

New Horizons in the Neuroscience of Consciousness

Advances in Consciousness Research (AiCR)

Provides a forum for scholars from different scientific disciplines and fields of knowledge who study consciousness in its multifaceted aspects. Thus the Series includes (but is not limited to) the various areas of cognitive science, including cognitive psychology, brain science, philosophy and linguistics. The orientation of the series is toward developing new interdisciplinary and integrative approaches for the investigation, description and theory of consciousness, as well as the practical consequences of this research for the individual in society.

From 1999 the Series consists of two subseries that cover the most important types of contributions to consciousness studies:

Series A: Theory and Method. Contributions to the development of theory and method in the study of consciousness; Series B: Research in Progress. Experimental, descriptive and clinical research in consciousness.

This book is a contribution to Series B.

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Volume 79

New Horizons in the Neuroscience of Consciousness

Edited by Elaine Perry, Daniel Collerton, Fiona LeBeau and Heather Ashton

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Elaine Perry

Daniel Collerton

Fiona LeBeau

Heather Ashton

Newcastle University

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List of contributors

Ehsan Arabzadeh

School of Psychology,
University of New South Wales,
Sydney, NSW, Australia.
e-mail: ehsan@unsw.edu.au

Heather Ashton

Department of Psychiatry,
Newcastle University,
Newcastle-upon-Tyne, U.K.
e-mail: c.h.ashton@ncl.ac.uk

Bernard J. Baars

The Neurosciences Institute,
San Diego, California, U.S.A.
e-mail: bbaars@nsi.edu

Ralf-Peter Behrendt

Older People's Services,
The Retreat Hospital, York, U.K.
e-mail: rp.behrendt@btinternet.com

Fabrizio Benedetti

Department of Neuroscience,
University of Turin Medical School,
Turin, Italy.
e-mail: fabrizio.benedetti@unito.it

Lucas Campos**Colin W. G. Clifford**

School of Psychology, University of Sydney,
Sydney, NSW, Australia.
e-mail: colin.clifford@sydney.edu.au

Daniel Collerton

Northumberland, Tyne and Wear NHS Trust,
Newcastle University,
Newcastle-upon-Tyne, U.K.
e-mail: daniel.collerton@ncl.ac.uk

Timoth J. Crow

SANE POWIC, Warneford Hospital,
Oxford, U.K.
e-mail: tim.crow@psych.ox.ac.uk

Armando D'Agostino

Department of Medicine,
Surgery and Dentistry, University of Milan,
Milan, Italy.
e-mail: arma.dagostino@gmail.com

Stan Franklin

Department of Computer Science
and Institute for Intelligent Systems,
The University of Memphis,
Memphis, TN, U.S.A.
e-mail: franklin@memphis.edu

Dominic H. ffytche

Section of Old Age Psychiatry
and Centre for Neuroimaging Sciences,
Institute of Psychiatry, London, U.K.
e-mail: d.ffaftche@iop.kcl.ac.uk

Bangalore N. Gangadhar

Department of Psychiatry,
National Institute of Mental Health
and Neuroscience,
Bangalore, India.
e-mail: kalyanybg@yahoo.com

Anthony A. Grace

Department of Neuroscience,
University of Pittsburg, PA, U.S.A.
e-mail: graceaa@pitt.edu

Justin A. Harris

School of Psychology,
University of Sydney,
Sydney, NSW, Australia.
e-mail: justin.harris@sydney.edu.au

Michael E. Hasselmo

Department of Psychology
and Program in Neuroscience,
Boston University,
Boston, MA, U.S.A.
e-mail: hasselmo@bu.edu.

Biyu J. He

Mallinckrodt Institute of Radiology,
Washington University School of Medicine,
St. Louis, MO, U.S.A.
e-mail: biyu.jade.he@gmail.com

Allan Hobson

Beth Israel Deaconess Medical Centre
and Harvard Medical Centre,
Boston, MA, U.S.A.
allan_hobson@hms.harvard.edu

Gustav Kuhn

Department of Psychiatry,
Brunel University,
Uxbridge, U.K.
e-mail: www.gustavkuhn.com

Valerie Laws

Writer in Residence,
Institute for Ageing and Health,
Newcastle University,
Newcastle-upon-Tyne, U.K.
e-mail: valaws@yahoo.co.uk

Fiona E. N. LeBeau

Institute of Neuroscience,
Newcastle University,
Newcastle-upon-Tyne, U.K.
e-mail: fiona.lebeau@ncl.ac.uk

