Copyright Statement

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand). This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- Any use you make of these documents or images must be for research or private study purposes only, and you may not make them available to any other person.
- Authors control the copyright of their thesis. You will recognise the author's right to be identified as the author of this thesis, and due acknowledgement will be made to the author where appropriate.
- You will obtain the author's permission before publishing any material from their thesis.

To request permissions please use the Feedback form on our webpage. http://researchspace.auckland.ac.nz/feedback

General copyright and disclaimer

In addition to the above conditions, authors give their consent for the digital copy of their work to be used subject to the conditions specified on the Library Thesis Consent Form
ON THE BORDERS OF CONSCIOUSNESS

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

Scott Laurence Fairhall

A thesis submitted in partial fulfilment of the requirements of the degree of Doctor of Philosophy, The University of Auckland, 2005.

This thesis is for examination purposes only and may not be consulted or referred to by any person other than the examiner.
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.
Acknowledgements

Firstly, I would like to thank my truly amazing parents, Sam and Joan Fairhall.

My supervisors Drs. Ian Kirk and Jeff Hamm are too deserved of many, many, thanks for their faith and support over the years. And the wonderful Suzanne Rolfe, certainly for her painstaking proof reading, but mostly for keeping me sane during this last year.

I would also like to thank Suresh Muthukumaraswamy, for the hours saved by your processing routines, and the good chats.

I would also like to thank the University of Auckland Early Career Excellence Award (awarded to Jeff Hamm) for paying my stipend and The Royal Society of New Zealand, The University of Auckland Graduate Research Fund and The New Zealand Neurological Foundation for travels grants during the course of this thesis.
# Table of Contents

ON THE BORDERS OF CONSCIOUSNESS .............................................................................. i

Abstract ..................................................................................................................................... i

Acknowledgements .................................................................................................................. ii

Table of Contents ...................................................................................................................... iii

List of Figures .......................................................................................................................... vi

List of Tables ........................................................................................................................... ix

Abbreviations ............................................................................................................................ x

Chapter 1 Introduction ............................................................................................................. 1

Coherence, Phase Synchrony and the Binding of Neural Activity ................................. 14

Lessons from Binding ............................................................................................................. 22

Anatomical Considerations in the Study of Consciousness .............................................. 25

Considerations on the Neural Correlates of Consciousness ............................................. 34

What Separates Conscious from Unconscious Processing – on the Borders of Consciousness......................................................................................................................... 36

Unconscious Processing ......................................................................................................... 36

Integration of Unconscious Processing with Neural Theories of Consciousness .......... 37

Conscious Capable Circuits Behaving Unconsciously ......................................................... 41

Integration into the Conscious Moment ............................................................................. 46

Chapter 2 Temporal Dynamics of Unconscious Word Reading ....................................... 49

Introduction ............................................................................................................................ 49

The Neural Mechanism of Backward Masking – a failure of reentrancy .................. 49

Insight from Word Reading ................................................................................................. 50

A Competing Model for the Distinction between Conscious and Unconscious Processing ................................................................................................................................. 52
List of Figures

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. ...................................................................................................64

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. ..........66

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’. ........68

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). .............................................................................................69

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). .................................................................69

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). .................................................................72

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). .................................73

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. .................93

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. .........................94

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). ...............95
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. ..............................................................96

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).................................................................................................................111

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.................................................................112

Figure 4-3 Scalp map of distribution of RP during the planned generation of movement averaged over the period 800ms to 500ms prior to movement onsets. Electrode labels correspond to the Geodesic Sensor Nets’ 10-10 International equivalents........................................................................................................113

Figure 4-4 The Readiness Potential proceeding 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.................................................................114

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............................................115

Figure 4-6 Normalised beta power during the spontaneous generation of movement as measured at electrode C3.................................................................117

Figure 4-7 beta (18-24Hz) band power averaged over the 1500-700ms prior to movement .........................................................................................................117

Figure 4-8 Normalised beta power during the planned generation of movement as measured at electrode C3..................................................................................118

Figure 4-9 beta (18-24Hz) band power averaged over the 1500-700ms prior to movement during the planned generation of movement. .................................118

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............................................119
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.................................132

Figure 5-2. An abrupt change in contrast triggers a change in the dominant stimuli...132

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.....................133

Figure 5-4 Morlet wavelet. The units on the abissca are $\sigma$. As frequency increases the $\sigma$ 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.............................................................................136

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)........................................................................138

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.................................................................139

Figure 5-7 Alteration in the topographical distribution of induced gamma across time. .......................................................................................................................................139
List of Tables

Table 2-1 Number of significantly different electrodes (α=0.05) between conditions, across time-windows. ........................................................................................................67

Table 4-1 Mean and standard deviation for the time at which subjects reported the first urge to move. Units are in milliseconds. .................................................................110
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