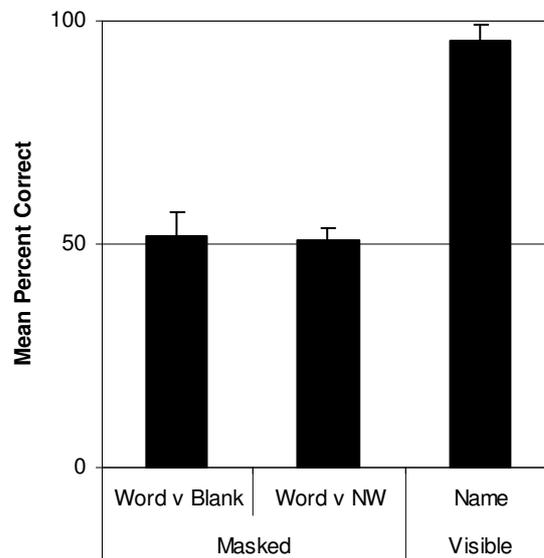


Figure 2-1 Results for stimuli discriminability. The mean percent of correct judgments across subjects is presented for two forced choice tests in the masked condition and an immediate recall test in the visible condition. The central horizontal line indicates chance performance for the forced choice tests. Error bars indicate 2 standard errors.

Time Window Selection

A previously employed technique for identifying time windows where evoked responses to masked words are present is to identify time windows through peaks in differential evoked response to visible words (Dehaene et al., 2001). To remove the affects of the masking pattern alone the 'blanks' condition was subtracted from both the word, and non-word, conditions. The resulting difference waves were then average and the Global Field Power (GFP) calculated. GFP is calculated by summing the squared difference between each electrode and all the other electrodes (So the squared difference is obtained for electrode 1 compared to electrode 1-128, this is repeated for electrode 2 and the remaining electrodes until all electrodes have been compared. The resulting squared values are summed. The square root of this is the GFP for that subject).

The GFP time series reflected activation predominantly due to the presence of the stimuli (word or non-word) and not masking stimuli. Importantly, this time series contained no information about differences between words and non-words allowing for the blind selection of time windows with respect to word/non-word differences. Further, it contained no information of differences within the masked condition, allowing blind time window selection for comparisons of all three levels of stimuli. Four time windows with distinct topographical distributions were observed (figure 2-2). Time windows were extended 20ms before and after the corresponding peaks. These were: 122-162ms, 226-266ms, 306-346ms and 422-462ms. These time windows and their respective topographic distributions were similar, though not identical, to those observed in Dehaene et al (2001).

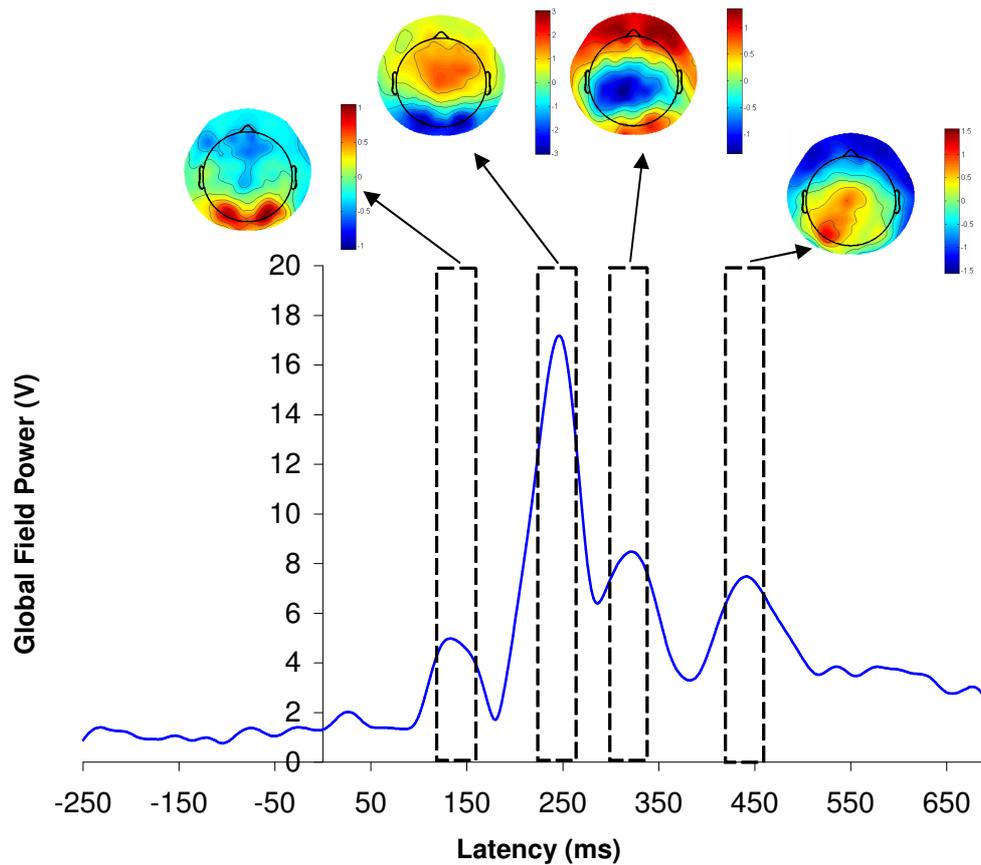


Figure 2-2 Time Window Selection. Global field power of the difference waveform between the average of visible words and non-words and visible blanks.

Analysis of Time Windows

To test for significant difference over the whole scalp in each time window a repeated measures ANOVA was performed with the within subject factors of condition and electrode. This analysis was repeated for all four time windows. Alpha was Bonferroni adjusted to compensate for the four comparisons ($\alpha_{\text{corrected}}=0.0125$). To compensate for the lack of independence between the electrodes the Greenhouse-Geisser adjusted degrees of freedom were used. A significant condition by electrode interaction indicates a different pattern of activations across conditions. Such an analysis is sensitive to differences in both topography and amplitude.

As a further index of the extent of difference the number of significant electrodes in each time window for each condition contrast was calculated and presented in table 1. In practice 13 or more electrodes are sufficiently unlikely to occur due to the inflated Type 1 error associated with 129 comparisons ($\chi^2_{(1)} = 7, p=0.01$).

Masked Condition

Analysis revealed a significant condition by electrode interaction in the first time window ($F_{(9.7, 165)}=2.390, p=0.012$). No significant difference was found in the three later time windows. Table 1 provides an index of the relative significance across the condition contrasts and time windows in the masked condition.

Table 2-1 Number of significantly different electrodes ($\alpha=0.05$) between conditions, across time-windows.

	Time Window			
	122-162ms	226-266ms	306-346ms	422-462ms
Words-Non Words	56	7	3	2
Words-Blanks	27	1	0	5
Non Words-Blanks	5	4	5	2

The significant effect of condition occurring in the first time window appears to coincide with a positive occipital activation typical of the p100 visual evoked potential. The presence of this p100-type component in the blank condition suggests that this component was the result of changes in the series of masking patterns.

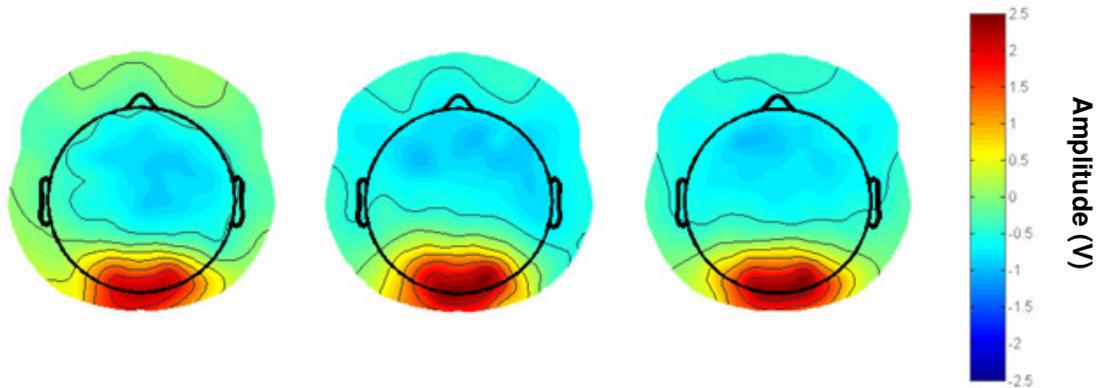


Figure 2-3: Topographic distribution of the non-subtracted waveform averaged between 122 and 162ms for (from left to right) Words, Non-words and 'Blanks'.

To investigate which conditions were contributing to the interaction a further post hoc pair wise ANOVA was conducted within each time window comparing the three two-condition combinations. The introduction of non-words into the mask stream did not produce a discernable change in the evoked potential ($F_{(7, 118.9)}=1.076$, $p=0.383$).

However, the inclusion of words in the masked stream produced an evoked response significantly different to that produced by either non-words ($F_{(7.2, 122.2)}=3.743$, $p=.001$) or blanks ($F_{(7.2, 123)}=2.517$, $p=.018$).

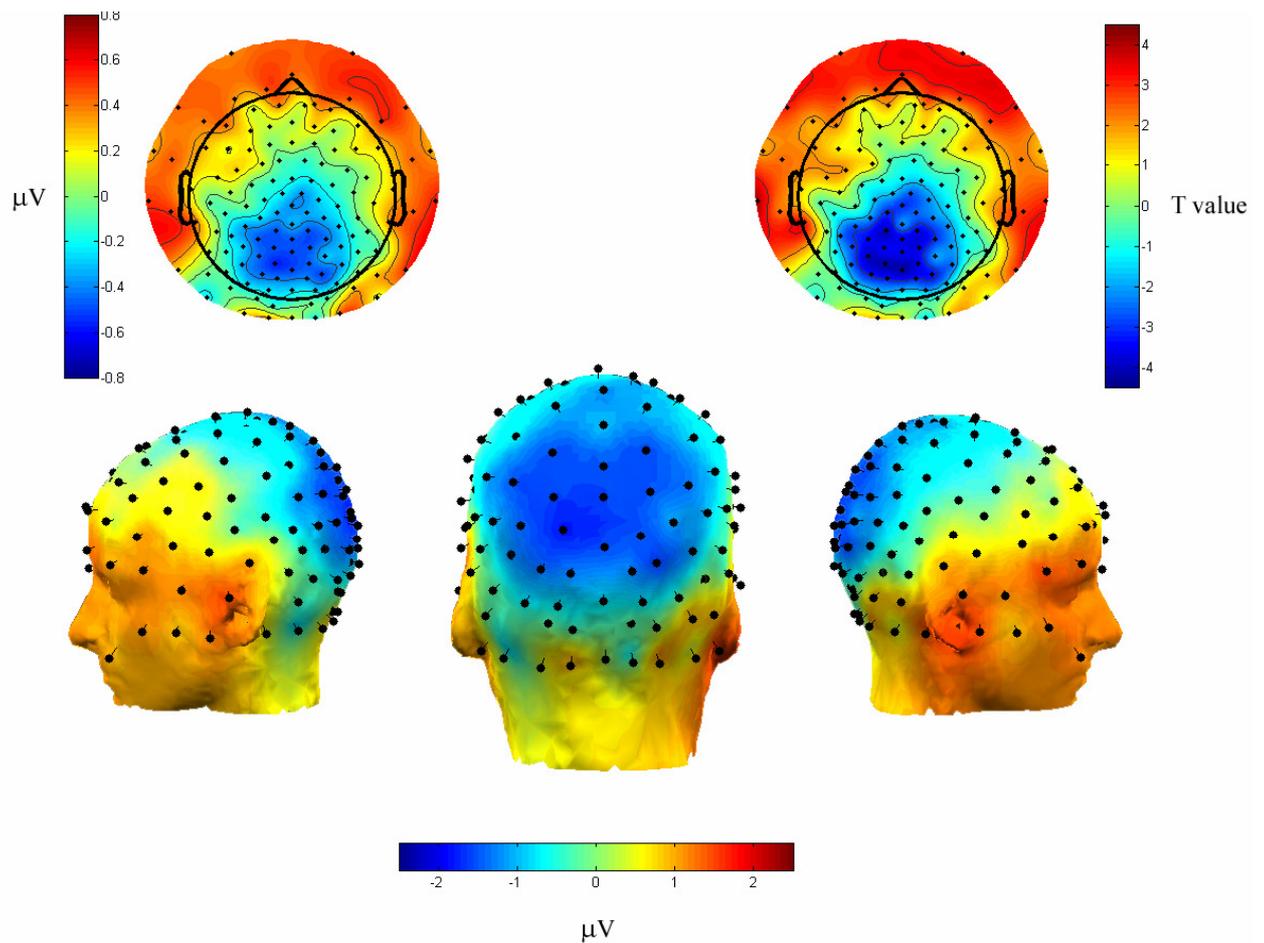


Figure 2-4: Topographic map of the average difference in the ERP between 122ms and 162ms to masked words and masked non-words: interpolated voltages across the scalp (top left); corresponding t value (top right); spline interpolation on the scalp (lower three).

Words elicited a greater parietal negativity and bilateral fronto-temporal positivity than did non-words. To assess whether this reflected a change in topography, and the recruitment of different neural populations, rather than a change merely in amplitude, individual subject data was normalised to a GFP of 1 and differences were compared to a distribution generated through 5000 permutation randomisation test (TANOVA, see Strik, Fallgatter, Brandeis, & Pascual-Marqui, 1998). This yielded a significantly different topography between word and non-word conditions ($p=0.001$).

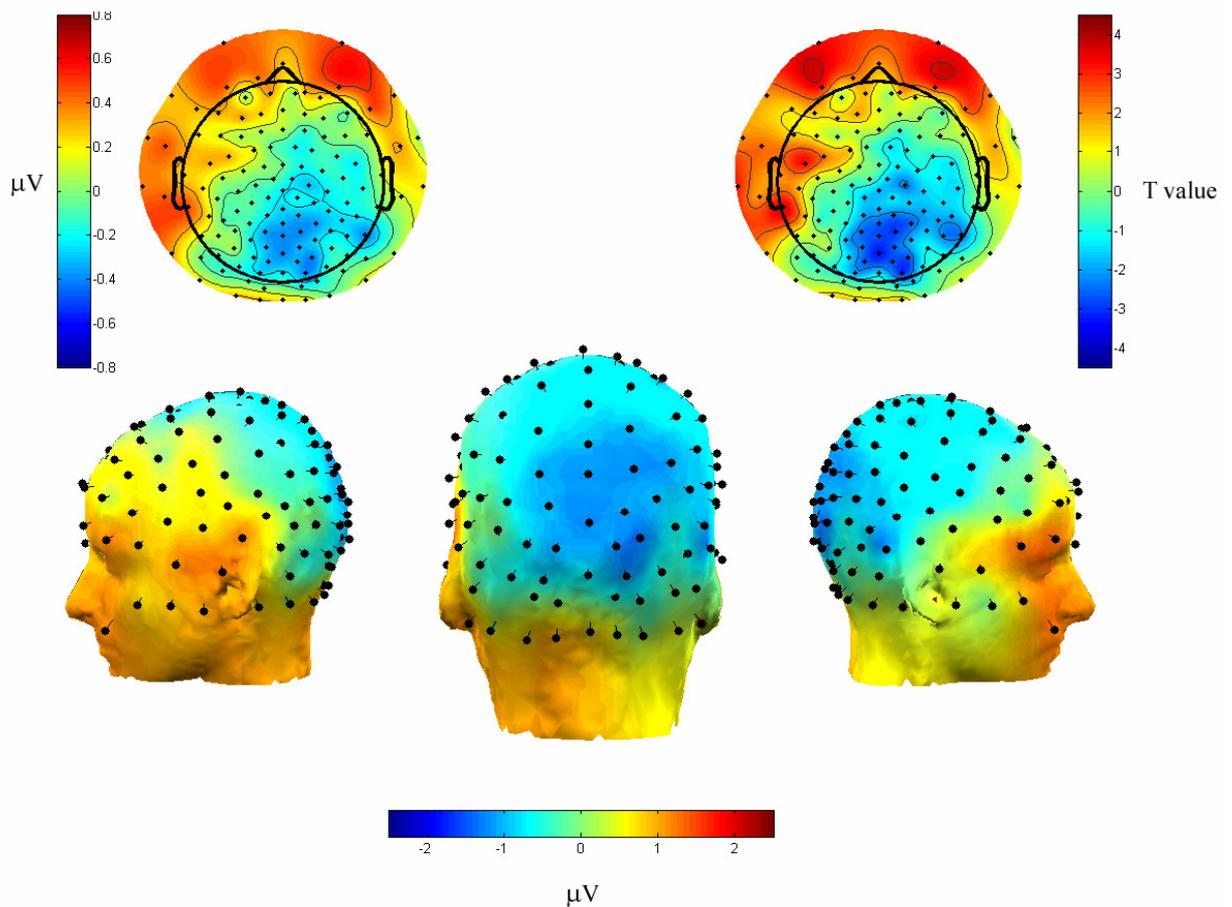


Figure 2-5: Topographic map of the average difference in the ERP 122ms to 162ms to masked words and masked 'blanks': interpolated voltages across the scalp (top left), corresponding T value (top right), spline interpolation on the scalp (lower three).

The differences between words and blanks were smaller than between words and non-words. The parietal negativity was less wide-spread and stronger over the right hemisphere though topography did not differ significantly between words minus non-words and words minus blanks ($p=0.099$).

Visible Condition

As the method used for selecting the time windows artificially biases differences between visible word and blanks and between non-words and blanks (but not visible

words and non-words), and because differences due to the visual perception of the stimulus were of little interest, contrasts were made solely between words and non-words. Such contrasts yielded only one significant difference and this was during the second time window ($F_{(9.2, 50.0)}=5.11, p=0.004$). Although the first time window did approach significance ($F_{(5.3, 95.4)}=2.44, p=0.037$), this did not survive correction for multiple comparisons ($\alpha_{\text{corrected}}=0.0125$).

During the 2nd time window, a left-lateralised occipital negativity was observed. This negativity was more prominent in the word than non-word condition. To assess whether laterality varied as a function of stimulus class an ANOVA on left versus right occipito-temporal electrodes (corresponding to the peak N1) was performed.

A significant main effect of both word type ($F_{(1,17)}=13.996, p=.002$) and hemisphere ($F_{(1,17)}=6.154, p=.024$) was present, though no interaction was observed between these factors ($F_{(1,17)}=.166, p=.689$). This confirms that the potential was left lateralised and stronger in the word condition but reveals that a uniform change in magnitude, rather than laterality, was occurring within this potential.