Ivan Limosani

Department of Mental Health,
San Paolo Hospital,
Milan, Italy.
e-mail: ilimosani@gmail.com

Antoine Lutz

Laboratory for Functional Brain
Imaging and Behaviour,
Waisman Centre, University
of Wisconsin-Madison, WI, U.S.A.
alutz@facstaff.wisc.edu

Mark F. Lythgoe

Centre for Advanced Biomedical Imaging,
University College London,
London, U.K.
e-mail: mlythgoe@ich.ucl.ac.uk

George A. Mashour

Department of Anaesthesiology,
University of Michigan Medical School,
MI, U.S.A.
e-mail: gmashour@med.umich.edu

Lucia Melloni

Department of Neurophysiology,
Max Plank Institute for Brain Research,
Frankfurt, Germany.
e-mail: lmelloni@gmail.com

Morris Moscovitch

Department of Psychology,
University of Toronto,
Toronto, Canada.
e-mail: momos@psych.utoronto.ca

Jaak Panksepp

Department of Psychology,
University of Cape Town,
South Africa.
e-mail: jpanksepp@vetmed.wsu.edu

Andrew C. Parrott

Department of Psychology,
Swansea University,
Swansea, U.K.
e-mail: a.c.parrott@swansea.ac.uk

Elaine K. Perry

Institute for Ageing and Health,
Newcastle University,
Newcastle-upon-Tyne, U.K.
e-mail: e.k.perry@ncl.ac.uk

Adrian Pichurko

Marcus Raichle

Mallinckrodt Institute of Radiology,
Washington University School of Medicine,
St. Louis, MO, U.S.A.
e-mail: marc@npg.wustl.edu

Dean Radin

Institute of Noetic Sciences,
Petaluma, CA, U.S.A.
e-mail: dean@noetic.org

Antti Revonsuo

School of Humanities and Informatics,
University of Skovde, Sweden.
Centre for Cognitive Neuroscience,
University of Turku, Finland.
e-mail: revonsuo@utu.fi

Ashish Ranpura

Centre for Advanced Biomedical Imaging,
University College London,
London, U.K.
e-mail: ash@ranpura.com

Naren P. Rao

Department of Psychiatry, National Institute
of Mental Health and Neuroscience,
Bangalore, India.
e-mail: docnaren@gmail.com

Edmund T. Rolls

Oxford Centre for Computational
Neuroscience,
Oxford, U.K.
E-mail: Edmund.Rolls@oxcns.org

Silvio Scarone

Department of Medicine, Surgery
and Dentistry, University of Milan,
Milan, Italy.
e-mail: silvio.scarone@unimi.it

William Sedley

Institute of Neuroscience,
Newcastle University,
Newcastle-upon-Tyne, U.K.
e-mail: willsedley@gmail.com

Michael Sharwood Smith

Department of Languages and Intercultural
Studies, Heriott Watt University,
Edinburgh, U.K.
e-mail: msharwood@blueyonder.co.uk

Signy Sheldon

Department of Psychology,
University of Toronto, Canada.
e-mail: signy.sheldon@utoronto.ca

Wolf Singer

Department of Neurophysiology,
Max-Planck Institute for Brain Research &
Frankfurt Institute for Advanced Studies,
Goethe University,
Frankfurt, Germany.
e-mail: singer@mphi-frankfurt.mpg.de

Mark Solms

Department of Psychology,
University of Cape Town,
South Africa.
e-mail: mark.solms@uct.ac.za

John Truscott

Department of Foreign Languages
and Literature,
National Tsing Hua University,
Hsincha 30012, Taiwan.
e-mail: truscott@mx.nthu.edu.tw

Katja Valli

Centre for Cognitive Neuroscience,
University of Turku, Finland.
School of Humanities and Informatics,
University of Skovde, Sweden.
e-mail: katval@utu.fi

Kai Vogeley

Department of Psychiatry,
University of Cologne, Germany.
e-mail: kai.vogeley@uk-koeln.de

Ursula Voss

JW Goethe-Universität Frankfurt,
Bonn, Germany.
e-mail: u.voss@uni-bonn.de

Prologue

Synopsis

We believe this is a unique book on consciousness. It is a fascinating cornucopia of new ideas on the subject, based on the fundamentals of neurobiology, psychology, psychiatry and therapy that extends the boundaries of current concepts of consciousness. We hope readers, not only neuroscientists and psychologists but also professionals from other quarters of the academic world with a general interest in exploring consciousness, will find this eclectic mix as stimulating and challenging as we do.