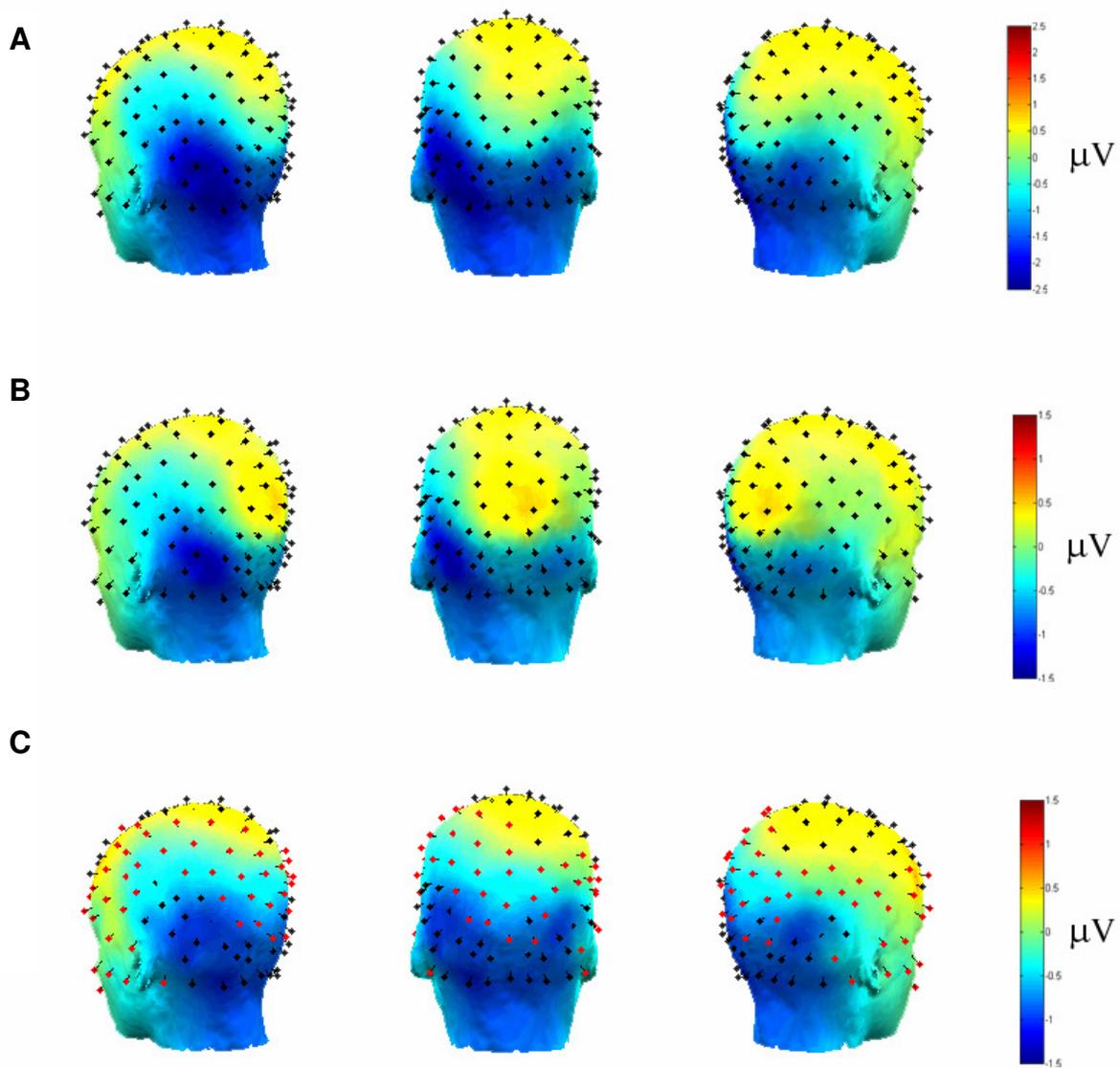


Figure 2-6: Topographical distribution of the left lateralised N1 component elicited by (a) words and (b) non-words and (c) the difference map (significant electrodes in red). Evoked potential were averaged between 226-266ms. Note the scale varies between (a) and (b) & (c).

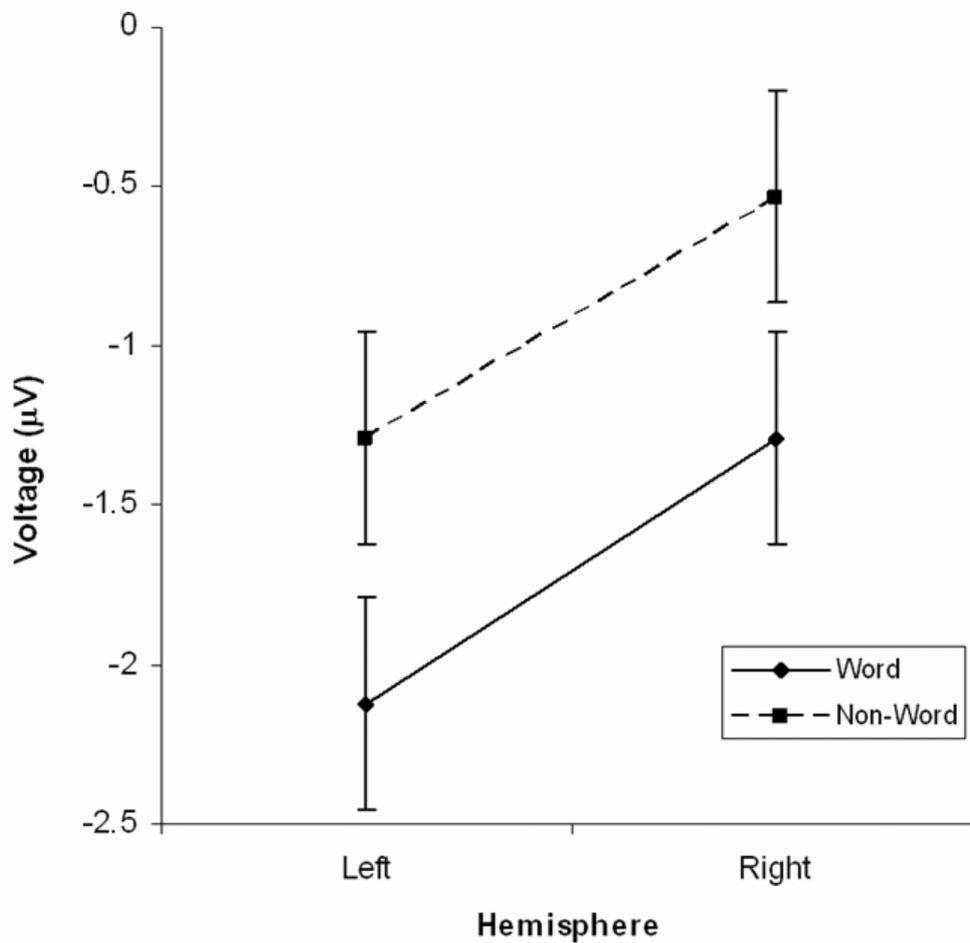


Figure 2-7: Lateralisation of the N1 component during the visible presentation of words and orthographically illegal non-words. This figure shows the averaged voltage for the period 226-266ms averaged over electrode P9 (left) and P10 (right) and the six electrodes surrounding each. Error bars represent 95% confidence intervals for repeated measures (Masson & Loftus, 2003).

Replication of previous analysis

Although not the central focus of this study, methodological similarities between this and the study of Dehaene and colleagues (2001) affords the opportunity to investigate the replicability of those results. To this end, an analysis of the difference between words and blanks was conducted in the same fashion.

Mean voltages for left and right occipital electrodes were calculated between 156 and 188ms. Words were more negative than blanks though this difference was not significant ($F_{(1, 17)}=0.49$, $p=0.49$, $\text{mean}_{\text{difference}} 0.094\mu\text{V}$).

To investigate a putative N1 component reported by Dehaene and colleagues, mean voltages were calculated for left anterior temporal electrodes. Words were more positive than blanks, though this difference was not significant ($t_{(17)}=0.09$, $p=.928$, $0.014 \mu\text{V}$ difference).

To investigate a potential observed between 400-500 ms average amplitudes were calculated for left precentral, central and right precentral electrodes. As in Dehaene et al. (2001), a significant interaction of stimulus and location was observed ($F_{(2,24)}=3.564$, $p=.039$), though only the significant right hemispheric negativity was replicated ($T_{(17)}=-0.165\mu\text{V}$). Left and central sites failed to reach significance and trended towards the opposite amplitude to that found in the Dehaene et al. study.

Interactions between word type and masking condition in time window one.

As a potential was observed to occur in the first time during masked stimulus presentation that was not present during visible word presentation a further analysis was conducted to see if this difference was significant. A three way repeated measured ANOVA was conducted with the factors word type (word, non-word or 'blank'), visibility and electrode. A significant interaction was observed between these three factors ($F_{(7.9, 135)}=4.187$, $p<.001$). When only two levels of word type (word and non-word) the interaction was likewise significant ($F_{(6.55,111)}=3.502$, $p=.002$).

Discussion

The behavioural studies show that subjects were unaware of the stimuli in the masked condition and that stimuli were easily observable in the visible condition. The masked condition can therefore be considered unconsciously processed as assessed by the objective threshold criterion (Merikle, Smilek, & Eastwood, 2001).

Unconscious word reading

Dehaene and colleagues demonstrated that perturbations could be detected in the ERP evoked by unconsciously perceived stimuli. Further, they showed in a supplementary experiment that under such presentation conditions, abstract information pertaining to the characteristics of the letter characters was extracted. Left ambiguous was whether the activation observed in response to masked words was a reflection of such abstract information processing, higher level abstract information, or merely due to the presence of the naked stimulus.

In this study, the differences observed between words and both non-words and blanks demonstrate that the recorded response was not due to physical characteristics of the stimulus. The significantly different evoked response between words and non-words provide direct evidence of abstract information extraction above the level of letter character information, demonstrating that during unconscious word reading words are processed to at least the pre-lexical level, in the absence of conscious awareness.

The evoked response observed in this study provides a qualitative distinction between conscious and unconscious conditions. A classic criticism of unconscious perception

paradigms is that the direct measure of awareness may not be sensitive to all aspects of conscious processing (Holender, 1986). Under such situations, undetected conscious cognition may seep into trials in the unconscious condition and produce an increase in performance that is erroneously attributed to non-existent unconscious processing. The observation of a temporally and topographically distinct pattern of activation in the masked condition amounts to a qualitative distinction. This qualitative distinction between conscious and unconscious processing could not be the result of conscious cognition's influence on the masked condition. Such qualitative distinctions offer rare evidence of dissociable unconscious processes. Such dissociations have been found in the process dissociation paradigm where explicit instruction is placed in opposition to automatic processing (Cheesman & Merikle, 1986; Debnar & Jacoby, 1994) and have previously been observed via modifications of the time course of the N400 evoked by masked and visibly primed target stimuli (Kiefer & Spitzer, 2000a).

The transient pattern of the evoked response is consistent with the transient pattern of the behavioural facilitation. Priming that requires extraction of the symbolic meaning of the word is maximal 60ms after stimulus presentation and disappears after 100ms (Greenwald et al., 1996). The single fleeting burst of activation related to the abstract nature of the word is consistent with the evanescent nature of masked semantic priming.

In a single subject (12 recording sessions) MEG study, difference in the evoked response were found over parieto-occipital sites to words of differing semantic strengths beginning 100ms post stimulus (Pulvermuller, Assadollahi, & Elbert, 2001). This response occurred to highly practised words (16 stimuli each presented 240 times)

which may have attenuated conscious processing. The authors speculate that, due to frequent repetition, the relevant memory traces may have been more active, facilitating the response to semantic word properties. The similarity of the distribution and time course (both peaked at 140) of the activation of this study of Pulvermuller and colleagues (2001) allows the possibility that the differences observed during this study may reflect the differences between the semantic content in the unconsciously processed non-words and words.

Three possible explanations exist for the surprising finding that the difference between words and consonant strings observed for masked stimuli was not found for visible stimuli. Two of these theories involve the signal getting lost amongst the noise. As the stimulus enters consciousness the amount of cognition for a given subject increases. Concomitantly, the amount of neural activity increases and so does the potential for intra-subject variability, the error term in the statistical tests employed. This concern was addressed by conducting a t-test on the standard deviations for masked and visible conditions in the word/consonant string subtraction. This test revealed no significant difference between conditions indicating that the failure to reach significance in the visible condition was not due to an increase in intra-subject variability. A second repercussion of increased activity is the greater likelihood that a neural population is activated that cancels out the homologue of the activation measured in the masked condition before it reaches the scalp. This is an unavoidable symptom of the inverse problem associated with scalp based EEG.

The third alternative has the furthest reaching theoretical implications. There exists the possibility that the masked pattern of activation was not observed in the visible

condition because as the stimuli enters consciousness the normal route of unconscious processing is reduced or removed. This supports a model where unconscious processing is actively suppressed during conscious processing leaving the elements of unconscious processing more active in the absence of awareness of the stimuli.

This counter-intuitive finding gains some support from previous research. A study of conditioned learning has shown a similar pattern. In this study the left amygdala was more active during masked than unmasked CS+ presentation (Morris et al., 1998). The authors suggest that the activation of the right amygdala during conscious stimulus presentation may inhibit the unconscious conditioned response. It is possible that a similar mechanism occurs with the conscious processing of words suppressing the automatic and unconscious processing of words.

Such a finding would have repercussions on existing theories of conscious and unconscious processing where unconscious processing is conceptualised as a constant that can be linearly added to the level of conscious processing, allowing the estimation of the degree of unconscious processing (Debner & Jacoby, 1994). However, if unconscious processing varies with stimulus perceptibility then such theories become untenable.

Evoked response to passive word viewing

The left lateralised negative occipito-temporal component of the current study is identical to that observed during similar stimuli presentation conditions (Dehaene et al., 2001). This waveform has the distinctive topography of the late N1, thought to reflect activity of the VWFA (Cohen et al., 2000) and demonstrated a delayed onset consistent

with other masking studies (Dehaene et al., 2001). During the visible presentation of words, differences between orthographic and non-orthographic stimuli have not been observed prior to the N170 (Simon, Bernard, Largy, Lalonde, & Rebai, 2004) post stimulus. If the VWFA is the site of the pre-lexical processing then there is a disparity between the results in the difference observed between words and non-words at 140ms in the masked condition and the difference observed at 240ms in the visible condition. The earlier activation in the masked condition suggests that visual word form has already been extracted 100ms prior to the potential usually attributed the initial extraction of the word form. It is suggested that this disparity is a reflection of the different time courses associated with an initial burst of high information firing.

The amplitude of the late N170 component related to visual word form showed a constant increase across electrodes from letter strings to words. This suggests that the putative VWFA may reflect bilateral generators and trans-hemispheric neural assemblies. The possibility of the presence of bilateral generators is supported by the finding of an increase in the BOLD response to words over non-words not only in the left VWFA of all subjects, but in the right fusiform area, observed in six out of seven subjects (Dehaene et al., 2002).

Discordant Findings

A reason for the disparity between these results and those of Dehaene and colleagues may reflect a difference in the focus of the analysis. The previous study searched for unconscious homologues to conscious processing in the time and location where evoked differences occurred during conscious processing. The failure of this study to replicate the findings of Dehaene and colleagues may reflect Type II error. However

several features of the analysis performed by Dehaene and colleagues suggest that the analysis employed in that study may have a heightened tendency to Type I errors.

Time window selection in the masked condition was corroborated with evoked difference occurring during the visible condition however, visual inspection of peak differences in the masked condition was used to refine time window selection (Dehaene et al., 2001). To select a time window based on maximal observed difference will massively inflate the chance of Type 1 error. The replication of only one finding out of three comparisons and the frequent trends in the opposite direction to the predicted, suggests that corrections for multiple comparisons may have been appropriate. This would have yielded no significant replication in the masked condition.

The evoked potential reported in this study was not reported by Dehaene and colleagues (2001) despite an almost identical experimental paradigm and examination of the same time window. This disparity may have arisen due to the type of analysis used.

Dehaene and colleagues focussed on a pair of occipital electrode (O1 and O2) where no significant difference was observed in this study. Another possibility is that the repetition of stimuli used during the study of Dehaene and colleagues may have attenuated the neural response through repetition suppression (Naccache & Dehaene, 2001)

In summary, this study provides evidence for a qualitatively different neural response during unconscious word processing. This response proceeded with a time course more rapid than that associated with visual word form processing during conscious cognition. The comparison of the evoked response to words and to letter strings demonstrates that

abstract information has been extracted despite the fact that subjects are unable to report the difference between words and non-words. The time course and distribution of this response are consistent with a component previously observed to be modulated by semantic processing (Pulvermuller et al., 2001). The earlier processing of information without awareness is compatible with an initial sweep of activations through neural circuits which is distinguished from conscious processing by its failure to develop reentrant stability.

The implications for the neural substrates of conscious cognition from this chapter are that these results seem to support the FFS model of unconscious processing and allow the possibility that recurrent processing may provide the distinction between conscious and unconscious processing. However, for the sweep model of unconscious cognition to hold, it is critical that all stimulus induced cognition, pre-lexical, lexical and semantic, are occurring concurrently. For this assertion to be tested it must be demonstrated that at the same time as disparities between word and non-word stimuli are being processed so are the semantic elements contained within the word stimuli. This shall be the focus of Chapter Three.

Chapter 3 Temporal Dynamics of Unconscious Semantic Integration: unconscious priming of unconscious targets:

Introduction

Semantic priming, the improvement in performance when a stimulus is preceded by a semantically related prime, is thought to involve both automatic and controlled processes (Posner & Snyder, 1975; Rossell, Price, & Nobre, 2003). The automatic processing is believed to be a reflection of the passive activation between related word representations (Collins & Loftus, 1975), while the controlled process is thought to involve the generation of the expected semantic cohort for the prime stimulus (Rossell et al., 2003). Masked semantic priming allows isolation of the automatic elements of this process and also affords the opportunity to explore the temporal dynamics of unconscious processes, and through this, the distinction between the neural events associated with conscious and unconscious cognition.

Semantic Access in the Brain

Using a direct subtraction method it is not possible to isolate the effects of semantics on unconscious cognition. There exists no stimulus set that can be subtracted from words to yield a pure distillation of the information related to the semantic content of word stimuli. The obvious candidate, pseudowords, paradoxically evoke a larger response in brain regions thought to process lexical and semantic content (Binder et al., 2003; Price, 2000).

Despite the lack of orthographically legal semantic-free referent stimuli, some gain in understanding semantic access has been made by studying words with differing semantic content. Words that serve a largely grammatical function, so-called function words, tend to activate only left hemispheric regions. In comparison content words, which possess deeper semantic associations, activate more widely distributed cortical networks (Pulvermuller, Lutzenberger, & Birbaumer, 1995). There is some evidence that verbs associated with motor actions activate regions of the motor cortex while high imageability nouns activate occipito-parietal regions (Pulvermuller et al., 2001; Pulvermuller, Lutzenberger, & Preissl, 1999). A comparison of verbs associated with facial or leg movement also revealed a difference in the evoked response consistent with the somatotopic organisation of the motor strip (Pulvermuller, Harle, & Hummel, 2000). These findings build a picture of semantic representation that cannot be localised to one particular cortical region but relies instead on the integration of information across the cortex.

One study that directly investigated the role of semantic content on the brain regions recruited during access (Giesbrecht, Camblin, & Swaab, 2004), compared pairs of highly imageable nouns to pairs of semantically related nouns and found differing regions of activation responses to the differing styles of stimulus relationship. Areas of the middle temporal gyrus were shown to be particularly responsive to word imageability, which is consistent with a previous PET study (Wise et al., 2000). In contrast, semantic relatedness influenced a network more traditionally associated with semantic access.

This network, typically attributed the governance of semantic access, includes the inferior frontal gyrus and the inferior parietal lobule and has long been implicated in tasks involving the semantically driven generation of words (Abdullaev & Posner, 1997; Petersen et al., 1988; Snyder et al., 1995). However, these tasks include a plethora of components extending beyond the semantic access of a words' meaning (Price, 2000). When ancillary task factors are controlled for, only the inferior medial temporal gyrus is activated (Price, 2000).

The electromagnetic measure most commonly associated with semantic processing is the N400, which responds to semantic context, and is more pronounced when a word is placed out of context within a sentence and in the 'oddball' paradigm. A putative generator for the N400 (Rossell et al., 2003) is the anterior inferior medial temporal lobe where the polarity reversed intracranial homologue of the N400, the P400, has been shown to be sensitive not only to semantic context but to the semantic content of words (Nobre, Allison, & McCarthy, 1994). Concrete nouns produced a P400 whereas purely grammatical function words did not (content effect) and the P400 was modulated by semantically primed target stimuli (context effect). However, attribution of the scalp recorded N400 to an anterior medial temporal lobe generator must be considered with caution, as the intra-cranial P400 has also been measured in the orbito-frontal cortex and other regions shown to be sensitive to semantics.

Creating a clear picture of the role of differing brain regions in the representation of the extraction of semantic meaning from words is in part hindered by unclear boundaries between the extraction of meaning from words and the representation of semantic information within the cortex. The transduction of semantic word content into an

abstract representation involves linguistic elements and presumably reflects left hemispheric regions such as the anterior inferior medial temporal lobe. The representation of semantic information rendered from words may more flexibly activate regions of the cortex reflecting the particular associations of the semantic content.

Investigation of Semantic Access through Priming

It is possible to access unconscious semantic priming through the manipulation of the relationship between stimuli. This is achieved by monitoring the effect of a masked semantically matched prime on a later behavioural or neural response to a target stimulus (the indirect response). This, however, involves imaging the repercussions of unconscious processing not the process itself. Cognition during the indirect task reveals little of the neural activity associated with the unconscious processing. Imaging the target response during semantic priming allows the study of the *site of influence* of priming but it does not reveal the *site of effect*, the neural mechanism that underlies semantic priming.

Repetition Suppression (RS) refers to the phenomenon where repetition of identical or similar stimuli results in a diminished neural response on subsequent occurrences. RS is a method for investigating the repercussions of priming. RS was first observed at the single cellular level in the Rhesus macaque during a working memory task (Miller, Li, & Desimone, 1991). The discharge of neurons in the IT cortex was shown to decrease as the items to be held in short term memory were repeatedly presented. In humans RS was first observed in the right posterior cortex when subjects completed stems that matched a previously studied list of items (Squire et al., 1992), a task believed to be sensitive to priming.

Activity in the left inferior prefrontal cortex has been shown to be attenuated during the successive semantic encoding of stimuli and during the semantically primed encoding of stimuli (Demb et al., 1995; Gabrieli et al., 1996; Giesbrecht et al., 2004). This activation is believed to reflect executive functions during semantic encoding and retrieval (Demb et al., 1995; Rossell et al., 2003) and, in the case of semantic priming, may reflect an increase in cognitive load demanded for incongruent pairs rather than a reduction to congruent pairs (Cardillo, Aydelott, Matthews, & Devlin, 2004). In a semantically primed lexical decision task, with a low demand on overt semantic encoding and retrieval, left middle temporal activation was observed in the absence of left IFG activation (Rossell et al., 2003). This represents a more pure reflection of semantic processing without the potential confounds created by other task-related cognitive elements

There is a diversity of methodology in the RS literature. Three different categories of studies have been used to provide support for RS: 1) the effect of stimulus repetition on neural activity; 2) the effect of studied items on later tests of implicit priming; and 3) the effect of primes on an immediately followed target. Considering the effects of previous exposure to stimuli assesses the effect of the stimulus *familiarity* (Brown & Aggleton, 2001). The second and third groups are more consistent with traditional studies of priming. Priming exerts an effect robust to both delay and distracter items (Dienes & Berry, 1997; Tulving & Schacter, 1990) and it is possible that RS due to both familiarity and traditional priming are manifestations of the same mechanisms. However, differences in the suspected neuroanatomical substrates exist. Familiarity mediated RS is suspected to involve perirhinal modulation and recognition memory is

dramatically impaired with perirhinal ablation (Meunier, Bachevalier, Mishkin, & Murray, 1993). In contrast, priming is observed in the absence of the hippocampal complex (Warrington & Weiskrantz, 1974) and is thought to rely on neocortical plasticity. The mechanism for enhanced performance on priming studies may reflect cortical RS while RS in the perirhinal cortex may lead to the longer term sense of familiarity necessary for overt recognition. Despite these apparent differences, both lines of inquiry have thus far yielded similar results (Schacter & Buckner, 1998).

Semantic RS is manifest in evoked potentials as a reduction in the N400 component (Kiefer, 2001). This finding has also been observed during masked semantic priming of a subsequent visible target word (Kiefer, 2002). Here the semantic prime was shown to exert influence only over prime-target delays of less than 200ms (Kiefer & Spitzer, 2000b). This duration of influence is consistent with behavioural measures of masked semantic priming which degrades after 60ms (Greenwald et al., 1996). Dehaene et al. (2001) found letter-case sensitive masked repetition priming in the extrastriate cortex and letter-case insensitive RS in the fusiform gyrus. These findings demonstrate how RS can be employed to investigate the effect of unconscious priming during overt semantic processing but does not allow insight into the role of semantics in unconscious processing.

The general rationale behind priming studies is to reduce the cognitive effort required to identify a given target stimuli by priming it with a related stimuli. The decrease in activation resulting from the target being primed can be considered to be a function of the nature of the relationship between prime and target, shedding light on this area of cognition during overt processing (Naccache & Dehaene, 2001). Repetition suppression

allows the assessment of relations between stimuli but to date has only been employed to measure the modulation occurring during conscious processing.

In the present study, to investigate the effects of semantic information on unconscious processing, both prime and target are masked so that they are presented below the objective threshold of awareness. In this way, the effect of semantic priming on unconscious processing associated with the target stimuli will be the dependent variable. As RS is measured during subsequent task performance, the neural events that associate passive presentation of semantically related pairs is uncertain. However, any difference in the evoked response between semantically related and unrelated word pairs will reveal the incorporation of semantic information into the current neural ensemble. This study should reveal information about the time course of semantic integration in unconscious processing and investigate whether repetition suppression occurs automatically without the need for performance on an overt task.

Methods

Participants

Fourteen right handed subjects (six female) participated in this study. The mean age was 26, ages ranged from 19-44 years. All subjects had normal or corrected to normal vision and no history of neurological impairment. All procedures were approved by the University of Auckland Human Subjects Ethics Committee.

Stimuli

160 pairs of semantically associated words were selected from University of South Florida Word Association, Rhyme and Word Fragment Norms (Nelson, McEvoy, & Schreiber, 1998). Word pairs with a cue to target associated strength of between 0.68 and 0.94 were selected. Word length ranged from four to eight letters in length and was identical in each condition.

In the semantically related condition words were presented in their initial cue to target pairings. In the semantically unrelated condition the target words were randomly shuffled. This permitted some semantically related word pairs in the ‘unrelated’ condition but the occurrence of these would be low and this is not a threat to the validity of the study. It was not deemed possible to ensure that word pairs were ‘semantically unrelated’ for each subject. This procedure ensured that the control and experimental condition consisted of one presentation of each cue and each target with the sole difference being the association within each pairing.

Procedure

Words were presented for 27ms with a 67ms mask separating word pairs. Before and after each word pair presentation a series of masking patterns were presented for 67ms each. At the end of each trial three to five intervening mask stimuli were presented before the initiation of the next trial creating a constant sequence of masks interrupted only by the presentation of the experimental stimuli (see Fig 3-1). The interval between the presentation of the experimental stimuli consisted of between 11 and 15 mask presentations and was 733-1000ms in duration.

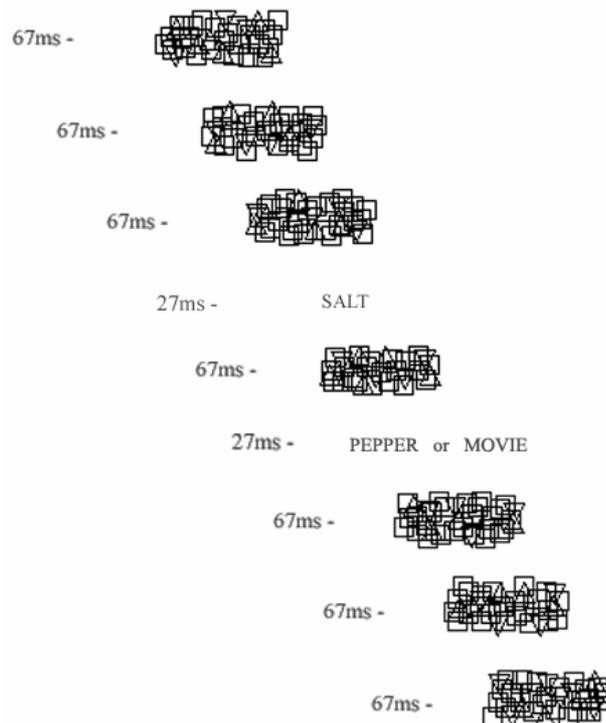


Figure 3 1. Sequence of events during a trial. Word pairs were preceded and succeeded by a series of masking patterns that was uninterrupted between trials. Words pairs were separated by a single 67ms mask and were either semantically related or unrelated.

A total of 320 trials were randomly presented to each subject (160 from each condition). Break periods occurred every eighty trials. To ensure that subjects attended to the location where stimuli were to appear subjects were given the overt task of detecting a series of red upper-case 'x's.

At the end of the imaging run a 40 trial word-consonant-string forced choice test was performed to assess stimulus perceptibility. Conditions were identical to the main experiment, subjects were required to distinguish between words and non-words by pressing the '1' or '2' key.

Electrophysiological Recordings

Recordings were made in an electrically shielded, sound-attenuated room, using a 128 channel Electrical Geodesic amplifier (200M Ω input impedance) with Ag/AgCl electrodes (Tucker, 1993). Recordings were sampled at 500 Hz with an analogue 0.1 to 100 Hz bandpass filter and referenced to Cz. All electrode impedances were below 40 k Ω which is within acceptable parameters for this system.

Analysis

Continuous EEG recordings were transformed to 950ms event related epochs including a 250ms pre-stimulus baseline. For each subject epochs were averaged within each condition and re-referenced to the algebraic average of all 129 electrodes. Average evoked potentials were then bandpassed filtered between 0.1 and 20Hz.

Conditions were compared using a 10000 permutation randomisation test (TANOVA) over all 129 electrodes (Strik et al., 1998). This test employs the dissimilarity between

conditions over all electrodes (i.e. the sum of the root means square of the difference between conditions A and B for each electrode).

This randomisation tests are preferred because a) they make *no* assumptions about the underlying distribution of the population, b) they do not suffer from the loss of power experienced by most non-parametric tests and c) this particular test deals elegantly with the inter-relatedness of observations across neighbouring electrodes.

These tests were not used in chapter 2 as the analysis required in this section required analysis across three different levels (words, non-words and blanks).

Results

Behavioural

Subjects performed at chance in the word versus consonant string two-alternative forced-choice test ($x_{\text{correct}}=50.07\%$ SD = 4.13%) indicating that subjects were unable to consciously identify word stimuli.

EEG Results

The initial ERP for each condition demonstrated a pattern of reversing polarity over occipito-temporal sites consistent with a visual evoked potential. The unsubtracted wave forms are presented in figure 3-2.

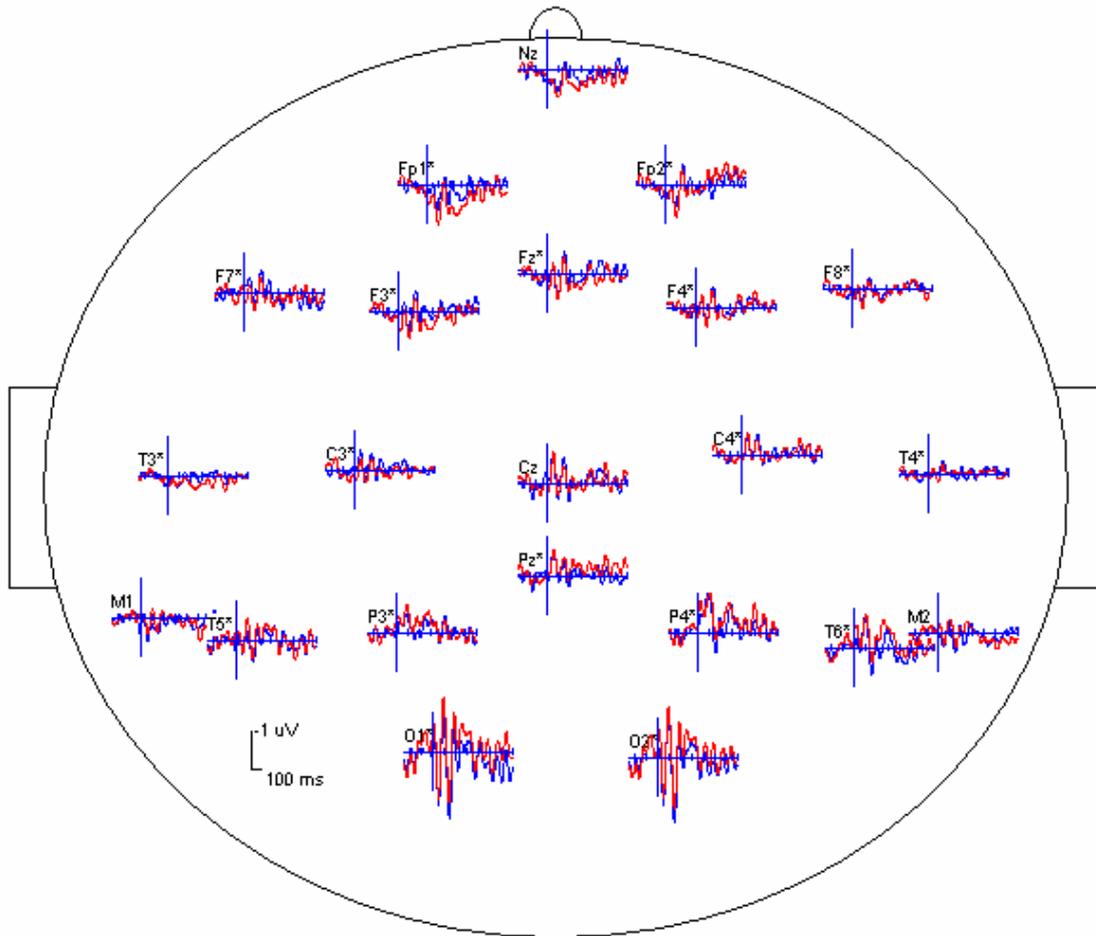


Figure 3-1 Evoked response to the target stimulus following priming by either a semantically related prime (blue) or semantically unrelated prime (red). Presented are electrodes corresponding to the international 10/20.

Analysis of the first time window, 130-150ms post target presentation, did not yield a significant difference between semantically related and unrelated conditions ($p=0.637$)

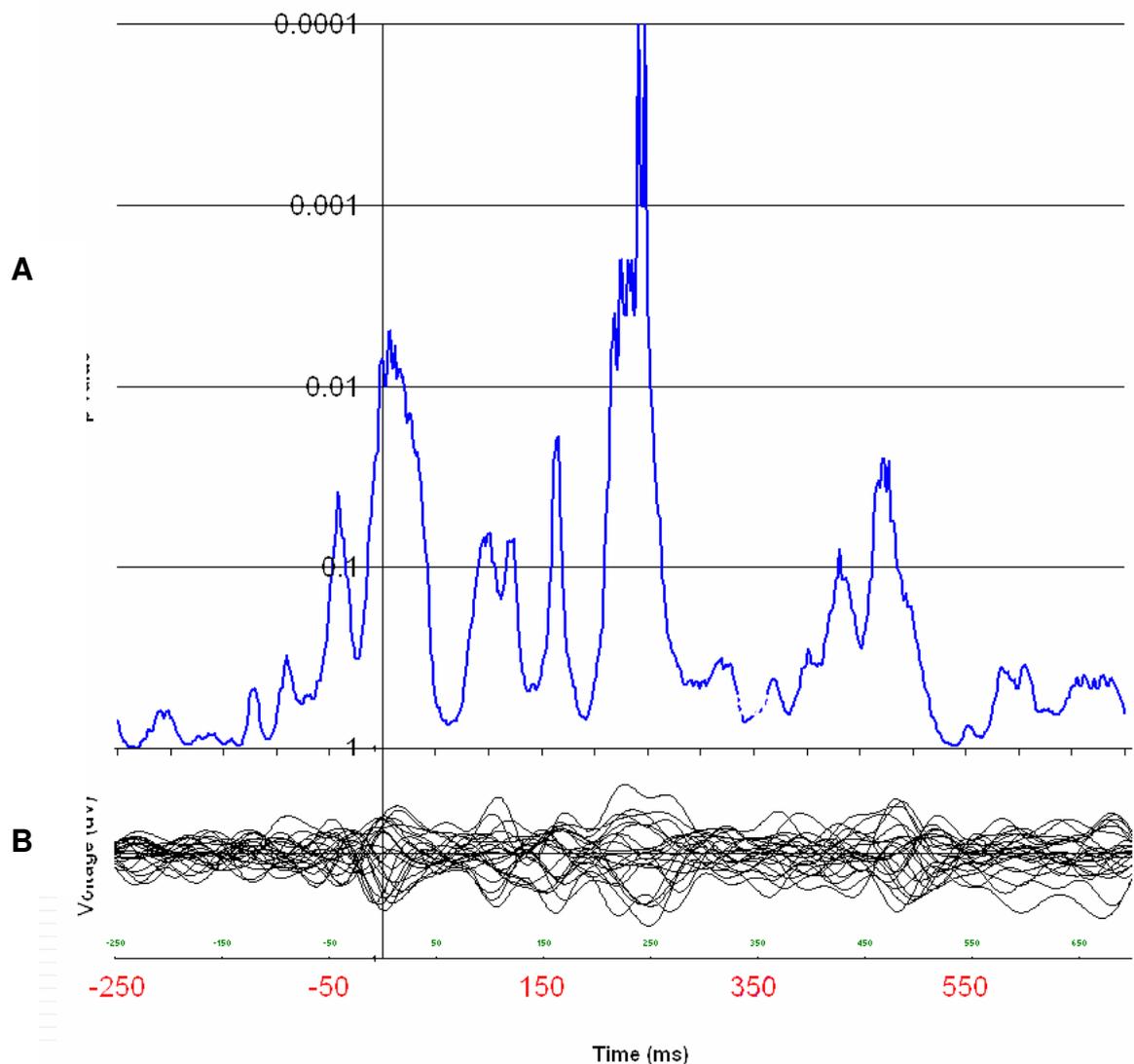


Figure 3-2 (a) The probability of the difference between conditions under the null hypothesis for each time point. P values were assessed using a randomisation TANOVA. The y-axis is presented on a logarithmic scale. (b) An overlay of electrodes corresponding to the international 10/20 system showing the difference in the evoked voltage values between conditions.

Statistical analysis of the difference waves between semantically primed and un-primed targets revealed a highly significant difference peaking 250ms after target presentation. Significance levels peaked at $p < .00003$. This significance level survives a Bonferroni correction for multiple comparisons across the 350 samples during the post stimulus epoch (a conservative measure considering the lack of temporal independence in EEG data and the consecutive nature of significant time points).

The modulation of the response to the second stimulus by the semantically related prime stimulus attains significance (at the 0.05 level) 210ms after stimulus onset and persists until 260ms.

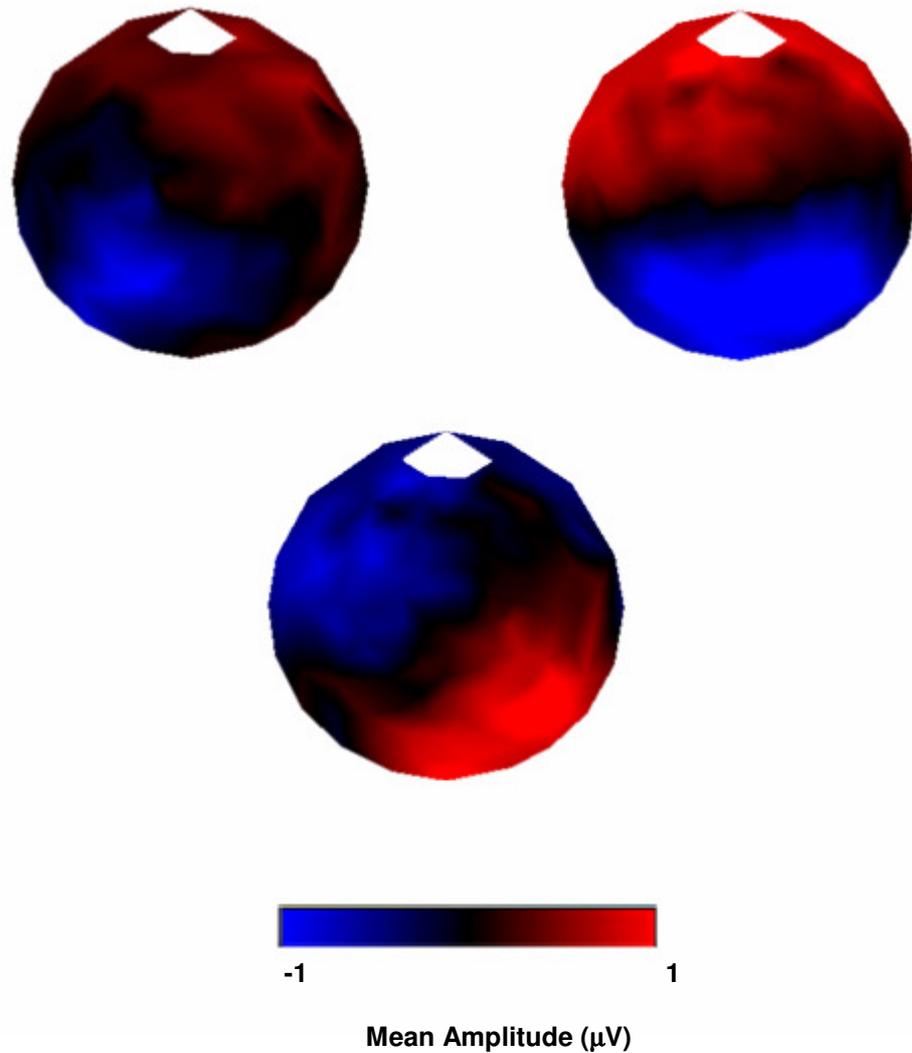


Figure 3-3 Topographical distribution of mean voltages between 230 and 270ms after target stimulus presentation. Top left: semantically related. Top right: semantically unrelated. Lower: difference (related minus unrelated).