Aims

When the Editor of this prestigious series, Maxim Stamenov, suggested a new edition of the volume published in 2002, 'The Neurochemistry of Consciousness', we found ourselves confronted with a challenge. The 1990s, and turn of the century, saw a plethora of texts on the neuroscience of consciousness following Christof Koch and Francis Crick's seminal notion that pursuing neural correlates of consciousness would unravel novel mechanisms and theories. These new books, based on brain mechanisms like neurotransmission, psychological functions like attention, and methodologies such as brain imaging, relevant as they are, have not (as might be expected) taken us nearer the central issue – how consciousness can be explained in terms of brain activities. Neither have they led to widely accepted radical paradigm shifts, such as have occurred in other areas of science like quantum physics. With time, even some die hard mechanistic neuroscientists have come to acknowledge that there may be an impasse – a gap between top-down subjective awareness and bottom up brain mechanisms as we currently understand them; the so called 'hard' problem of 'qualia', – that is not apparently bridged in current approaches.

The subject nevertheless continues to intrigue scientists and philosophers. Neuroscience, we believe, continues to play a central role in providing information on the brain that will inform thinking on the subject. Enlisting two new Editors and after much debate we decided to encourage some thinking 'outside the box'. We extended a wide net by approaching experts in the area of the neuroscience

of consciousness, seeking new concepts and approaches. We were greatly encouraged to elicit positive and enthusiastic responses to our plea for short, sharp contributions from a number of top researchers either working directly in the field of consciousness or in related areas. Although we initially suggested a focus on conscious – non-conscious interactions, many contributions have gone beyond this boundary and demonstrated the diversity of ideas that the term ‘consciousness’ can elicit.

There were various ways we could have grouped the contributions: as we had done in the previous edition into normal states (controlled or otherwise) and disease or drug induced states; bottom up – how consciousness is related to and affected by molecular/neuronal/systems, versus top down – how consciousness itself affects these brain mechanisms; academic approaches relating to theories of consciousness versus those with more pragmatic implications.

More than most books on consciousness, this volume has been structured by the ideas of individual contributors rather than any preconceived editorial plan. As ideas and concepts accumulated it seemed to us that the most logical and meaningful categorization was fourfold grouping chapters which:

1. Potentially pave the way for new research into consciousness relating to basic scientific – physiological, pharmacological or neurochemical – mechanisms underpinning conscious experience (the ‘bottom up’ approach).
2. Provide directions based on how psychological processes are involved in consciousness and related brain activity (the ‘top down’ approach).
3. Indicate how including consciousness in the equation could lead to new approaches to understanding mental disorders, such as schizophrenia, depression, dementia, psychosis in general (in particular hallucinations) and addiction, including, amongst therapeutic approaches, an understanding of the power of the placebo.
4. More provocatively, but still based on scientific evidence, explore ways that consciousness can be considered beyond conventional boundaries, including some which indicate the potential for radical new thinking or possible ‘quantum leaps’ in neuroscientific theory.

These divisions are not absolute and one of the book’s strengths is that each chapter stands alone and can, therefore be read in any order, over any period of time.

Below each Editor has highlighted what they consider to be the main points of interest for each of the contributions in the book. We hope this overview will guide the reader to chapters related to their particular field of interests, but also that it will entice readers into areas outside their fields of expertise. This has certainly been our journey as Editors and we hope that it is one that readers will also undertake and enjoy as much as we have done.

Neuronal mechanisms

Slow cortical potential hypothesis of consciousness. Biyu He and Marcus Raichle postulate that the slow cortical potential recorded from the surface of the brain is a key neural substrate that could facilitate integration across wide cortical areas – a prerequisite for conscious awareness. In view of the link between the slow cortical potential and the fMRI signal, their hypothesis can be tested empirically.

Distinct characteristics of conscious experience met by large scale neuronal synchronization. Lucia Melloni and Wolf Singer propose that synchronization of distributed neuronal activity patterns meets most requirements for the neuronal mechanisms supporting consciousness. The challenge of identifying neuronal correlates of consciousness is distinguishing between the processes that lead to conscious experience and those that follow once contents have become conscious. Criteria for this distinction are outlined, separating the contribution of each subsystem and characterizing how they interact; providing a real alternative to the ‘ever lurking homunculus’.