The topographical distribution during a 40ms window centred at 250ms is presented in figure 3-4. The difference map showing a left fronto-temporal negativity balanced by a

right occipito-parietal positivity. During this window 45 electrodes significantly differed between conditions ($\alpha = .05$; figure 3-5).

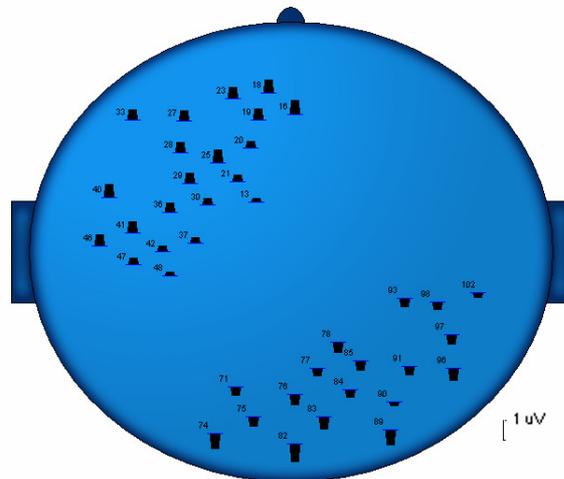


Figure 3-4 Head Map indicating the topographical distribution and amplitude of electrodes that significantly differed between semantically related and semantically unrelated word pairs in the timewindow 230-270ms post target presentation. Up is negative.

Discussion

The major finding is a significant response to the semantic relationship between words during purely unconscious processing. The occurrence of a semantically related prime evoked a different neural response to an unconscious target stimulus compared with the response to the same target stimulus when it was preceded by a semantically unrelated prime. This fits with studies that have demonstrated that unconsciously perceived stimuli can influence behavioural and neural responses to later stimuli. However, this is the first imaging of a direct effect of semantic processing within unconscious cognition and demonstrates that semantic relationships are assessed without the requirement of a conscious awareness of either stimulus.

The topographical distribution of this difference waveform does not resemble any classical EEG evoked potentials. During the studied time window ($250 \pm 20\text{ms}$), in the semantically unrelated condition, a posterior negative potential consistent with the visually evoked N1 component is present. This potential occurs without the typical left lateralised distribution usually associated with word stimuli (Cohen et al., 2000; Dehaene et al., 2001). During the presentation of semantically related word pairs this N170 component, though possibly present, is certainly altered or attenuated. It is unlikely that semantic relatedness affects the purely visual response to the mask stream. This leaves the existence of a dipole that is countering the current of the N1 generators as the most plausible reason for the observed difference in the evoked potential. The emergence of such a dipole in the related but not unrelated condition suggests a gain in cerebral activity as a result of unconscious semantic priming. This is in sharp contrast to the findings of repetition suppression observed during the conscious perception of target stimuli. These results suggest that, whereas repetition suppression may reflect a

reduction in the cognitive resources needed to process a primed stimulus, the mechanism of priming results from facilitation of neural activity in responding neural assemblies. This repetition facilitation would result in a reduced requirement for top-down intervention as less alternative interpretations have to be excluded, which would in turn result in RS.

The observed difference occurs earlier than is normally associated with the evoked response changes caused by semantically related primes, both visible and masked, which usually occur after 350ms (Kiefer, 2001; Kiefer & Spitzer, 2000a). However, these tests investigated the evoked response to the processing of a second (visible) stimulus and the reported effects may reflect moderation of overt conscious processing of the second stimulus.

This temporal disparity suggests that unconscious processing proceeds more rapidly than conscious processing. Such a finding argues against a model of unconscious processing being a degraded and delayed form of conscious cognition (Dehaene et al., 2001).

The latency of this effect has repercussions for the theory of unconscious/conscious distinctions in neural activation patterns raised in the preceding chapter. It was suggested that unconscious neural activity can be dissociated from the neural activity underlying events that create a conscious representation by a sweeping flood of activation that fails to lead to sustained neural discharge. The single, early (~140), evoked response to masked words (in comparison to random letter strings) is consistent with this hypothesis. The findings in this chapter suggest that unconscious word

processing is still occurring 250ms after stimulus presentations. The two stage 'sweep' and 'sustain' model holds that unconscious activity proceeds in a non-reverberatory fashion. This requires that all empirically observed unconscious activity occurs in close temporal proximity. The findings of this study suggest that the 'sweep' during unconscious processing persists for at least 100ms.

Under the FFS model, neuronal populations respond in an initial burst. This burst then stimulates on-flowing cortical regions, which respond with their own burst and activity sweeping across appropriately excited cortical regions (Lamme & Roelfsema, 2000; Rolls & Tovee, 1994). Under the FFS model, during masking the sustained phase of activity is prevented, and neural activation relating to the masked stimulus will only persist for as long as it takes for this burst to traverse cortical regions (Lamme & Roelfsema, 2000; Rolls & Tovee, 1994).

In the macaque, a delay of 80ms was observed between the presentation of the face stimulus and the bursting response in IT of the macaque (Rolls & Tovee, 1994).

Neurons in the LGN respond to light stimuli approximately 20 (parvocellular) to 30ms (magnocellular) after presentation of a light stimulus (Maunsell et al., 1999). These signals reach V1 approximately 65ms after visual stimulation (Schmolesky et al., 1998). After V1 is activated there is a rapid spread of activation across many visual areas (including MT and the medial superior temporal area) approximately 75ms after stimulation (Schmolesky et al., 1998).

This gives an approximate time frame for the passage of the sweep (from V1 to STS) of approximately 15ms. In a metanalysis (comparing across multiple studies with varying

latencies reported across studies within the same cortical region), reports that the mean difference (across studies) that the upper limits of a non-recurrent feed forward sweep may be in the order of 70ms. With differences in conduction delays between the macaque and humans, the 100ms delay observed during unconscious word processing may remain possible. The above figure of 70ms refers to a duration of the sweep between V1 and TE1 (one of the five inferotemporal areas) while the EP observed between words and non-words in Chapter One, occurring at 140ms, is presumably occurring in an area later than V1 (therefore reducing the 'distance' to travel and therefore the estimated travel time). It seems unlikely that a 100ms longevity of the FFS is plausible without some form of reentrant activity to maintaining it over this period. However, whereas longevity of 300ms might have provided unequivocal evidence that recurrent processing was occurring, the 100ms observed here suggests recurrent processing but the evidence is equivocal. When the possible role of sub-cortical loops through the basal ganglia are considered it becomes apparent that a 100ms delay is not sufficient to reject the hypothesis that recurrent processing is sufficient for consciousness.

The main purpose of these last two chapters was to ascertain whether unconscious processing occurred in a manner consistent with the FFS model and thereby whether Lamme's RPM, that recurrent processing is necessary and sufficient for conscious awareness, is viable. The findings are sadly inconclusive. The degree of longevity observed during unconscious processing was longer than expected but not long enough to make reentrant neural activity mandatory.

The finding of a semantically influenceable component of cognition 250ms after stimulus presentation does not necessitate the absence of semantic processing in the 140ms component observed in the previous study (Chapter Two). Although this may be the case but it is also possible that different elements of semantic content contribute to both the observed components. An unequivocal conclusion is not possible based upon these two studies.

This study demonstrates that semantic processing can produce a measurable neural response in subjects who are completely unaware of either prime or target stimuli. The latency of this response is too long for unconscious processing to be the result of a sweep of cortical activation that fails to attain reentrancy. However the observations of a neural response during masked semantic priming that is earlier than is usually associated with conscious semantic priming also argues against a model of unconscious processing which is an impoverished form of that usually occurring during conscious cognition.

Chapter 4 beta ERD during Spontaneous and Planned Movement

Introduction

In the preceding chapters, the boundary between conscious and unconscious cognition was investigated through the manipulation of incoming sensory information. However, this is not the only means by which information may enter consciousness. Thoughts, actions, and imagery can enter consciousness without the necessity of immediate sensory input, but rather from the intrinsic activity of the brain. As with cognition that derives its impetus from sensory information, internally generated cognition can have both conscious and unconscious manifestations. Under a Crickian model conscious awareness of external events is explained in terms of competing interpretations of sensory information vying for dominance and attaining neural monopolies (Crick & Koch, 2003). A similar process is thought to occur during volition with the driving force from the internal emergent neural activity likewise forming into coalitions and establishing dominant neural assemblies. The aim of this chapter is to investigate the distinction between these unconscious and conscious premonitions of action and in doing so to investigate the neural underpinnings that distinguish conscious and unconscious cognition.

The spontaneous generation of movement is the exemplar of free will, and a means by which one can study the endogenous generation of consciousness. Since the work of Libet et al. (1983), investigating the illusory nature of free will, it has been known that pre-conscious mental activity can be detected in the form of slow wave currents

originating from motor and prefrontal regions of the cortex, the implication being that early stages in the emergence of volition occur prior to the formation of a conscious representation.

In his now classic study Benjamin Libet, (Libet et al., 1983) asked subjects to spontaneously and capriciously move their hand, while recording EEG. The Readiness Potential (RP), a negative deflection in the EEG prior to movement, preceded the subjects' reports of the first urge to move (denoted as W-time for "wanting to move time") by, on average 350ms and by at least 150ms. Libet's interpretation of this was that the decision to initiate the movement had been made by the cortex, with the self merely receiving an *ex parte* edict before the movement is actuated, hinting at the possible illusionary nature of free will.

Libet's work has been controversial, particularly with respect to the assertion that free will is illusionary and over the veracity of introspective reports (e.g. Latta, 1985; Rugg, 1985). The validity of the W-time estimates has been questioned and may be slightly earlier or later than the actual event (Klein, 2002). Other authors have raised concern over whether the early component of the RP is the best measure of preparatory movement activity (Haggard & Libet, 2001). However none of these criticisms are in conflict with the assertion that the RP offers a measure of widely distributed neural activity in the absence of awareness that precedes spontaneous voluntary movement (Merikle & Cheesman, 1985). These are the elements of Libet's work that are relevant to this study.

The RP investigated by Libet affords the opportunity to study the neural activity associated with unconscious cognition. Such neural indices are usually subtle and ephemeral. In contrast, the RP is robust and often observable in single subjects. As such it offers a powerful tool for studying the differences between conscious and unconscious forms of neural activity. The RP occurs during self paced movement and is characterised as a fronto-central negativity. The RP can be further divided into an early central component and a later lateralised, component contralateral to the response hand (Deecke, 1996). It is thought that the early component reflects activation of the supplementary motor area (SMA), while the later lateralised component reflects activation of the primary motor cortex (M1) (Deecke, 1996). MEG dipole modelling of an individual with a right SMA lesion (allowing precise location of the generator without bilateral generators cancelling each other out) located the early component in the SMA and the late component over contralateral M1 (Lang et al., 1991). Intracranial recordings have revealed both SMA and contralateral M1 generators of the RP but failed to find differences in the chronometry of these two generators in the three seconds preceding movement (Rektor, Feve, Buser, Bathien, & Lamarche, 1994).

Libet et al.'s initial study, which focussed on the early central RP measured at vertex locations, has been replicated and also extended to consider the temporal relationship between the first urge to move and the late RP. These studies have shown that the early RP precedes movement by between 500 and more than 2000ms (Haggard & Eimer, 1999; Keller & Heckhausen, 1990; Trevena & Miller, 2002). When evoked potentials are aligned to the urge to move, rather than to the motor response itself, the early RP still precedes the urge to move, ruling out the possibility that the observed potential is

the result of artefacts created by trials where early awareness is present (Trevena & Miller, 2002).

The relationship of the late RP to W-Time has also been considered. The late RP has been variously found to precede movement by between 500ms and 1500ms when averaged across subjects (Haggard & Eimer, 1999; Trevena & Miller, 2002). However some W-times do occur before the emergence of the late RP (Trevena & Miller, 2002) though the significance of this is hard to ascertain in the face of error variations in W-time.

Earlier W-times have been found to be associated with earlier onset of the late RP suggesting an interplay between the late RP and awareness of the ensuing movement (this trend could not be examined with the early RP due to the lack of a stable baseline) (Haggard & Eimer, 1999). This suggests that there is interplay between changes in direct current potentials and consciousness. However these studies together show that, although there exists a relationship between the RP and conscious awareness, these direct current changes do not manifest the conscious awareness.

The initiation of self paced movement is also preceded by changes in the spectral power of the ongoing EEG with a pre-movement decrease in induced mu (10-12Hz) and beta (18-24Hz). These rhythms initially manifest contralateral to the moving body part and typically become bilateral with movement onset (Pfurtscheller, Graimann, Huggins, Levine, & Schuh, 2003; Pfurtscheller, Woertz, Supp, & da Silva, 2003). Beta ERD has been suggested as a more localised variant of the desynchrony involved in both these oscillatory changes (Beisteiner, Hollinger, Lindinger, Lang, & Berthoz, 1995).

Intracranial recordings have shown that beta de-synchrony measured over SMA may precede movement by more than three seconds (Ohara et al., 2000).

Beta rhythm is believed to exert an inhibitory influence in movement (Pfurtscheller, Woertz et al., 2003) and is known to be modulated by GABA agonists such as barbiturates and benzodiazepines, which increase the amplitude of beta oscillations (Lindhardt, Gizurarson, Stefansson, Olafsson, & Bechgaard, 2001; Nunez, 1995), although alpha oscillations are not (Baker & Baker, 2003). GABA inhibition is believed to play a critical role in the establishment of reverberant networks (Jefferys et al., 1996; Wang, 2003). Modelling studies have further shown that beta oscillations may increase in amplitude if greater numbers of GABA channels are open (Pauluis, Baker, & Olivier, 1999). In this way beta oscillations may provide an index in the level of inhibitory activity occurring within the motor cortex.

The aim of the current study is to investigate the interplay between the DC changes and beta ERD associated with spontaneous and non-spontaneous movement. The hypothesis is that beta indexed GABA inhibition has the capability to prevent the formation of reentrant networks necessary for the conscious representation of an act and that beta de-synchrony, as an index of such reentrancy, will be more closely related to an internal representation than DC potentials. The finding that beta ERD is largely independent of conscious awareness would suggest that these oscillations are not related to the form of neural activity underlying conscious awareness, while the finding that beta ERD is less evident preceding spontaneous movement would suggest the beta ERD is related to the neural activity underlying conscious awareness.

Methods

Participants

Thirteen subjects (nine male, three left handed) participated in this study. Participants' ages range between 21 and 58 years with a mean age of 27. All experimental procedures were approved by the University of Auckland Human Subjects Ethics Committee.

Stimuli

A clock face was generated on a computer monitor subtending six degrees of visual angle. The hand completed a rotation every 2560ms. Behavioural responses were entered using a standard computer keyboard.

Procedure

Subjects were instructed to fixate on a central cross and make their response by pressing the 'j' key with their right hand. In the spontaneous condition subjects were instructed to try to avoid planned movements responding 'spontaneously and capriciously' and attempting to 'try and surprise yourself'. After a response was made the clock hand continued to rotate for a randomly determined interval between 213 and 453ms (to minimize the amount of information contained in the final stopping point of the hand). After the hand stopped moving the screen went blank for 500ms. A prompt was then displayed asking the subject to note the time on the clock when they first felt the urge to move. During the planned condition subjects were asked to make their response when the hand passed a point indicated at the beginning of each trial. Subjects

were instructed to respond the second time the clock hand passed the mark (to ensure at least 2500 ms baseline). Following the response the screen blanked for 500 ms and the same response field present as in the spontaneous movement condition was presented for a further 500ms, although the subject did not make a response.

The experiment was divided into two blocks of 80 trials per condition. The order of the blocks was counterbalanced across subjects.

Electrophysiological Recordings

Recordings were made in an electrically shielded, sound-attenuated room, using a 128 channel Electrical Geodesic amplifier (200M Ω input impedance) with Ag/AgCl electrodes (Tucker, 1993). Recordings were sampled at 500 Hz with an analogue 0.1 to 100 Hz bandpass filter and referenced to Cz. All electrodes impedances were below 40 k Ω which is within acceptable parameters for this system.

Analysis

Event Related Potentials

Following data acquisition EEG recordings for each subject were averaged across trials. Automated artefact rejection algorithms were employed to remove trials contaminated by eye blinks or other artefacts. Initial cuts were made 2000ms prior to movement to ensure a stable baseline period. Once a stable baseline period had been identified cuts were shortened to minimise the number of artefact contaminated trials. Resulting ERPs are 1000ms prior and 100ms post movement.

Event Related Desynchronisation

Initially data were cut into 2000ms pre movement and 1000ms post movement epochs. These epochs were then tested for non-ocular artefacts as ocular artefacts do not influence the beta spectrum (Hagemann & Naumann, 2001)). Data were band-passed filtered between 18 and 24 Hz using a bidirectional Butterworth filter (Alarcon, Guy, & Binnie, 2000). To prevent start and end effects associated with filtering, epochs were buffered, before and after, by 200ms of EEG recording which was not included in the output. The resulting voltages were squared then outliers were rejected using the sliding criterion method (Vanselst & Jolicoeur, 1994). The remaining segments were then averaged for each condition and each subject.

The resulting measure yields an index of the beta range oscillations present which are present prior to movement. By squaring the filtered waveform from each trial the oscillation do not have to be phase locked to the onset of the movement (as is the case with traditional ERPs).

When considering individual electrodes, normalisation for differences in the magnitude of ERD across subjects was accomplished by dividing each voltage value by the range of that channels' voltage across the entire (averaged) epoch.

Results

Behavioural Results

Participants' reports of the urge to move preceded key presses by an average of 162ms (SD 91ms). Average scores ranged from 80ms before stimulus onset to, in one case, 400ms prior. The spread of reaction times, as indicated by the standard deviation, is reasonably wide. Individual W-times are reported in table 4-1.

Table 4-1 Mean and standard deviation for the time at which subjects reported the first urge to move. Units are in milliseconds.

Mean w-Time	SD w-Time
86	72
87	35
92	46
101	64
106	71
112	91
120	83
130	137
200	90
210	130
218	407
244	77
402	311

Evoked Potentials

Spontaneous Movement

The readiness potential was observed over central (Cz) and frontal-central (FCz) electrodes (see figure 4-1). The RP began 800ms prior to the button press and was statistically evident by 600ms prior to button press (see figure 4-2). The RP was accompanied by an anterior frontal negativity (see figure 4-1) with a similar time course though slightly earlier onset.