Cellular components of gamma oscillations. Fiona LeBeau explores the role of key neuronal elements in the generation of cortical gamma frequency oscillations. She discusses how new techniques for labelling and activating in isolation specific sub-classes of neurons (optogenetics) can be used to explore the cellular components that underlie the generation of a brain activity that may be specifically linked to aspects of consciousness.

Dopaminergic decision making. Anthony Grace discusses how changes in dopamine levels in the limbic system (prefrontal cortex, hippocampus and nucleus accumbens) guide behavioural responses and modulate decision-making. He proposes that dopamine can serve to focus conscious attention to a particular task and can flexibly alter behaviour to achieve goals.

Endocannabinoid system and undercurrents of consciousness. Heather Ashton stresses that unconscious processes set the ‘tone’ for all conscious moods, thoughts and feelings. These unconscious processes are mediated by modulatory neurotransmitter systems, of which the endocannabinoid system is one of the most powerful. This system modulates almost all vital functions including those clearly involved in consciousness (cognition, mood and others) and many that do not normally reach consciousness (motor control, endocrine activity and others).

Disconnecting consciousness in general anaesthesia. George Mashour and colleagues explore molecular and cognitive mechanisms of general anaesthesia and their relevance to the science of consciousness. They suggest that general

anaesthetics serve as an important but still relatively under used tool to explore transitions from conscious to unconscious processing, as these drugs rapidly induce a complete and reversible cessation of consciousness. With vast numbers (over four million patients each year in North America alone) undergoing general anaesthesia, the highly controlled and monitored setting of the operating room could become the ultimate consciousness laboratory.

Neural mechanisms of mental time travel underpin the continuity of consciousness across time. Michael Hasselmo uses the term neural time travel to describe the processes of drawing on distributed cortical perceptual processes for detecting the state of the self along multiple dimensions. These include spatial location, head direction, speed, temporal duration, and egocentric relationships to items. He provides evidence that one particular set of cerebral circuitry, mediated by cholinergic muscarinic receptor mechanisms, activates neuronal properties involved in seamless internal representation of self that is based on memory.

Psychological processes

Explicit and implicit memory share underlying processes. Signy Sheldon and Morris Moscovitch remind us of the commonly held assumption that consciousness is a defining feature that distinguishes explicit memory (with conscious awareness) from implicit memory (without conscious awareness). Although early studies support this notion, recent evidence suggests that conscious and non-conscious memory systems may share crucial underlying processes. They propose that one locus of interaction between some types of explicit and implicit memory may be the non-conscious processes associated with recollection or detailed remembering, that are mediated by the hippocampus.

More than one type of non-conscious processing. Stan Franklin and Bernard Baars suggest that unconscious processes come in two varieties – the preconscious, whose contents may become conscious, and the never-conscious, whose contents may not. They enlist their Global Workspace Theory and a related model to catalogue never-conscious and preconscious processes. They suggest that the functional distinction between never-conscious and preconscious processes derives from one of the major purposes of the consciousness mechanism – to select the most salient portion of the current situation to which to attend and to broadcast this globally, in order to choose the best next action.

Gambling as a measure of awareness. Colin Clifford and colleagues remind us that most of the processing of incoming sensory information is not accessible

to consciousness. These authors are concerned with methodological issues in exploring the limits of unconscious processing and evaluate the intriguing tool of post-decision wagering as a candidate method for measuring awareness.

Magical methodology. Gustav Kuhn shows us how magicians have developed powerful techniques to manipulate our perception and awareness. Many of these techniques share similarities with phenomena typically investigated by psychologists and neuroscientists. His novel approach to the study of consciousness is to utilize the magician's expertise to complement more traditional experimental laboratory based research. This approach offers new and exciting insights into wide areas of consciousness, such as attention, visual awareness and how top-down processes modulate perception.

The advantage of a noisy brain. Edmund Rolls focuses on decision making and the advantages of noise caused by randomness in the spiking times of neurons in the brain. Noise results in the brain operating effectively as a non-deterministic system, which has implications for free will. It also results in decisions being taken probabilistically between the reasoning system and the implicit reward system. If free will describes the operation of the reasoning system, consciousness is then a property of a reasoning system that must use higher order syntactic thoughts to correct its first order thoughts. Decision making in an implicit system potentially involves confabulating a reason for the decision with the feeling of being free an illusion.

Social consciousness as a key function of the default network. Kai Vogeley describes the neural correlates of the reciprocal nature of social interaction using fMRI. Self-consciousness, as awareness of ones own mental states, and social consciousness, as knowledge of the mind of others, overlap with the default mode of brain function. A key biological function of this default network, irrespective of task, may be social consciousness. Humans thus have a built in disposition for social cognition that is reflected in this neural default mode.

Linguistic processing at two levels. Mike Sharwood Smith and John Truscott point out that knowledge, use and acquisition of language is largely an unconscious process for a child acquiring its first language. However, it leaves conscious footprints in the form of a 'voice in the head'. Learning a second language in later years, the mature learner can and often does develop a conscious understanding of what is being acquired. This understanding springs from a knowledge that is separate from the unconscious and inaccessible system developed within the language module. It is an open question how much that separate knowledge and the voice in the head that it engenders actually enhances or hinders development and on-line performance.

Dreaming as key to understanding consciousness. Antti Revonsuo and Katja Valli suggest that dreaming as a state of subjective awareness, essentially independent of input and output, best lends itself to the challenge of bridging the top-down / bottom-up divide. They go so far as to indicate that if the internally generated state of dreaming is not accounted for by any neuroscientific theory of consciousness that theory is lacking.

Lucid dreaming and the bimodality of consciousness. Allan Hobson and Ursula Voss argue that, in the context of the widely accepted division between primary and secondary or reflective consciousness, dreaming is dominated by the primary type. Intriguingly, lucid dreaming, during which rational thought and volition emerge in a state of sleep dominated by primary consciousness, provides a new investigative tool. Exploring dreaming is proposed as a cornerstone of higher level consciousness research.

Psychopathologies and therapies

Why depression feels bad. Mark Solms and Jaak Panksepp highlight the urgent need to restore conscious experience to psychiatric practice. They provide evidence for the failure of bottom-up antidepressant drugs or theories of serotonin deficits to deal with the problem of depression. Their idea of depression as a kind of bereavement based on loss of self connectedness and separation is, they suggest, a pathological extension of a natural survival mechanism. Accordingly continuing to ignore such conscious experience is, they suggest, likely to be perilous in clinical practice

Consciousness abhors a vacuum. Daniel Collerton considers the question of what kind of consciousness is experienced by people with dementia and suggests they have not diminished, but different conscious awareness. Resulting from brain pathologies which impair perception and other aspects of cognition, gaps in normal conscious awareness are not left unoccupied but are 'filled in' resulting in, for example, hallucinations or delusions. This view encourages empathy in those interacting with people with dementia that could impact on care strategies.

Consciousness as the spin-off and schizophrenia as the price paid for language in man. Tim Crow puts forward a novel and thought provoking theory of schizophrenia based on the asymmetry (torque) of the human brain as the foundation of the faculty of language. Focusing on the symptoms of hearing voices, the experience of thoughts as not one's own, and incoherent speech as core symptoms of schizophrenia, he follows three new lines of argument. First, this torque is

the feature that defines the human brain as four chambered by comparison with the two chambers of the generalized mammalian brain. Secondly, by separating thought from speech production in the frontal lobes, and meaning from speech perception in occipito-parieto-temporal association cortex, torque confers on our species the capacity for language. Thirdly, the phenomena of psychosis can be seen as 'leakage' from one to another of the four quadrants of association cortex.

Hippocampal seat of consciousness and hallucinations in schizophrenia. Ralf-Peter Behrendt argues that a hippocampal auto-association network (CA3) pin-points a spatiotemporal and emotional context for the purpose of event memory formation. Representing a continuous flow of complex symbols, conscious experience may be irrelevant to the workings of the brain, although neural activity underlying event memory formation influences behaviour (via output to medial prefrontal cortex, ventral striatum and lateral septum). Excessive pyramidal cell activity in the CA3 area, due to deficient inhibition (by GABAergic basket interneurons), leading to event memory formation unrestrained by input from areas such as entorhinal, may be a mechanism for the generation of altered consciousness such as hallucinations in schizophrenia.

Perspectives from the Charles Bonnet Syndrome. Dominic ffytche examines evidence derived from visual hallucinations in the context of eye disease – the Charles Bonnet Syndrome – to examine the nature of the visual unconscious. Forcing us to reconsider the nature of the unconscious, this hidden system of processing underlies our apparently seamless conscious experience of the world, with many of its complex functions yet to be recognised by visual science.

Believing is hearing is believing: the reciprocal nature of consciousness. Will Sedley provides an analysis of the neural correlates of auditory hallucinations including tinnitus, musical and verbal hallucinations, misperceptions and imagery. All types of auditory consciousness involve auditory cortex activation which can often be measured as synchronised gamma band oscillations, but disruptions in connectivity, such as cochlear damage, can lead to positive feedback cycles that cause and enhance hallucinations.