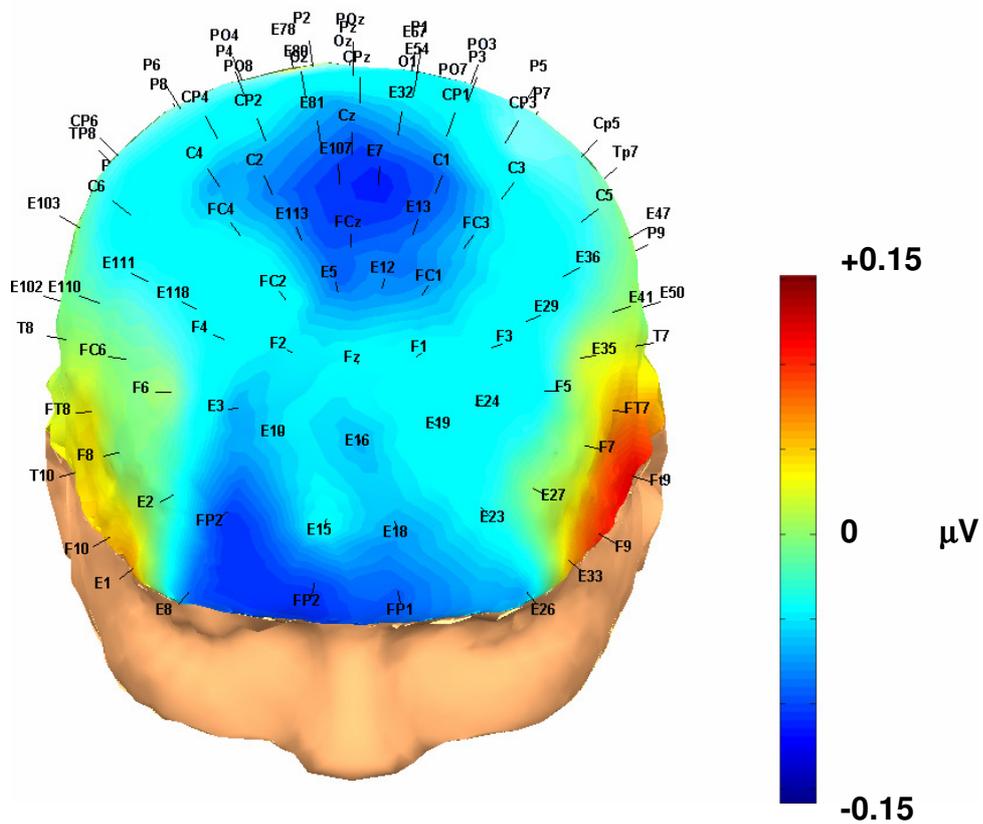


Figure 4-1 Scalp map of distribution of RP during the spontaneous movement condition averaged over the period 800ms to 500ms prior to movement onsets. Electrode labels correspond to the Geodesic Sensor Nets' 10-10 International equivalents (Luu & Ferree, 2000).

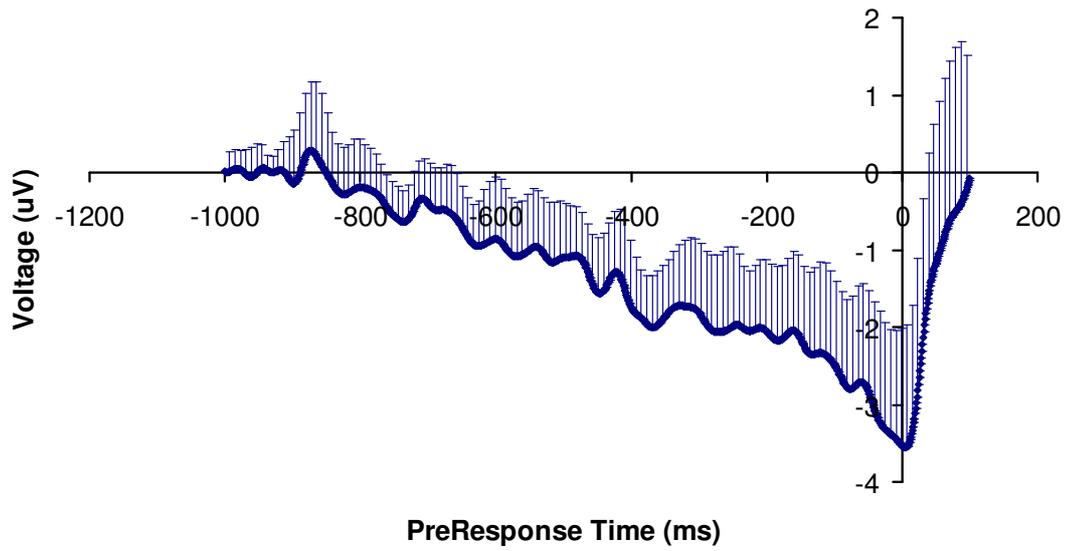


Figure 4-2 The Readiness Potential preceding the spontaneous initiation of voluntary movement as measured at FCz. Error bars reflect +2 standard errors. Time 0 is the time at which the response was made. The trace has been smoothed using a 20ms moving average.

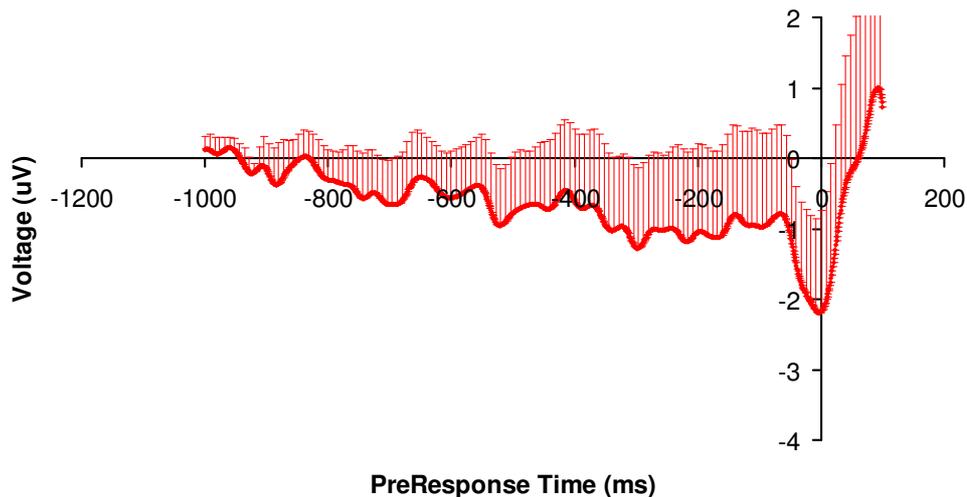


Figure 4-4 The Readiness Potential preceding the planned initiation of movement as measured at FCz. Error bars reflect +2 standard errors. Time 0 is the time at which the response was made. The trace has been smoothed using a 20ms moving average.

Comparison of conditions

To statistically examine the onset and differences in the Readiness Potentials, evoked potentials at FCz were divided into four time bins, 800-600, 600-400, 400-200 and 200-0ms prior to the response. Screening of the data for the assumptions of parametric testing revealed unacceptable differences in the variances between conditions (min 0.530, max 4.412).

A Friedman test performed on the factor time revealed a significant effect in the spontaneous condition ($\chi_r^2(3) = 15.5, p < .001$) but not in the planned movement condition ($\chi_r^2(3) = 4.6, p = .206$), indicating that the increase in RP with time was significant during spontaneous but not planned movement. Non-parametric tests do not afford the means to assess interactions between time and condition. The results of

Wilcoxon signed-rank tests assessing the onset of the RP and differences within each time-window are presented in figure 5.

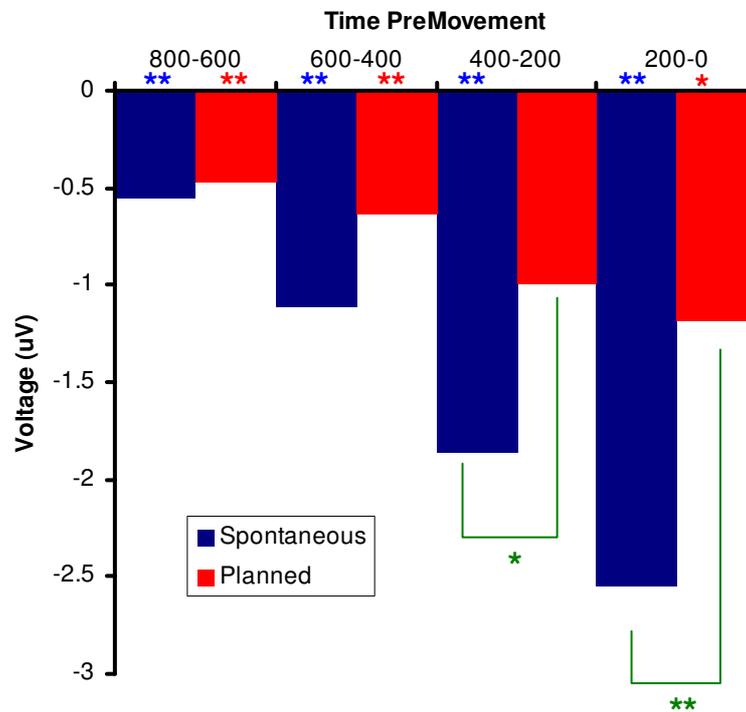


Figure 4-5 Voltage as a function of time prior to movement for four time bins in both conditions as measured at FCz. Red and blue asterisks above the x-axis indicate significant deviation from baseline (one-tailed). Green asterisks indicate significant differences between conditions within a time window (two-tailed). Single asterisk indicate uncorrected significance. Double asterisk indicate that significance remains after Bonferroni correction.

Significant differences from baseline were evident in the RP potential 800-600 ms in both movement conditions (this is different to that reported in the preceding section as temporal resolution has been traded for a higher signal to noise ratio). During later stages of the RP this difference was more robust during spontaneous movements, being both reliably distinguishable from baseline and the RP of the planned movement condition.

beta ERD

During spontaneous movement beta ERD occurred in the 500ms preceding movement. Figure 4-6 illustrates the time course of beta ERD at the Geodesic equivalent of C3, an electrode overlying the motor strip contralateral to the response hand.

beta ERD during the planned execution of movement was present 1500ms prior to movement (fig 4-8). The beta ERD was present over midline central sites (Cz, CFz) electrodes and central-parietal sites contralateral to the response hand (CP3).

Comparison of Conditions

For statistical comparisons data were divided into seven 200ms time windows covering the 1400ms prior to movement. A Friedman test performed on the factor time revealed a significant effect in both the spontaneous condition ($\chi_r^2(3) = 52.2, p < .001$) and planned condition ($\chi_r^2(3) = 26.9, p < .001$) indicating that the increase in beta ERD across these time bins was significant. Wilcoxon signed-rank tests revealed that beta ERD was evident in the planned movement condition 1400ms prior to movement in comparison to its emergence 400 ms prior to spontaneous movement. Planned and spontaneous movement conditions differed across the four time bins covering the period 1200 to 400ms. In the 400ms prior to movement no significant power difference was observed.

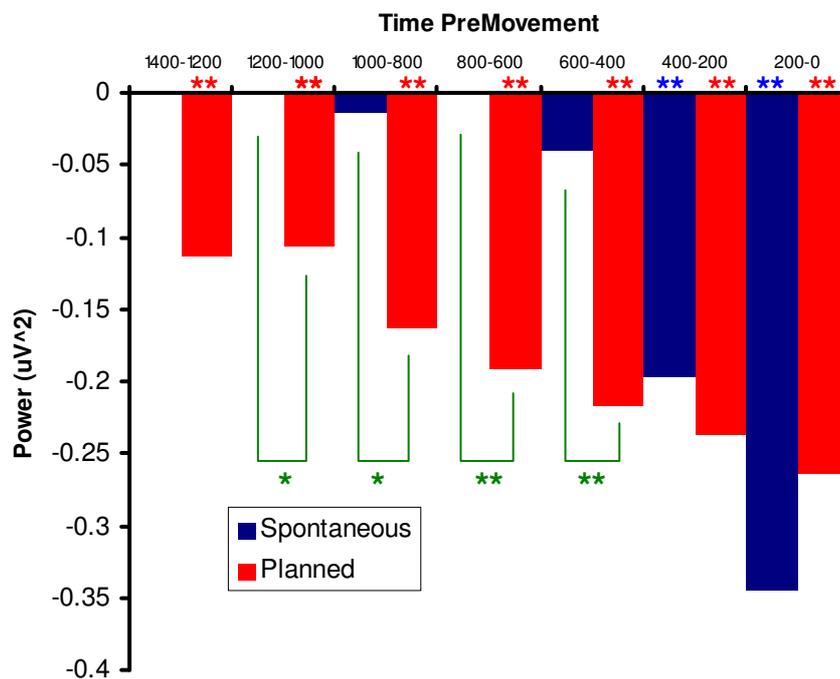


Figure 4-10 Change in beta power from baseline as a function of time prior to movement for seven time bins in both movement conditions. Red and blue asterisks above the x-axis indicate significant deviation from baseline (one-tailed). Green asterisks indicate significant differences between conditions within a time window (two-tailed). Single asterisk indicate uncorrected significance. Double asterisk indicate that significance remains after Bonferroni correction.

RP and beta ERD Independence

If beta ERD and the RP are dependent processes then one would expect the magnitude of each individual's beta ERD and RP amplitude to be related. To this end a correlation was carried out between these two measures within each task condition. There was no correlation between individual RP amplitude and beta ERD in either the spontaneous ($r=-0.025$, $p=0.936$) or planned ($r=-0.052$, $p=0.867$) movement conditions in the 200 to 500ms preceding the key press.

Discussion

The RP potential was found to precede spontaneous movement by several hundreds of milliseconds, confirming previous studies (Haggard & Eimer, 1999; Libet et al., 1983; Trevena & Miller, 2002). Beta ERD, which is known to precede by several seconds the self paced, non-spontaneous, initiation of movement (Ohara et al., 2000; Pfurtscheller & Berghold, 1989; Pfurtscheller, Graimann et al., 2003) was observed during the planned task but was absent until 500ms prior to the spontaneous generation of movement.

The observed differences in the RP must be interpreted with caution in light of the high pass filter used during the recording of the EEG. The high pass filter (0.1 Hz) may serve to attenuate the measured RP. Although the same filter was present in both conditions, if the RP in the planned movement condition has an earlier onset but reduced gradient then this would result in the selective attenuation of this waveform. The presence of the RP in both waveforms is genuine, but comparisons between these two conditions must be made cautiously.

This indicates that two separable processes, with different neuronal signatures, occur during the initiation of movement with and without awareness. The RP occurred well before either the conscious initiation of movement in the spontaneous condition, or, in both conditions, the motor act itself. This is in sharp contrast to the pattern of beta de-synchrony, which proceeded movement with awareness by 1400ms and spontaneous movement by 500ms. This dissociation suggests that qualitatively different neural processes comprise the preparation for movement with and without awareness. This

assertion is further supported by the finding that there was no consistent relationship between the magnitude of an individual's RP and the extent of the beta ERD.

The possibility exists that the observed differences in beta ERD between planned and spontaneous movement could result from temporal anticipation being stronger in the planned movement condition. This is thought to be unlikely, as during the self-paced initiation of movement, where temporal anticipation is absent, beta ERD is present seconds before movement (Pfurtscheller, Graimann, Huggins, Levine, & Schuh, 2003; Pfurtscheller, Woertz, Supp, & da Silva, 2003). Indeed, self-paced movement this was the initial choice for the control condition of this experiment but as it had already been shown to produce beta ERD, as it did not control for possible effects of attending to the clock-stimulus and as it was thought that potential confusion might arise between instructions to self pace movement and to spontaneously generate movement, the planned movement control was chosen instead.

If it is taken that beta ERD is a correlate of movement-awareness, then consideration of the causal nature of this relationship must be made. It is clearly ridiculous to say that the decrease in oscillatory activity between 18-24 Hz causes consciousness. Beta ERD presumably reflects changes in the properties of the neural networks when a representation of a cognition becomes conscious. Beta ERD reflects a modulation of the properties of the network and may alter the interaction between members of neural population currently encoding the impending movement. It has been proposed that the distinction between conscious and unconscious elements of brain activity may be dependent on the formation of reentrant connections (Dehaene & Naccache, 2001; Tononi & Edelman, 1998). In terms of IIT (Tononi, 2004), the persistence of tonic inhibition may serve to decrease the effect which the various sub-complexes encoding

the impending movement may impact on other sub-complexes. That is to say the effective connectivity within the 'complex' may be low, allowing the preparation of the movement to form, but preventing the integration of information necessary for conscious awareness.

Do plausible mechanisms exist which would allow this to happen? One possible mechanism is that a decrease in the activity of GABA-ergic interneurons (indexed by the beta ERD) may allow the internal representation of the movement to enter into a dispersed, reverberant, neural assembly and subsequently into conscious awareness. The possible mechanism by which assemblies may form into reverberant networks could be mediated synchronous oscillatory gamma activity (Wang, 2001, 2003). The establishment of synchronous networks is sensitive to GABA levels (Pauluis et al., 1999) and beta ERD is found co-localization with gamma (30-80Hz) ERS (Crone, Miglioretti, Gordon, & Lesser, 1998; Pfurtscheller, Graimann et al., 2003). Under this tentative model the presence of tonic inhibition prevents the integration of information through modulations of gamma range synchrony.

A second possibility is that increased inhibition may alter the interconnectivity of the neural assemblies involved in movement preparation through some generalised mechanism, rather than through modulation of gamma related activity. Increased inhibition may permit the persistence of widespread cortical activity but lower the effective connectivity amongst active populations. Massimini and colleagues (2005) have recently shown that during slow wave sleep effective connectivity is reduced and neural activity induced by TMS stimulation is limited in both time and space (in comparison to that induced during wakefulness). It is possible that beta indexed

inhibition is having a similar effect here. In models that explain oscillations through inhibitory activity, excitatory activity is periodically silenced by the inhibitory modulators. Such periodic silencing (at the beta frequency) could prevent the processes that lead to large scale reentrancy. This may create the same effect as observed by and colleagues (Massimini et al., 2005). This hypothesis would predict that TMS neural activity induced in the presence of beta oscillations would likewise induce activity confined in space and time.

It is not suggested that beta ERD causes the neural activity to form into a reverberant network or, conversely, that reverberant activity removes beta ERD. Rather, it is suggested that an interplay between these two states exists. In the case of spontaneous movement, the persistence of inhibition during spontaneous movement until the moment just before awareness may prevent the internal representation of the action, indexed by the RP, from entering into conscious awareness. It is proposed that activity measured by the RP reaches a threshold where it overcomes the beta rhythm linked inhibition, allowing the feed-forward emergence of reentrant networks. Once the reentrant connections have stabilised, awareness of the urge to move is available to conscious awareness. This awareness is shortly followed by the initiation of the movement. In contrast, during planned movement attentional mechanisms which are focussed on the motor impending movement may come into play. It has been suggested that attentional mechanisms may alter the effective connectivity of a network (Tononi, 2004). It is suggested that this modulation may be realised by reductions in beta oscillations. In this case the reduction in beta lowers the threshold needed for reverberant assemblies to form, resulting in a conscious awareness of the impending movement forming earlier during planned movement. These mechanisms are tentative

and many other potential mechanisms may account for a decrease of connectivity in the presence of tonic inhibition.

The time course of beta ERD in the spontaneous condition is consistent with the emergence of a feed forward set of reentrant connections. It has been shown that for the formation of a conscious representation of an incoming stimulus to occur, thalamic stimulation must persist for several hundreds of millisecond (Libet et al., 1991). The rise of beta desynchronisation several hundred milliseconds prior to movement in the spontaneous condition is on a temporally compatible timescale with the formation of such a neural assembly from the direct current input of the RP.

Forming an internal representation of an action without performing it, mental imagery, results in both DC changes (Beisteiner et al., 1995) and changes in the mu and beta rhythms (Pfurtscheller & Neuper, 1997) leaving it unclear whether beta inhibition and DC changes play dissociable roles in mental imagery. Unlike sensory-related mental imagery, where the input stimulus is known to be absent, motor mental imagery, where the output stimulus is generated by the brain, may be present to a greater or lesser extent. Mental imagery involves not only the formation of an internal 'image' of an action, but can also involve the generation of a set of motor commands involved in performing the motion. During mental imagery the specific muscles corresponding to the imagined movement are activated (Wehner, Vogt, & Stadler, 1984). Viewed in this light it is not surprising that a dissociation between internal representation and mundane generation is not observed in imagery.

Limitations

A cause for concern in the interpretation of this experiment is that it relies on the subject's report of when the 'urge to first move' occurs. This measure can be criticised in that all the conscious information available to the individual may not be reported (Holender, 1986). It is possible that an 'urge' is consciously available but that the subject does not recognise it and report it. This concern is in part answered by the dissociation found between the RP potential and beta desynchronisation. This dissociation suggests that qualitative, not quantitative, differences are occurring when the subject is aware or unaware of the approaching initiation of movement.