Dreaming as a model of psychosis. Armando D'Agostino, Ivan Limosani and Silvio Scarone investigate the long neglected dream state of consciousness in psychiatry. They argue that the similarity between normal dreaming and states of psychosis provides a novel fertile area for psychopathology and consciousness research. In particular, they suggest that lucid dreaming, whereby there is awareness of the dream state during sleep, whether induced by psychological or pharmacological means, could be a new tool for investigation and therapy in psychiatry.

If only drug users were aware of why they choose to use. Andrew Parrrott presents new evidence based on reports by users of ecstasy/MDMA that their choices are governed by largely non-conscious optimistic beliefs focused on desired aims rather than actual consequences, with low levels of or little attention to, conscious awareness of all the issues. He describes how users become aware of the adverse effects of MDMA and make the conscious decision to use less frequently and quit permanently.

Brain body interactions in placebo responses. Fabrizio Benedetti presents a host of fascinating data on how placebo responses, involving a range of cues, depend on both conscious and non conscious processes, and how these can mimic therapeutic drug effects even inducing cellular and molecular changes in the patient's brain (e.g. receptor function or neuronal circuitry). He argues that this evidence provides the basis for the efficacy of cognitive and other psychological therapies in terms of neurobiological mechanisms. This raises the intriguing question of how we might deliberately self modify our mindset at both conscious and non conscious levels to promote healing processes.

Expanding boundaries

Paradox of creativity. Ashish Ranpura and Mark Lythgoe describe a neurobiological theory that explains the process of creativity – possibly the most impressive facet of secondary consciousness. The authors explore how three paradoxes of creativity, the paradox of ego, of focus, and of quality are defining features of this quintessentially human experience. The frontal lobes appear to play a critical role in creativity and the authors draw upon a Darwinian selection theory that allows conscious creativity to emerge from a series of unconscious mental activities.

How research on meditation contributes to the neuroscience of consciousness. Antoine Lutz examines initial findings of neuroscientific research on meditation and reveals how these identify new horizons of further inquiry in consciousness research. While such studies of contemplative practices are still in their infancy, early findings promise to contribute in three key areas. These include: neuroplasticity – physiological and psychological indices of short and long terms responses of the brain circuits that underlie complex mental functions associated with specific types of meditation techniques; mind body interactions – revealing mechanisms by which such training may exert beneficial effects on physical health; and subjectivity – well developed introspective skills of practitioners potentially shedding new light on the neural counterpart of subjectivity.

Exploring consciousness based on self induced altered stated techniques. Bangalore Gangadhar and Naren Rao provide a fascinating perspective on methods used to alter personal conscious experience using a variety of procedures commonly practised in India including meditation. Together with Eastern concepts of the nature (levels or states) of consciousness which diverge markedly from Western ideas, for example belief in a cosmic consciousness as a source of all conscious experience, he provides food for thought on potential paradigm shifts in theories of consciousness. At the same time, how physiological and brain imaging markers are affected as a result of meditation provides neuroscience with down to earth tools for investigating an area hitherto regarded by most neuroscientists as esoteric at best.

Models of conscious and non-conscious perception may need radical revision in unexpected ways. Dean Radin provides evidence from anecdotal to controlled scientific experimentation (published in refereed journals) that telepathy is a genuine phenomenon. He raises the question of how to account for such conscious interactions beyond the 'common' senses and what kind of new neuroscientific theories might have to be generated. An intriguing theory of 'entanglement' based on principles of quantum physics is discussed as a possible explanation of such 'non local' phenomena – food for thought for neuroscientists looking beyond continuing shortcomings of reductionism to explain conscious experience.

Plants of the gods and shamanic journeys. Elaine Perry and Valerie Laws suggest that knowledge and experience of shamanic practitioners may have more to offer consciousness studies than psychedelic plant chemicals. Among agents which alter the boundary between conscious and non-conscious cognition, the ritualistic use of plant species provides an example of long-standing empirical knowledge subsequently verified by scientific (chemical, pharmacological and psychological) evidence. Based on such an impressive 'track record' for obtaining validated information about consciousness, further investigation of shamanic experiences including reports of other 'dimensions' of consciousness are warranted. Evidence obtained in such areas, rooted firmly in scientific methodologies (though no doubt incorporating factors not normally part of scientific methodology such as mind training, belief, past experience and empathy), could potentially contribute material for radical new scientific theories of consciousness,

Conclusions

This book clearly reflects the individuality of its contributors more than most. In seeking novelty, it contains new 'streams of consciousness' on the subject of neuroscience and consciousness that we think provide new directions for future research.