Linking the 'urge to first move' to a visual stimulus is not a very precise way of time-stamping the temporal origin of volition. Although results were consistent with previous studies the backwards referencing caused confusion, with many subjects reporting a rough estimate based on the clock time when the movement was initiated. Despite concerns with this measure, subjective reports were of a very brief interval between volition and movement. The interval was clearly briefer than the time-span of the RP potential.

In summary, the beta desynchrony preceding internally generated voluntary movement (Ohara et al., 2000; Pfurtscheller, Woertz et al., 2003) and externally cued movement (this study) did not emerge during spontaneous movement until 500ms prior to movement. This showed a clear distinction from neural activity reflected in DC changes over the cortex. It is tentatively argued that this distinction reflects neural processes that differentiate conscious from unconscious information representation in the cerebrum.

Chapter 5 Induced Occipital Synchrony during Binocular Rivalry

Introduction

Binocular rivalry provides a means to study changes between conscious states independent of change in the sensory system. During binocular rivalry two percepts are available, yet despite both percepts being represented within the brain (Leopold & Logothetis, 1996), only one enters the conscious moment. A key to understanding the neural underpinnings of consciousness is an understanding of the neural activity associated with the determination of the dominant or subordinate state of the rival images.

Single unit recordings in animals suggest that changes in the consciously perceived image result in a change in the rate of firing in higher order visual association areas IT and the STS (Shenberg & Logothetis, 1997), but not in primary visual areas V1, V2 and V4 (Leopold & Logothetis, 1996). This suggests that rate of neuronal discharge in primary visual areas does not influence the contents of consciousness and that percept dominance is a reflection of activity in higher association areas.

An alternate mechanism by which percept dominance may be expressed in the visual cortex is through an increase in the synchronisation in neural discharge. Support for this theory comes from a study of strabismic cats where it was found that neural synchrony increased when a competing image is presented to their non-dominant eye (Fries et al., 1997).

The view that rivalry does not affect the magnitude of activity in the early visual cortex has been recently challenged (Andrews, 2001; Tong, 2001). In humans fMRI studies have shown that higher visual association areas respond to houses (the parahippocampal place area) or faces (the fusiform face area) preferentially when their preferred stimulus is dominant, as in the macaque. However, metabolic changes in V1 have also been reported in response to alterations in the conscious percept (Lee & Blake, 2002; Polonsky et al., 2000; Tong & Engel, 2001) suggesting that rivalry may be resolved within the striate cortex. Changes in synchrony, such as that observed by Fries and colleagues (1997), cannot account for this metabolic increase.

MEG studies, using the steady state response to flickering (~10Hz) stimuli to distinguish neural activity relating to each rivalrous image, have shown that widespread brain regions respond to both the dominant and subordinate elements but respond preferentially to the dominant (Tononi, Srinivasan et al., 1998). As well as these changes in spectral power, cortical coherence at the driving frequency also increases with conscious perception (Srinivasan et al., 1999). However the pattern of coherence is unreliable across subjects even with simple stimuli. This makes it difficult to draw inferences about the changes in the anatomical distribution of neural assemblies associated with conscious perception.

Although steady state responses provide information on the relative distribution and magnitude of the neural activity related to the two perceptual alternatives, they cannot provide insight into the natural oscillatory dynamics. The use of a steady state driving frequency eclipses endogenous synchrony that may be involved in rivalry. Although the

relative oscillations can be isolated by Fourier analysis this represents the *driving* frequency not a *natural* frequency.

Such endogenous synchrony may be important to the study of binocular rivalry as it is believed to play a role in feature binding during object representation (Engel, Fries, & Singer, 2001). Due to spatial summation local synchronous neural activity will constructively summate allowing its measurement at the scalp (Varela et al., 2001). Synchronous gamma range oscillations, that are not phase-locked to the onset of the stimuli (or induced), have been measured during the Gestalt perceptual closure of visual stimuli (Rodriguez et al., 1999; Srinivasan et al., 1999; Tallon-Baudry et al., 1997; Tallon-Baudry et al., 1996; Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998; Trujillo, Peterson, Kaszniak, & Allen, 2005). Such induced gamma activity is characterised by an increase in gamma synchrony spanning from two hundred to three hundred milliseconds after the presentation of the stimulus. Using single unit recordings gamma synchrony has been observed in the cat cortex when two neurons are responding to the same horizontal line (Gray et al., 1989) and it is thought that induced gamma is a reflection of this binding process (Tallon-Baudry & Bertrand, 1999; Tallon-Baudry et al., 1997).

Phase synchrony has also been observed to occur over distributed cortical regions during the perceptual closure of Mooney faces (Rodriguez et al., 1999). In this study, the pooled synchrony amongst thirty electrodes was shown to increase during the perception of upright Mooney faces but not during the perception of meaningless inverted Mooney faces. However this study must be interpreted with caution. Rodriguez and colleagues selected peak gamma band activity from the upright

condition and used this band to measure synchrony. When the peak gamma band is selected for both upright and inverted conditions, synchrony is present for both the upright (with perceptual closure) and the inverted (no perceptual closure) conditions, with no difference between these conditions (Trujillo et al., 2005). This argues against a specific role of long distance synchronous gamma band activity as a mechanism for perceptual closure.

In binocular rivalry displays, the transition in dominance from one stimulus to the other is not a simple fading in and out between percepts. Rather the change originates at one focussed point and spreads outwards like a wave, until the previously suppressed image attains dominance. This effect is enhanced with stimuli that subtend larger areas of visual space (Wilson, Blake, & Lee, 2001). Wilson and colleagues (2001) employed an abrupt change in contrast to invoke a rivalry wave and investigate the speed of change as it travelled around an annulus stimulus. Using a computational model these authors suggest that the transfer of dominance is consistent with wave propagation through the primary visual cortex.

Using similar stimuli during fMRI scanning Lee and colleagues (Lee, Blake, & Heeger, 2005) mapped the passage of the perceptual change across the primary visual cortex. Using the retinotopic organisation of V1 and the effect of alterations in contrast between the two rivalrous images on the BOLD response, Lee and colleagues found that the delay in change in the BOLD response was contingent on the passage of the perceptual rivalry wave.

It is the goal of this study to investigate the dynamics of oscillatory activity during binocular rivalry. Using the cuing method employed by Wilson (2001) and colleagues it is hoped to reliably determine the point at which dominance changes. This will allow the assessment of the role of gamma oscillations in the *formation* of a conscious representation. Such a design has the benefit over frequency tagged electromagnetic studies in that it allows precise time information about rivalry and the assessment of endogenous oscillatory cortical activity.

Method

Participants

Subjects were selected for stable perceptions of the rivalrous stimuli and for reliably switching between percepts in response to the contrast cue. A total of 18 subjects were screened. From these subjects the five (three male, mean age 26.4) who showed the greatest stability and most reliable cuing were included in the EEG study. Participants excluded from the study showed rapid alterations in the dominant percept, too rapid to allow reliable cuing and time locked averaging of the evoked response. Alterations in stimulus contrast were found to increase periods of image dominance but to prevent reliable cuing. There was no consistent difference in eye dominance between subjects who did and did not experience stable percepts. Subjects who experienced stable percepts reported stronger dominance for the same rivalrous image (the blue diagonal lines, see next section). In four of the five subjects this was independent of which eye perceived the stimulus.

Stimuli and Apparatus

A dichoptic image was presented to each eye through red/blue filtered glass. Diagonal blue lines were overlaid on three horizontal red bars against a green background (figure 5-1). When viewed through the bi-chromatic glasses the horizontal red lines were indistinguishable from background when viewed through the blue lens (right eye) while the blue diagonal lines were indistinguishable from background when viewed through the red lens (left eye). Stimuli subtend 9.5 degrees of visual angle horizontally and 1.8 degrees vertically. The green background covered the entire screen.

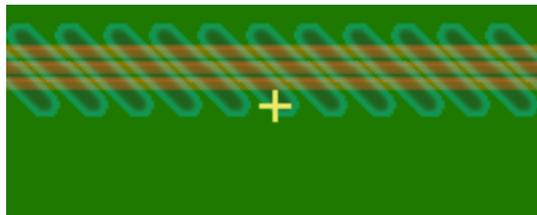


Figure 5-1 Experimental Stimuli. Diagonal lines are indistinguishable from background through blue monochromatic lenses. The horizontal lines are indistinguishable from background through red monochromatic lenses.

An abrupt change in contrast in the non-dominant image is known to cue binocular rivalry (Wilson et al., 2001). To initiate rivalry waves contrast was increased on the right end of the red horizontal line stimuli for 100ms (figure 5-2).

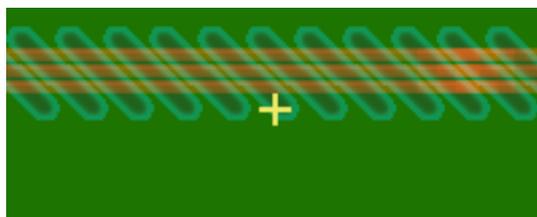


Figure 5-2. An abrupt change in contrast triggers a change in the dominant stimuli.

A yellow fixation cross was located in the lower part of the stimulus (figure 5-1). Subjects were instructed to fixate on this cross to prevent eye motion during recordings. The fixation cross was presented in the lower part of the stimuli as off-centre stimuli are more likely to yield measurable effects of early visual cortical activity.

Procedure

Subjects were instructed to fixate on the yellow cross and to press and hold the space bar when the diagonal stimulus was dominant. 100 or 200ms after the key press (randomly assigned with equal probability) the contrast change in the horizontal bar was triggered. Subjects were instructed to release the space bar once the horizontal stimulus had attained full dominance. 800ms after the space bar was released subjects were presented with two options, 'good' and 'bad'. The 'good' response indicated that rivalry had been triggered and the rivalry wave travelled in a continuous fashion (figure 5-3). A 'bad' response indicated a reversal of the dominance change or bi-stable chimeric percepts.

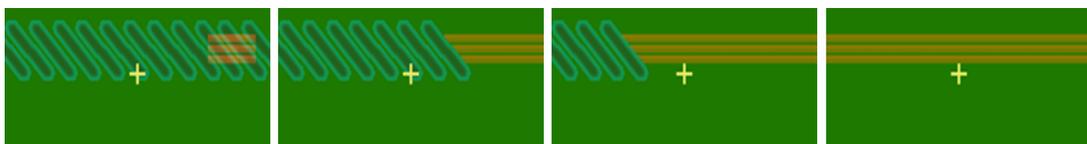


Figure 5-3. Cartoon of the subjective sequence of events constituting a 'good' trial. A rivalry wave is cued in the right visual field and travels from right to left, ending in complete dominance of the horizontal component of the stimuli.

A control condition was also included to control for the change of contrast and the motor response. This was the same as the experimental condition with the exception that the blue diagonal stripes were absent from the presented stimulus. Subjects were

instructed to press the space bar at will and to release it after approximately the same duration as during the experimental trials. Following the trial the same ‘good’ or ‘bad’ option was presented to the subject. The subject was instructed to answer ‘good’ on each trial.

The experiment was run in four blocks of 50 (sequential) experimental trials and 50 (sequential) control trials. Subjects altered response hand each block.

Electrophysiological Recordings

Recordings were made in an electrically shielded, sound-attenuated room, using a 128 channel Electrical Geodesic amplifier (200M Ω input impedance) with Ag/AgCl electrodes (Tucker, 1993). Recordings were sampled at 500 Hz with an analogue 0.1 to 100 Hz bandpass filter and referenced to Cz. Recordings were the high pass filtered at 15Hz. All electrodes impedances were below 40 k Ω which is within acceptable parameters for this system.

Time Frequency Analysis

Data were re-referenced to the average reference. Following re-referencing data from ‘good’ trials were segmented from 600ms prior to the rivalry cuing flash to 1200ms after. The resulting epochs were then screened for ocular and non-ocular artefacts using automated detection algorithms.

The segmented waveforms were then convolved with a Morlet wavelet (figure 5-4) (Tallon-Baudry et al., 1997). Morlet wavelets have a Gaussian shape in both the time and frequency domains. The formula for a Morlet wavelet is given in Equation 1.

$$w(t, f_0) = A \exp(-t^2 / 2\sigma_t^2) \exp(2i\pi f_0 t)$$

Where A relates to the normalisation factor:

$$(\sigma_t \sqrt{\pi})^{-1/2}$$

which normalises the total energy of each wavelet to 1 (figure 5-4.). The wavelet family is selected with a constant ratio of $f_0/\sigma_t=7$.

The resulting wavelet is longer in the time domain at lower frequencies and shorter at higher frequencies. In the frequency domain the wavelet has a tighter frequency range at lower frequencies and a broader range at higher frequencies (Tallon-Baudry et al., 1997). This results in maximal time resolution at higher frequencies and maximal spectral resolution at lower frequencies.

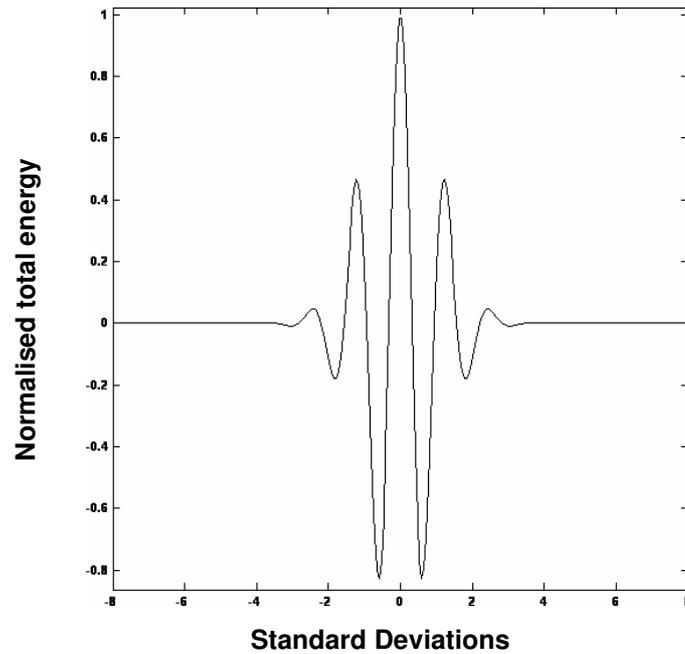


Figure 5-4 Morlet wavelet. The units on the abissca are σ . As frequency increases the σ decreases in the time domain, squashing the wavelet. As in this study the ratio of $f_0/\sigma_f = 7$ two standard deviations of the wavelet are about two oscillatory cycles at a given frequency.

The wavelet is then convolved with the recorded signal $[s(t)]$ to yield an estimate of energy across time and frequency.

$$E(t, f_0) = |w(t, f_0) \times s(t)|^2$$

This value is then squared to attain spectral power.

The resulting time frequency values were averaged across trials for each condition, electrode and subject. As contamination by condition contingent muscular artefacts is thought to distort results during this form of analysis (Trujillo et al., 2005) the median was chosen as the measure of central tendency.

Median time-frequency values were then normalised to baseline and baseline variance according to the formula:

$$P(t, f)_{norm} = \frac{P(t, f) - \mu_{base}}{\sigma_{base}}$$

This transformation yields a measure of change from baseline proportional to the variance observed within the baseline. This transformation has been used in previous electrophysiological investigations of induced gamma (Rodriguez et al., 1999; Trujillo et al., 2005).

Normalised wavelet values were then averaged across subjects within each condition.

Results

Behavioural

91% of trials were marked as ‘good’ indicating that rivalry had been cued and dominance had exchanged fluidly. The average amount of time taken for the rivalry change was 843ms (SD =151ms). The yoked key depress in the control condition lasted on average 659ms (SD =103ms).

Electrophysiological Results

Analysis of an *a priori* time window (200-300ms post rivalry cue) and electrodes of interest (01 and 02) revealed significantly greater gamma range (30-70Hz) power during rivalry (*i.e. greater in the experimental rather than control condition*) ($x_{diff} =$

0.74σ , $t_{(4)} = 5.75$, $p < .005$, values were averaged across electrodes). When compared to power during the stable perception of one of the alternative images, there was an increase in gamma power during rivalry, though this only tended towards significance ($x_{\text{diff}} = 0.19\sigma$, $t_{(4)} = 2.31$, $p < .082$). During the control condition there was a significant decrease in gamma power ($x_{\text{diff}} = -0.55\sigma$, $t_{(4)} = -6.06$, $p < .005$) in this window.

Figure 5-5 illustrates the focussed distribution of gamma power over the occipital recording sites. The peak of the distribution is slightly right lateralised

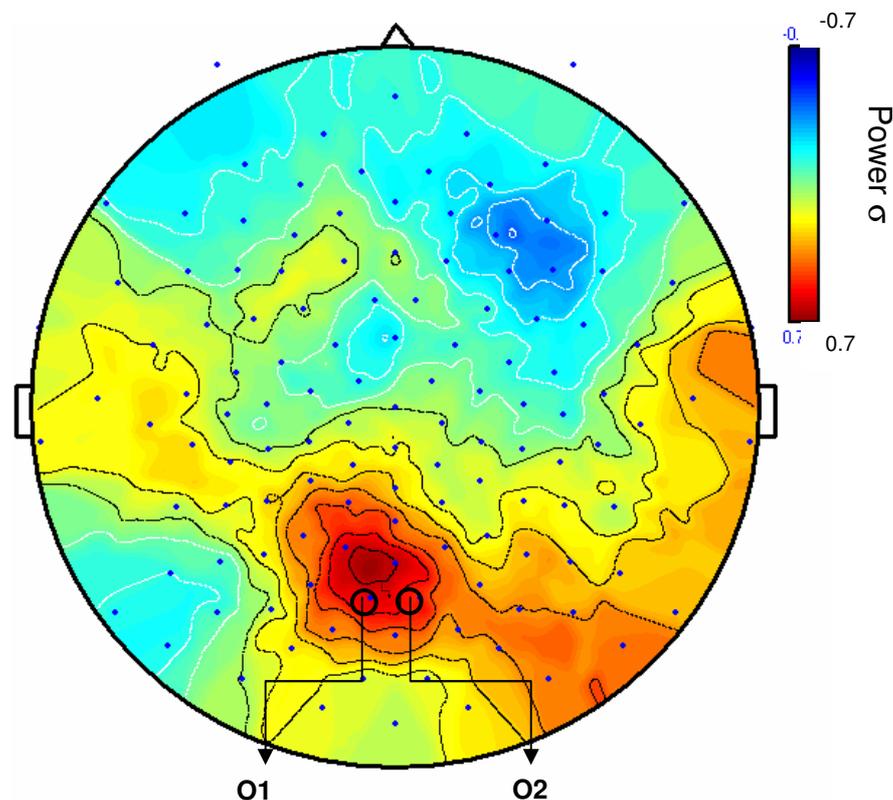


Figure 5-5. Topographical distribution of gamma activity between 200-300ms after the initiation of rivalry. The plot shows the *difference* between control and experimental conditions. The electrodes that correspond to the international 10-20 system O1 and O2 are indicated in black. (Topographic plotting routine by S. D. Muthukumaraswamy, 2004)

Analysis of the cross spectral density at electrodes O1 and O2 reveals the expected burst of gamma activity spanning 30 to 70 Hz. This burst begins 200ms after the onset

of rivalry and ends approximately 100 ms later. No other significant increases in gamma synchrony were present in the 1000ms epoch. The second burst of oscillatory activity evident 500ms after rivalry cuing (figure 5-6) did not approach significance ($t_{(4)} = -0.30, p = .78$; time window 500-600ms frequency range 30-50Hz).

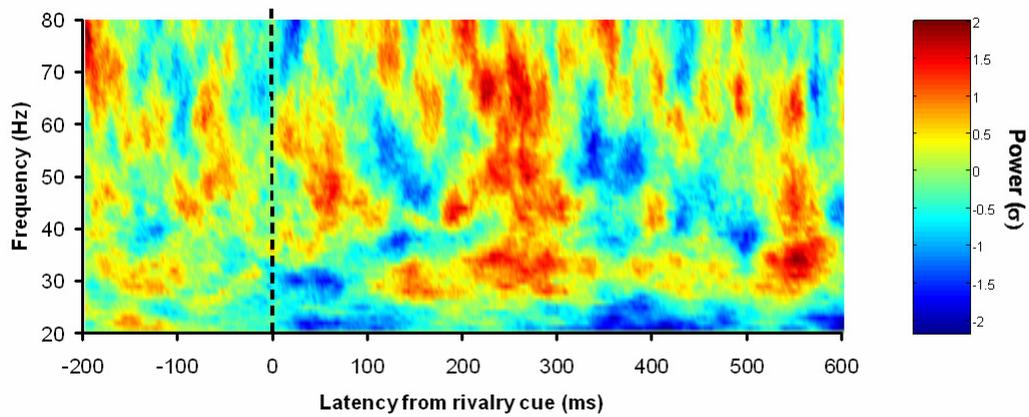


Figure 5-6 Time-frequency plot of 20-80Hz spectral power for the period 200 ms preceding and 600ms succeeding rivalry cueing. Results are averaged across electrodes O1 and O2 and across subjects. Presented is the difference between the rivalry and control conditions.

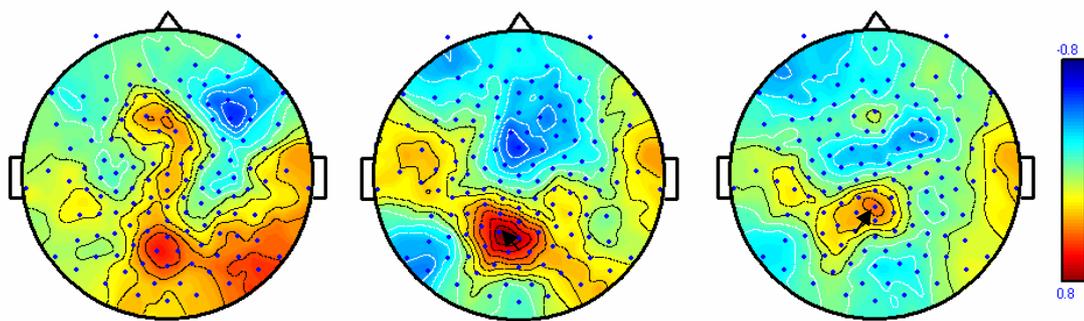


Figure 5-7 Alteration in the topographical distribution of induced gamma across time.

200-250ms

250-300ms

300-350ms

As part focus of this study is to investigate how oscillatory neural activity relates to the travelling of the rivalry wave through primary visual areas, topographical transition of induced gamma power across time is shown in figure 5-7. Perceptually, the rivalry wave initiates in the right visual field and spreads to the left (figure 5-3). This predicts a pattern of gamma activity originating over left occipital sites and spreading rightward as the perceptual rivalry wave moves left. As can be seen in figure 5-7, gamma activity originates over central occipital sites and is slightly left lateralised (fig 5-7a). Between 250 and 350ms after rivalry is initiated gamma activity is greater and more left lateralised (fig 7-5b). By 300-350ms the activity has moved in an anterior/superior direction returning to midline sights (fig 7-5c).

Discussion

A shift in rivalry, the exchange of the dominant percept for the subordinate, induces a burst of high frequency gamma activity over the occipital cortex. This is consistent with previous research that has shown that gamma activity is induced, not so much by the sensory elements of a percept, but by binding of these elements into a Gestalt whole. Binocular rivalry reflects only a change in conscious awareness of the stimuli, not the stimuli themselves. These findings demonstrate that reorganisation in the contents of conscious awareness during binocular rivalry is accompanied by an increase in neural synchrony in the occipital lobe and that a change in conscious state alone is sufficient to produce this change in occipital synchrony.

Gamma activity related to perceptual closure has been shown in some studies to be maximal over the occipital cortex (Tallon-Baudry et al., 1997; Tallon-Baudry et al., 1996) and in others to be homogeneously distributed across the posterior two thirds of the scalp (Rodriguez et al., 1999). During percept changes in binocular rivalry, induced gamma is focussed on central occipital sites overlaying the external boundary of the calcarine sulcus. Although it is not possible to state with certainty the neural generators of an EEG signal, this pattern of activity is consistent with activation of early visual areas (Bonmassar et al., 2001) and inconsistent with generators in higher visual association regions equivalent to IT and STS in the macaque. If rivalry was resolved above the level of the early visual cortex, as suggested in single unit recording studies (Shenberg & Logothetis, 1997), then early visual activity would not alter during rivalry change. The occipital activation observed in this study argues against this case, supporting studies showing early visual cortical areas are involved in image dominance (Fries et al., 2001; Lee et al., 2005; Tong & Engel, 2001).

The topographical distribution of induced gamma during perceptual closure may reflect the complexity of the inducing stimuli. Relatively complex Mooney faces were reported to induce gamma oscillations over the posterior two thirds of the head (Rodriguez et al., 1999). Likewise, perception of an ambiguous Dalmatian dog induced gamma-band activity over occipital and parietal sites (Tallon-Baudry et al., 1997). However, the perception of a relatively simple triangle produced a focal activation with a distribution identical to the one observed in this study, including the slight leftward bias (Tallon-Baudry et al., 1996). The greater extent of activation by the inducing stimulus may reflect the differential recruitment of visual association areas to more complex visual stimuli.

The induced gamma burst observed between 200ms and 300ms after stimulus presentation is believed to reflect perceptual closure of the gestalt image. It has been suggested that this oscillatory synchronisation may reflect the temporal binding of the elements of the percept (Tallon-Baudry & Bertrand, 1999). During this experiment the Gestalt binding of the three horizontal bars was prolonged, extending over the 850ms of the subjective transition. Despite this extended duration, induced gamma has the same time-course as during the binding of static images, which occurs over a much shorter duration. This suggests that occipital induced gamma may reflect a realignment of the neural assemblies contributing to the new perceptual Gestalt but may not communicate the bound response of neurons responding to a perceptual object through synchrony.

The idea that gamma oscillations are a reflection of coordinated neural activity, rather than being the medium for feature binding, is also supported by the time course of gamma synchrony during non-rivalrous perceptual closure. Induced gamma activity

lasts for a mere 100ms but the subjective experience of the bound image does not degrade to its component parts after this time. This suggests that these gamma oscillations do not communicate perceptual belonging, as posited by the Temporal Binding Hypothesis, as the object continues to be bound beyond the duration of the gamma burst. It is argued that the higher degree of inter-communication of neurons responding to perceptual closure creates a coordinated discharge of these elements. Due to the higher degree of inter-communication the discharge is correlated and therefore demonstrates some degree of synchrony. Induced gamma, as measured on the scalp, may be an index of this integration of activity. However, it is suggested here that this synchrony is a by product of this process and does not carry information in itself.

Consideration of the frequency distribution of induced gamma observed over the occipital cortex, spanning 30-70Hz, also argues against the hypothesis that synchronous discharge of neurons is used to communicate their bound response. The range of frequencies means that neurons in the higher frequency ranges are firing with a period twice that of the lower frequency range. Although synchronous activity is occurring within each band, such a range of oscillatory cycles makes it unlikely that synchrony is being used to identify elements of a coordinated neural assembly across this frequency range.

An original aim of this study was to investigate whether the subjective transition of rivalrous stimuli resulted in a corresponding transition from right to left of the induced gamma activity. Figure 5-7 shows the erratic nature of the migration of scalp recorded induced gamma power, which may be due to the unpredictable effect of dipoles along the convoluted calcarine fissure. Both the transitory nature of induced gamma and the

focal distribution of this oscillation make EEG induced gamma a poor tool to measure the spread of rivalry waves.

An unexpected finding in this study was the significant decrease in induced gamma during the control condition. Gamma desynchronisation has been reported in the interval between perception and response in previous studies (Rodriguez et al., 1999; Trujillo et al., 2005). The desynchronisation in the present study may be related to the key-press response used to indicate the transition of dominance. The high similarity between this study and previous studies that have investigated visually induced gamma suggest that this putative movement induced gamma desynchronisation was equivalent in both control and experimental conditions and was effectively removed via subtraction.

Using binocular rivalry to measure induce cortical synchrony this study has shown that the neural events occurring in the early visual cortex reflect dominance change. This indicates that binocular rivalry is not a phenomenon of the higher order visual association cortices. In addition three factors are presented as evidence against the view that induced gamma is a reflection of the synchronous neural activity binding the response of the various neurons responding to elements of a grouped visual object (Tallon-Baudry & Bertrand, 1999). Firstly, the duration of induced gamma is not extended in situations when the binding process is extended across time by the migration of rivalry waves across the visual cortex. Secondly, during the binding of static images induced gamma does not persist for as long as the object is bound. Thirdly, the frequency range present in the gamma band is so broad as to make information contained in synchronous discharge minimal. It is suggested gamma range

synchrony reflects a reorganisation and coordination (and therefore correlation) of neural activity in response to complex stimuli, rather than perceptual binding through temporal synchrony.

Chapter 6 General Discussion

Summary of Research Findings

In Chapter Two, the evoked response to word-type stimuli was used to investigate the level of information available during unconscious processing. Rather than assessing the effects of masked stimuli on later judgements to target stimuli, a novel approach was used where the evoked response to two classes of unconsciously presented stimuli were directly compared. The classes of stimuli contained differing levels of abstract information content but identical perceptual features, the rationale being that any difference observed in the evoked response is evidence that the brain is processing this difference in abstract information during unconscious cognition. This revealed direct evidence that abstract information is extracted from word stimuli during unconscious perception. Although abstract information contained within the word stimuli altered the evoked response, the response to the physical features of the letter stimuli, in the absence of abstract content, was indistinguishable from the absence of stimuli. This demonstrates that the evoked response during unconscious word processing is contingent on cognitive, rather than perceptual, processes.

Chapter Two saw the introduction of a model that distinguished conscious and unconscious processing based upon predictions made by a functional model of consciousness. This model predicted that, in comparison to conscious cognition, unconscious cognition would be a rapid process that was not capable of stimulus independent sustenance. This model incorporated work on backward masking in the single unit recording literature. Work on the macaque has demonstrated that during the presentation of masked stimuli an initial 20-30ms burst of neural activity was still

evoked in the STS (Rolls & Tovee, 1994). The presentation of the mask interrupted the subsequent 300ms low frequency firing of the neuron. It was argued that the initial burst has the properties of unconscious processing. Namely that, at the level of the single neuron, the initial burst was computationally rich, containing 65% of information contained in the entire neural response (Tovee et al., 1993); and it is resistant to backwards masking, known to elicit unconscious word reading (Cheesman & Merikle, 1986; Greenwald et al., 1996).

This model posited a two stage process of neural propagation and is very similar to Lamme's FFT model. In the first sweeping stage, neural activity induced by a stimulus travelled rapidly across a distributed neural assembly in a high information burst of non-synchronous activity. This stage underlies unconscious cognition. During the second stage, following the computational operations of the initial stage, neural discharge forms into a coherent pattern, reducing the ability to contain information, but forging a sustained representation of the result of computations occurring in the first stage. This coherent pattern allows the representation of information in conscious awareness.

The empirical findings of Chapter Two were consistent with this model. The single evoked response to the abstract information contained in the word occurred rapidly, peaking at 140ms after stimulus presentation. This response preceded by 100ms the recorded evoked response during conscious stimulus processing that is believed to underlie the processing of the first stage of word identification, identification of word form (Cohen et al., 2000).

The data from Chapter Two provided support for a two stage model of the distinction between unconscious and conscious neural activity. However, for the unconscious stage of this model to be fully supported, it must be shown that all information is processed at this point in time. Chapter Three tested this hypothesis through consideration of the time-course of unconscious semantic information processing.

The effect of a masked prime on processing of a later target stimulus has been demonstrated by both behavioural (Greenwald et al., 1996) and neural (Kiefer, 2002) measures. This approach cannot be used to investigate the time-course of the unconscious neural response to masked stimuli. Chapter Three used the masked semantic priming of a masked semantic target to investigate the influence of semantic information during unconscious cognition. This experiment revealed that masked semantic priming occurs even during unconscious target-stimulus processing. Semantic information contained within the masked prime influences processing of the masked target stimulus 250ms after target onset. This delay, between the lexical/semantic process observed in Chapter Two and the purely semantic process observed in Chapter Three, was longer than would have been expected between V1 and IT regions, based on transmission times in the macaque brain (Schmolesky et al., 1998). In the macaque, the longest delay between V1 and another cortical region (the perirhinal cortex) is in the order of 100ms (Lamme & Roelfsema, 2000). However the activity observed in Chapter Two (differentiating words and non-words) presumably occurred beyond primary visual areas with both the observed activations hypothesised to stem from neighbouring elements of the language system. This would limit the distance that the sweep could travel, leaving this time span an overestimate. The neuronal lifespan of the sweep was initially predicted to be very brief between these neighbouring structures.

The observed latencies are therefore thought to argue against a FFS model of unconscious processing. *However*, the delay was not sufficiently large to exclude potential feed forward connections definitively. The findings of the first two experimental chapters argue against recurrent/reentrant processing being the mechanism of conscious awareness but these findings remain equivocal.

During the spontaneous generation of movement, the subjective occurrence of the first urges to move precedes movement by a few hundred milliseconds. Yet neural activity can be observed to occur up to a second prior to movement. This provides a method to measure the neural characteristics underlying the unconscious generation of movement. Chapter Four contrasted the neural premonitories of movement when participants were consciously aware of the impending onset of movement and when they were unaware. This study found that slow direct current cortical potentials were present in both conditions but that the presence of beta ERD distinguished the neural activity prior to movement with awareness from spontaneous movement. Beta ERD preceded movement with awareness by 1400ms, while beta ERD during spontaneous movement emerged in the 500ms prior to movement.

It is argued from this finding that beta ERD plays a role in the formation of a conscious awareness of future intentions. More specifically it is argued that preceding prescient movement, the inhibitory processes of motor related beta synchrony (Pfurtscheller & da Silva, 1999) is reduced and that this allows the establishment of reentrant connections amongst the dispersed neural populations (Rektor et al., 1994) that participate in movement preparation. It is possible that this decrease in integration is mediated by an increase in GABA activity, either through an influence establishment of stable reentrant

assemblies (Wang, 2003) or in a more generalised effect of increased inhibition. During the spontaneous generation of movement, the activation of dispersed neural populations is insufficient to manifest a conscious representation of the impending urge to move. It is noted that the time scale of the emergence of the beta ERD during spontaneous movement and the removal of the reentrancy blockage, 500ms prior to movement and – 350ms prior to estimates of awareness, is consistent with the time taken to kindle conscious awareness during direct electrical stimulation of the thalamus (Libet et al., 1991). It is suggested that a similar process may be occurring here. The conclusion of this study is that a failure to coordinate neural discharge across the members of a neural assembly may result in a failure to form a conscious representation.

It has been suggested that increases in beta synchrony reflect the binding of movement related neural activity (Brovelli et al., 2004). This study suggests the reverse is the case. If the internal conscious representations are seen to reflect more integrated neural assemblies, then this increase in neural activity is seen to be associated with a decrease in beta synchrony.

Chapter Five investigated the importance in local synchrony in resolving which of two rivalrous images would be represented in conscious awareness. Image competition during rivalry is resolved by changes in the internal states within the cortex, although the site, or sites, of this change in internal states remain contentious (Tong, 2001).

Using a cuing paradigm, rivalry resolution was triggered. Rivalry resolution induced local gamma synchrony focussed over occipital recording sites with the same frequency and temporal characteristics as observed in previous studies of perceptual closure

(Tallon-Baudry & Bertrand, 1999). These results indicate that change in image dominance is reflected in an increase in gamma power within the occipital cortex, suggesting that synchronous oscillations may play a role in determining image dominance. As rivalry changes are associated with changes in the occipital lobe, this study joins the growing body of evidence (Lee et al., 2005; Tong & Engel, 2001) to suggest that rivalry dominance is not determined purely in higher association areas.

During rivalry changes the alteration in the conscious percept follows a wave-like dynamic change (Wilson et al., 2001). In Chapter Five stimuli were manipulated to create a prolonged transition from one percept to the next. This created a situation where object closure and feature binding were spread out in time, beyond that normally occurring during object recognition. Despite the increase in subjective object-closure time, the purported neural correlate of this object closure (induced gamma) demonstrates a typical duration of persistence. This finding, along with the general transience and large frequency range of induced gamma, led to the conclusion that induced gamma synchrony observed during object closure is not a suitable vehicle for feature binding in accordance with the Temporal Binding Hypothesis. It was argued that synchrony may be a correlate of the reorganisation of neural alliances in response to the new percept but that, as synchrony is not maintained across the percept closure process; this synchrony cannot be the mechanism that binds the percept.

Although the duration of scalp-measured gamma synchrony induced by static images has repeatedly been shown to span from 200-300ms, the relationship of scalp recorded, intracranially recorded and single-/multi-unit recorded gamma is uncertain. Intracranially recorded gamma has been observed to persist for several hundred

milliseconds following the presentation of static images (Rols et al., 2001; Lachaux et al., 2005; Tallon-Baudry et al., 2005). This suggests that gamma oscillations sampled intracranially and at the scalp may reflect heterogeneous samplings of the underlying gamma-producing neural activity which may prevent generalisations of the present result to gamma recorded elsewhere than the scalp. Most single-/multi-unit studies have used moving or flickering stimuli, as this produces robust oscillatory activity in the anaesthetised animal (although static images do induce oscillatory activity in the awake macaque (Friedman-Hill et al., 2000)). With such changeable stimuli, as has been reported at the level of the scalp recordings in humans (Muller et al., 1996; Muller et al., 1997), oscillatory gamma synchrony across cortical columns has been reported to last for several hundreds of milliseconds (Gray et al., 1992; Samonds and Bonds, 2005). However, the relationship between the often transient (Gray et al., 1992) and localised gamma response measured at the level of the single unit, multiple unit or LFP and the global, temporally predictable gamma synchrony measurable at the scalp, is uncertain at this stage and may indeed represent to different functional manifestation of gamma range synchrony.

Implications for the Neural Substrates of Consciousness

In the literature review and introduction in Chapter One it was argued that a search for the Neural Correlates of Consciousness is a less profitable approach than searching for what amounts to the Neural Distinctions of Consciousness. Chapters Two through Four investigated the distinctions between conscious and unconscious forms of neural transmission. Chapters Two and Three confirmed that unconscious processing can integrate information across dispersed brain regions, those relating to orthographic, lexical and semantic information. The significance of this is that the activation of

distributed brain regions in itself does not result in, or require, conscious awareness. These chapters demonstrated, for the first time, that the speed of unconscious neural transmission is more rapid than is seen during studies of conscious cognition, with semantic information being extracted unconsciously at roughly the same point in time that letter information is extracted during conscious processing. This suggests that the neural processes underlying conscious representation require more time to establish.

These chapters also *suggest* that some form of reentrant neural activity is present during unconscious processing. In contrast, the findings of Chapter Four suggested that the dispersed neural population involved in motor preparation do not form a conscious representation unless ‘idling’ cortical oscillations are absent perhaps through some block to reentrancy. This indicates that reentrancy over distributed regions may be required for conscious representation. However, synchrony within these reentrant assemblies may not be the mechanism that communicates belonging in these assemblies. The findings of Chapter Five question the importance of neural synchrony in the binding of a dispersed neural coalition as the features of gamma synchrony, as observed in the occipital cortex, make it an improbable medium for communicating differentiation.

These Findings in the Context of Existing Theories of Consciousness

The findings of the first two chapters argue against the RPM of consciousness, or at least that recurrent processing is sufficient for conscious awareness. Again it should be emphasised that this evidence is not conclusive. Rather, a more prolonged lifespan of

the FFS was observed than was hypothesised. Given the multi-stage nature of conscious word reading it was considered a risky prediction that neural activity spreading across the neighbouring cortical regions would process different levels of word-related information almost immediately. This prediction was not met. However, it is possible to refine the model and allow for longer possible conduction delays and retain the RPM of consciousness. But, I would argue that, in themselves, these findings lend more credibility to the potential for unconscious modular processes to remain stably active over time as suggested by Dehaene and Naccache (2001).

Chapter Four suggests that alterations in tonic activity over entire cortical regions (i.e. the motor cortex) may influence the dynamics of active neuronal populations and through this determine whether conscious awareness is generated. In this case the distributed neural activity underlying the RP does not endow conscious awareness in itself while the formation of conscious awareness is preceded by a removal of tonic beta oscillations. The effect of the 'idling' beta oscillation on this absence of conscious awareness can be considered in terms of attentional mechanisms. When attention is directed elsewhere, beta oscillations persist in the motor cortex. In the case of planned movement, attention is already focussed on the impending movement, acting either as a gateway to awareness (Lamme & Roelfsema, 2000) or an amplifier (Dehaene & Naccache, 2001) of the existing neural activity.