We would hardly expect readers, any more than the Editors as it transpired, to agree with all the arguments raised within this book. A unitary definition of consciousness was neither sought nor provided. In originally setting an interface between conscious non conscious processes as a target focus, we may have been overly optimistic that agreement on any such division could be reached. Categorizing distinct levels of consciousness or considering continuity are clearly far from being resolved. Contributors have incorporated a range of definitions or states of consciousness in addition to or other than the conscious non conscious divide: Gerald Edelman's division between primary or first order and secondary or reflective consciousness; divisions within non conscious processing itself; self consciousness; dreaming as a neglected but core state for investigating consciousness; and Eastern concepts of multiple states that challenge the Western mind.

Drawing together what we consider the most stimulating and challenging ideas into emergent themes for neuroscience based consciousness research, key questions emerge:

Are boundaries between conscious and non conscious processing less obviously demarcated than previously considered, with multiple levels or states or perhaps a boundless continuum?

How much of cognitive or perceptual conscious awareness is based on illusion versus reality?

How many other non-conventional activities and investigative tools (like magic and gambling) might be incorporated into research into consciousness?

Is it time to reinstate dream research into brain research as a model for investigating the essence of conscious awareness in normal and pathological states?

Which if any, or all, of candidate electrophysiological measures is most likely to reflect the mechanisms which are specifically involved in conscious awareness?

Do individual signalling (e.g. neurotransmitter) systems govern specific aspects of consciousness and, if awareness is but a minute portions of pre/unconscious processing, is any one system primarily in control of the transition?

Why is general anaesthesia not a mainstream tool in more basic consciousness studies?

Can psychiatric practice thrive or survive without attending to the state and nature of consciousness in individual patients?

Can pathologies associated with common disorders of the human mind be analysed more in relation to consciousness and so inform basic mechanisms of consciousness?

If the placebo effect is so robust and associated with the same mechanistic changes in brain and body as those induced by drug treatment, why is it not the subject of more therapeutic research?

Is it time for neuroscientists to seriously consider scientific evidence for so called anomalous phenomena such as telepathy, and in this context contemplate paradigm shifts in theories of consciousness?

Should more attention be given to concepts of time honoured mystics about consciousness which could be relevant to neuroscientific enquiry?

In the process of gathering contributions for this book it became clear that a second volume could easily have been generated, as there are many topics we have not had sufficient space to cover in this volume. For example, consciousness in the vegetative state springs to mind as an omission that reminds us of the need for new tools to assess individual subjective states of conscious awareness. New neurophysiological findings of a novel type of high speed cohesion between distant groups of neurons remind us how exciting it is when a new and unexpected observation emerges at the level of observational science to inspire new thinking about neural network integration relevant to consciousness. Default mechanisms that include a kind of continual 'day dreaming' as a fall back position in the awake state remind us of the essentially and continuously creative nature of the conscious stream. And brain body interactions referred to in passing in some chapters may cause us to consider consciousness as a more global phenomenon.

Acknowledgements

The Editors gratefully acknowledge: Maxim Stamenov for not only for suggesting this new volume but also for his guidance and wisdom in the shaping of the book; Valerie Laws and Susan Aldworth, currently Writer and Artist in Residence respectively at Newcastle University, for the poetic and artistic inclusions; Brian Moore for suggesting contributors; Peter Whitehouse for formulating ideas for the prologue; Peter Fenwick for guidance on 'beyond the brain' issues; Peter Russell and Ervin Laszlo for agreeing their article on the primacy of consciousness could be included (and we refer readers interested in this con-

cept, relevant to some of the chapters in the last section to the relevant website [<http://www.redicecreations.com/specialreports/2006/02feb/primacyconsciousness.html>]); our respective Heads of Department for supporting our work on the book, and to the Publishers John Benjamins.