The emergence of awareness preceding spontaneous movement is perhaps best considered in terms of IIT. The removal of the beta oscillatory activity alters in some way the effective connectivity of active neural population. This allows integration of information across the neural population and it is the integration of this information that

forges awareness. However, although the results from Chapter Four can be fitted to these models, these were not tested predictions and do not, in this form support, any particular model.

Although some models weight more the importance of synchrony on the formation of conscious awareness (Crick & Koch, 1990; Dehaene & Naccache, 2001) than others (Crick & Koch, 2003; Lamme, 2004), none stand or fall with the role of synchrony in awareness. The finding of Chapter Five, that gamma synchrony (at least occipital gamma) is dissociable from conscious experience, argues more against theories that ascribe synchrony a global role in the formation of conscious awareness (Engel et al., 2001) than against any of the particular theories discussed.

In general, the findings of this thesis suggest that conscious neural processes are not clearly distinguished from unconscious neural processes by the presence or absence of reentrancy, dispersed neural activity or the presence of synchrony.

Considerations on the Neural Substrates of Consciousness

The importance of synchrony in cognition grew out of the work of Gray, Singer and colleagues in the cat cortex (Gray et al., 1989; Gray & Singer, 1989). Here synchrony was observed in a very orderly fashion. Spike coincided in time with a zero phase lag and a very tight frequency distribution. Indeed, in relation to the binding of the elements of consciousness, authors today still talk of “*neural synchrony with precision in the millisecond range*” (Engel et al., 2001, p706).

Forty Hz became the exemplary frequency of gamma, and the purported vehicle for the temporal binding of cortical neural assemblies. Forty Hz corresponds to the maximal driving frequency at which a steady state response can be elicited and is thought to reflect a natural resonant frequency of the brain (Tallon-Baudry & Bertrand, 1999).

The enthusiasm for synchrony grew, spreading from theories of perceptual binding to theories of global binding across the thalamo-cortical system. Initially synchrony was seen as solving many of the challenges facing a neural system capable of conveying conscious awareness (Crick & Koch, 1990). This mechanism has the capacity to unite fleetingly an almost infinite number of combinations of cortical populations with the potential to access all information within the cortex and to differentiate activity from one conscious moment to the next. This enthusiasm is nicely encapsulated by Steven Pinker, “*probably sooner rather than later, we will have a fine understanding of what in the brain is responsible for consciousness in the sense of access to information*” (Pinker, 1997).

However the majority of empirical findings, as applied to these theories, do not match this simplified pattern. The correlation between two synchronous neurons is often weak (Shadlen & Movshon, 1999). Neurons participating in a synchronous assembly do not all fire on each cycle of the oscillatory wave but rather fire stochastically during selective cycle peaks (Wang, 2003). Synchronous activity is often observed with a phase lag across distant cortical sites (Varela et al., 2001). Gamma synchrony is often conspicuously absent in regions where its presence would be thought to be vital, for example, in the monkey cortex gamma has not been reported outside of primary sensory regions in the awake, alert animal (Bair et al., 1994; Young et al., 1992). If

such synchrony underlies conscious experiences it should be prevalent in association cortices.

Theories emphasising the vital role of synchrony in both the generations of cortical integration and conscious representation remain prevalent (Thompson & Varela, 2001; Varela et al., 2001) despite the alterations to the empirical landscape that led to their inception that has caused some theorists to reduce the importance placed on synchrony (Crick & Koch, 2003). Current theories emphasising synchrony acknowledge the immense complexity of synchronous relationships across the thalamo-cortical system with nested synchrony across multiple frequency bands (based on ratios of 1:3 or 2:3 cycles) and phase lag across the cortex. However, with increasing explanatory power the information contained within these 'synchronous' assemblies diminishes. Under these models synchrony may help coordinate but it no longer has the capacity to differentiate.

The two empirical findings most often called to support the role of synchrony in perception (Rodriguez et al., 1999) or in the contents of consciousness (Srinivasan et al., 1999) remain either unreplicated or over-generalised. The study of Rodriguez and colleagues demonstrating increased gamma synchrony with perceptual closure has recently come under close scrutiny. Trujillo and colleagues (2005) replicated the original findings of the Rodriguez study. However, in the Rodriguez study, the peak gamma frequency for each subject was identified in the perceptual closure condition and then subjected to synchrony analysis.

When Trujillo (2005) selected the peak gamma frequency from each condition for subsequent analysis of phase synchrony, synchrony was observed to accompany the presentation of both upright and inverted Moony faces. The selection of the frequency range from the maximal band in the experimental condition artificially biased synchrony estimates in favour of this condition. When a non-biased selection method was used, there was no effect of perceptual closure on widespread cortical phase synchrony. Further, synchrony was seen to increase in the control condition, in the absence of perceptual closure, questioning its role in this process.

The study of Srinivasan and colleagues (Srinivasan et al., 1999) found an increase in cortical coherence at the driving frequency of the dominant image during binocular rivalry. Coherence here is a reflection of the steady state driving frequency. It is a leap to state that this reflects the mechanisms of endogenous cerebral synchrony.

Throughout this thesis it has been suggested that the synchrony observed during tasks thought to relate to the elements of conscious awareness may be an epiphenomenon of the coordinate neural activity induced by these tasks. Such an assertion requires that consideration be made as to the ability of non-synchronous neural activity to carry consciousness and the ability of neuroscience to study it.

The problem at the heart of this issue is how a population, or subpopulation, of neurons contributes to conscious perception at one point in time and another at a second point in time. An alternative device to the temporal binding of these subpopulations is that the information of 'belonging' is coded in the simple strength of connections between these

populations. If the interconnectivity within a neural population increases then so will the correlation of discharge. The synchrony within the population will now increase, as there is now greater shared neural information flowing between these two populations, but this synchrony does not entail information exchange in itself. It is possible that the promiscuous sharing of reciprocal excitation is a sufficient mechanism to dynamically bind elements of the cortex. If inhibition of neurons outside this coalition is included in this repertoire, then this model is essentially that described by Crick and Koch (Crick & Koch, 2003)

There are benefits to a model of neural coordination that does not rely on synchronous firing to communicate membership. Within the brain, information can be represented in the pattern of connections between neurons and in their rate of discharge. If the timing of firing is used to bind, then there is a reduction in the amount of other information that can be represented in the rate of firing of neurons. It is possible that a neuron could fire at any peak of an oscillating frequency, for example, increasing the rate of discharge from once every four cycles to once every two cycles, but such a quantum system would lose sensitivity. As an example, in the monkey cortex there has been found evidence for a parametric representation of tactile information being held in working memory (Romo et al., 1999). Neuronal discharge increased or decreased as a function of the frequency of stimulus vibration. The detail represented in these neurons would not be possible if this population was constrained to keeping its neuronal discharge aligned with the neural discharge in another population.

Further Directions

If formation of reentrant assemblies is the sole mechanism of the representation of consciousness, is it possible to measure this process and is it possible to distinguish it from other processes occurring outside of consciousness? Tononi and Edelman (Edelman & Tononi, 2000; Tononi & Edelman, 1998; Tononi, McIntosh, Russell, & Edelman, 1998) propose a model of measuring consciousness in terms of their Dynamic Core. This model does not rely on synchrony, rather it is proposed as a measure of functional clustering. This is the measure of which neural activity underlies the same *complex*, as discussed in the general introduction. By this it is meant that elements within the functional cluster interact more strongly with each other than they do with elements outside the functional cluster. This provide a novel approach for the assessment of the clustering of computational neural models (Edelman & Tononi, 2000). It is not certain if this method will be applicable to human imaging studies. This approaches has been used to investigate the degree of clustering in schizophrenic and neurotypical subjects, in PET voxels during response, letter search and semantic judgement tasks (Tononi, Srinivasan et al., 1998). This study found evidence for functional clustering, but the low temporal resolution and the concomitant lack of intra-subject degrees of freedom make this study a poor estimate of the merits of this approach. Functional clustering has recently been used to compare the electroencephalographic response to steady state response to photic and auditory stimuli in schizophrenics and neurotypical controls (Jin, Ham, & Kim, in press). The results of this study may reflect volume conduction rather than functional clustering, as neighbouring electrodes will tend to cluster for this reason alone. The difference observed between the two groups may be a reflection of the apparent increase in the noise present in the signals of the clinical group, as functional clustering would be

sensitive to this confound. The analysis of functional clustering may be a promising avenue but needs to be tested further.

The functional clustering technique identifies clusters within which units vary more with each other than they do with units outside the cluster. Conceptually this is similar to a correlation analysis (with the proviso that correlation analysis does not factor in the lack of shared information outside the cluster). And it could be equally argued that correlation will identify clusters of integrated neural activity within the brain. The functional clustering technique of Tononi, Edelman and colleagues may be a more efficient and theoretically sound measure of coordinated neural activity but it does not differ fundamentally from correlation based estimates, such as coherence and phase synchrony.

The theoretical implication of functional clustering, the IIT of consciousness, provides perhaps the most parsimonious explanation of present theories as to how awareness is formed by the neural activity of the brain. This theory states that information integration in and of itself is the process by which conscious awareness is generated (Tononi, 2004). It follows from this, the perhaps controversial claim that *any* system that integrates information of sufficient complexity will form an awareness. This will occur even if the system is an artificial one (Tononi, 2004). This is a very strong claim but if information integration is seen as the generator of conscious awareness then it must be made. There is a certain appealing simplicity to this account of consciousness in that according to the RPM recurrent connections form the integration of information. That is to say, those context driven alterations in neural activity observed in later stages of neural discharge are formed by the context contained in the changes in recurrent

connections shared by that neuron. This process in itself is the integration of information. IIT theory posits, without having to resort to additional mechanisms, that fundamental manifestation of this will be awareness. The richness of this awareness will be determined by the complexity of the information being integrated. Tononi likens information integration to a fundamental property. Just as mass or energy will have repercussions on a physical system so will information integration and this repercussion is subjective experience. Although this theory is parsimonious in attributing awareness to a fundamental quality of the universe it sidesteps the need to provide insight into how information integration *creates* awareness.

Although there are many measures providing tools for investigating functional integration, if synchrony is not seen as a vehicle for consciousness these tools may not in themselves be capable of identifying consciousness. If both synchrony and reentrancy are deemed insufficient vehicles, in themselves, for consciousness then, from what is known of cortical function at this time, there is no clear mechanism that distinguishes conscious cognition (information integration is a quantitative measure). The lack of a clear delineation in the neural substrates of conscious and unconscious processing may reflect a lack of delineation between conscious and non-conscious cognition. Consciousness does not emerge fully formed but is a reflection of the neural processes which are, in some way, selected to partake in the moment. The lack of a clear delineation in neural activity allows the possibility that participation in consciousness could operate on a sliding scale, with the activity of some assemblies closer or further from the centre of consciousness with the perception of unity and a clear delineation within the subjective experience being an illusion of our internal perceptual system.

Consciousness within a wider framework of cognition and theoretical considerations

If the consciousness system is viewed as a high-end representation of the processes occurring in the brain, our 'conscious' experience is that of a user of this system. Here 'high-end' is not synonymous with complexity. In fact in many ways it is the reverse of this. This is perhaps best illustrated with a metaphor. The interaction we share with our desktop computer is (generally) governed through Graphical User Interface (GUI). The operations and processes occurring inside our computer, when we say resize a window, are far more complex than what is necessary for us to efficiently interact with the system. The GUI allows us to open documents, to move files, to interact with information in an abstract way but hidden beneath is the real computational power. Information is represented in a simplified iconographic style, which allows a simplified command of the complex, routine, processes underlying file copying or window-resizing. Likewise, a Brain User Interface (BUI) allows the user to interface with the brain, the simplified experience of the user being conscious awareness. In the computer, the part of the operating system that is involved in creating the icons and managing the information and commands representing the relationship of these icons is the GUI. In the brain the routines which govern the interaction operations and representation represent the neural substrates of consciousness. Here the metaphor of the computer fails as the computer relies on an outside source (a human user) to generate complex solutions to novel problems. In the brain however, the brain creates not only the BUI and the command sequence but also generates the solutions to novel complex problems.

The representation of the GUI is responsible for a fraction of the operations of the computer. Likewise as the BUI represents, but does not encapsulate, the cognitive processes of the brain, it might require a modest amount of cerebral computation. The computational activity of the user interface is intimately tied to the underlying computations. Theories which emphasise the interrelatedness of conscious-related neural activity may fail to discern the distinction between this user interface and the underlying unconscious, computations that feed into it. These computations in themselves may be highly integrated and yet not contribute to the tapestry of consciousness. The processes that create the contents of consciousness are computationally mind boggling. However, these processes are, by and large, not incorporated into the conscious experience. Although it has not been possible to teach a machine to perceive with anything like the sophistication of the human visual system, it is within the capability of current computers to handle and render enough information to fill the contents of the conscious perceptual system.

This illustrates the difficulty in delineating conscious and unconscious actions. If consciousness is seen as a mere interface, then how is it we delineate, either empirically or theoretically, the elements of the user interface from the commands which they issue? An example is the process of sentence construction, one of the most complex, generative, operations the human brain can perform. During the process of conversation words emerge. However the words being used are often unknown to the speaker until they are issued. The user of the system is granted a representation of this complex cognitive operation, but this is a limited and largely post hoc representation of the result of the process. The challenge facing the investigation of consciousness is to tease apart complex cognition of the mind from the internal representation of that cognition.

It is often, if tacitly, assumed that the information contained in the internal representation of consciousness represents the sum of all that kind of information available in the brain. As mentioned above, there appears no clear delineation between the neural substrates of consciousness, and conscious awareness itself may lie on somewhat of a continuum. The division between user interface, as a representation of cogitation, and the process of cogitation itself, allows that, at times, these two divisions may separate. Such an example may exist in the form of moments of insight, where a complex integrative process is solved outside of conscious awareness.

It is possible that the information contained outside of consciousness is highly integrated in itself *and the integration across the system is limited*. The oneness of conscious awareness may be created by heuristics present in the perception of cognition. It is hard to determine philosophically and introspectively the distinction between cognitive processes inside and outside of awareness as there is at least some evidence that the conscious self applies the same perceptive heuristics internally as have been so adaptive in external perception. As investigated in the Fourth Chapter of this thesis, the conscious self perceives itself as the author of actions, even though it is shown electrophysiologically that the decision to move, in some form, had been initiated prior to the formation of a conscious representation. This bias is perhaps best exemplified in the actions of the split brain where the left hemisphere, observing the obviously non-reflexive behaviour of the right, seamlessly confabulates authorship for those actions (Baynes & Gazzaniga, 2000).

A second heuristic assumes environmentally valid temporal relationships between events. When asked, people will report that they would experience both pain and sensation concurrently if their finger was spiked by a needle. Yet the delays between stimulus and pain, due to modest conduction velocities along the responsible axons, are in the order of half a second. Through their life span it is assured that the individual had multiple experiences with this delay and when overtly tested the individual can clearly discern the delay. Yet despite possessing all necessary perceptual information, the conscious system demonstrates a bias towards seeing these events as they should occur. This analogical example has been supported within the perceptual system by empirical studies which have shown that the location of a stimulus in the flash-lag illusion is backward referenced in time depending on subsequently occurring events (Eagleman & Sejnowski, 2000). This heuristic is reflected in Libet's (1991) theory that due to the delay in time required to recruit the reentrant assemblies necessary for conscious awareness, the entire conscious experience is backward referenced in time. Although this theory is contentious and the evidence supporting it far from overwhelming, I include it here to emphasize the potential for internally directed heuristics to bias the interpretation of our subjective conscious experience.

The lack of a discrete neural substrate between conscious and extra-conscious cognition may be reflected in a less than discrete border between conscious and extra-conscious cognition, without a distinguishing feature to identify activity relating to the conscious representation of cognition

These factors together suggest that the relationship between consciousness and cognition may be far more entwined than they would appear to be. Because of the

potential for heuristics to distort our internal perception of consciousness, particularly to attribute actions and thoughts to our own initiation, the framework through which we look at consciousness may be several degrees of latitude off course. The integrative process believed to be important in distinguishing neural activity related to consciousness may in fact serve to entangle it with neural activity outside of the conscious sphere. If no clear distinction is found between the neural correlates of consciousness and the neural correlates of other cognition, then untying the knot of consciousness will be a continual challenge in the future of the cognitive neuroscience of consciousness.

Limitations

The first two experiments hypothesised that unconscious neural activity would be fleeting; but an idea of just how fleeting is constrained by current knowledge of the forward propagation of information across the cortex. Estimates of latencies of neural response in a given cortical region vary from study to study (Lamme & Roelfsema, 2000) limiting the certainty with which estimates of the duration of FFS can be made. Secondly, the passage of neural activity from the visual cortex is not linear, with more distal regions being activated, often considerably, before more proximate regions (Lamme & Roelfsema, 2000). This, coupled with the fact that this information is derived from the macaque, make it very difficult to estimate with precision how long delays in purely feed forward *linguistic* processing may be. The longevity reported in this thesis, ~100ms, did little to help uncloud this uncertainty, as this figure is greater than was expected but not great enough to exclude purely feed forward propagation.

A second limitation of the first two studies, if they had been interpreted as supporting the FFS model, is that this would rely on the absence of later activity. Although there are strong and justified grounds for not interpreting the absence of evidence as evidence for absence, this is particularly compelling in the case of EEG (an inherently noisy and sometimes blind system) and unconscious cognition (an extremely weak signal).

The third study used the controversial paradigm of Libet and colleague. As expressed within the chapter, the validity of estimates of awareness-time is questionable. This requires subjects, using varying criteria, to make reliable estimates of a completely non-tangible and non-verifiable 'stimulus'. The validity of this measure as an index of the timing of the origin of conscious is questionable and the author feels that it is merely a way to spuriously transfer numbers onto the feeling that one decides to move shortly before one does. It is uncertainty what Libet's W-time actually measure (Haggard & Libet, 2001). Having said this, as our subjective selves clearly do not decide to move half a second before we do, I still remain confident that neural activity during the first part of the RP remains an example of preparatory neural activity in the absence of awareness.

A second limitation of the third experiment is the impossibility of controlling perfectly for all task-elements except for conscious awareness. Although care was taken to select a paradigm where the task itself remained the same, it is impossible to limit flow on effects of conscious awareness and the potential influence they may have had on oscillatory beta activity.

Future Research

The concept of using imaging technique, independently of behavioural measures, to fathom unconscious processing is, to my mind, an under-exploited application of this technology. Further studies would not only increase understanding of the neural dynamics of unconscious processing but also allow the investigation of automatic elements of cognition, independent of particular tasks demands.

Theories of the neural substrates of consciousness emphasise the integration of neural activity across the thalamo-cortical system. This is the area that most needs to be investigated in the study of consciousness. However, studies of wide spread cortical integration remain limited. This limitation lies largely on practical constraint. Within EEG, volume conduction provides a major impediment. Both EEG and MEG are too general, being constrained in that they are able only to measure the summed neural activity from large populations of neurons. Invasive recording techniques are (presently) too specific, in that they can record from only a limited number of sites. Perhaps the technique with the most potential is that of fMRI. However, these measures are constrained by the specifics of the haemodynamic response. Even advanced measures such as dynamic causal modelling (Friston, 2003) have yielded little success in tracing function integration through the cortex and may be terminally limited by the indirect nature of the BOLD response.

Conspicuous by their absence are studies that attempt to measure neural integration through functional clustering in fMRI data. These techniques have been applied to PET (Tononi, McIntosh et al., 1998) but the superior temporal and spatial resolution of fMRI would provide a particular advantage in the application of this technique. Lastly,

fMRI studies have shown distributed neural populations to be activated in the absence of awareness (Moutoussis & Zeki, 2002). I cannot think of a more appropriate test of both theories of consciousness and of measures of integration than to consider through functional connectivity and functional clustering whether these regions are more tightly integrated in the presence of awareness than in its absence, which is an area I intend to pursue.

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