Seeing myself think

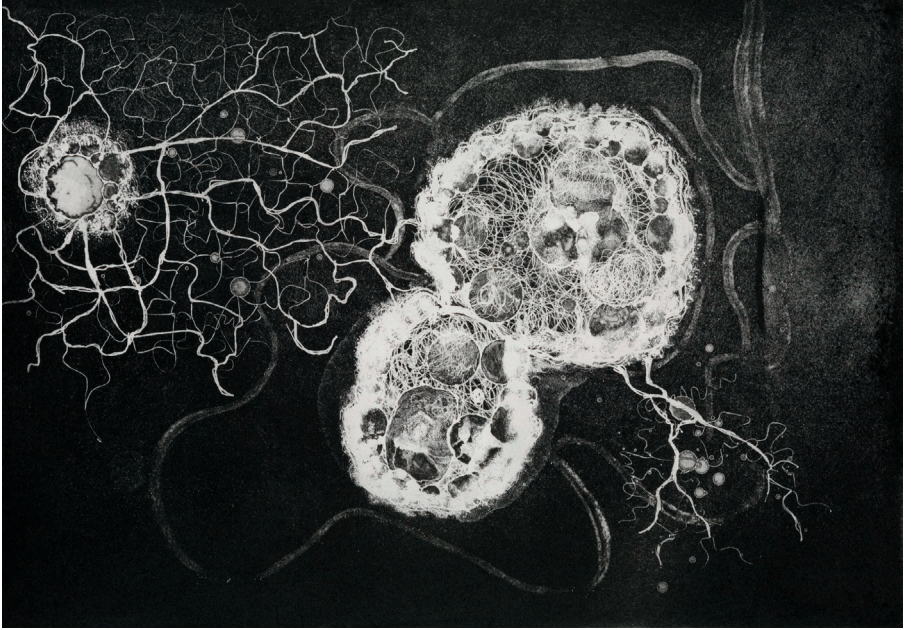
Last night I saw myself think;
I caught myself out. Just
As I went to sleep
I saw the ideas, a sea
Of winking sparks like mackerel
Under the moon or the flutter
Of cameras flashing
In a dark auditorium; or
The bioluminescence
Of deep sea creatures signalling
In the black cold. Each thought
Was a light leaping a synapse
Where pairs of nerve cells
Reached out to each other, their touch
Kindling. Whole galaxies
Of consciousness glittered before
My eyes.

And I saw myself thinking, our sun
Might be a spark of thought
In an enormous mind
Which sees its thoughts flash
In the birth and death of stars.

Valerie Laws
(formerly published in *Quantum Sheep*,
Peterloo Poets)

SECTION I

Neuronal mechanisms



Birth of a Thought 2. Susan Aldworth (2007) etching and aquatint, 35 × 50 cm

The slow cortical potential hypothesis on consciousness

Biyu J. He and Marcus E. Raichle

We propose a neurophysiological hypothesis on the emergence of consciousness, which postulates that the slow cortical potential (SCP) recorded from the surface of the brain provides an index of the activities of superficial-layer pyramidal neurons that directly contribute to the emergence of conscious awareness. This hypothesis is supported by existing data from manipulations of conscious awareness in normal human subjects and by data from altered states of consciousness such as general anesthesia and recovery from vegetative states; it further makes experimentally testable predictions. Given a relationship between the SCP and the functional magnetic resonance imaging (fMRI) signal that has now been revealed, this hypothesis also provides a potential bridge between existing neuroimaging and electrophysiological studies on consciousness.

Since its introduction in the early 1990's, fMRI has become the most widely used tool in cognitive neuroscience and has produced a formidable array of brain maps depicting both localization (as in traditional activation studies) and integration (as in more recent functional connectivity studies) of brain activity. As the fMRI signal measures directly blood oxygenation and only indirectly neuronal activity, an important need for understanding the neural events contributing to the fMRI signal has been widely recognized. Such a need is further stressed by the inconsistencies between a number of human fMRI and monkey unit physiological studies employing the same tasks (Logothetis, 2008). Responding to this need, a number of studies have compared the fMRI signal or its close relatives (including tissue oxygenation, blood flow, optical intrinsic signals) with simultaneously recorded electrophysiological signals. The convergent results from these studies suggest that the fMRI signal is contributed predominantly by synaptic activity representing inputs and local processing in an area as measured by local field potentials (LFP). The spiking activity, though often correlated with both the LFP and the fMRI signal, can be dissociated from the latter two in a number of conditions

including adaptation, drug modulation, manipulations of excitatory and inhibitory inputs, and a spatial separation between input and output activity (for reviews see (He and Raichle, 2009; Logothetis, 2008)).

Whereas multiple frequency ranges of the LFP (e.g., 5–30 Hz, 20–60 Hz, ~25–90 Hz, see references in (He and Raichle, 2009)) have been correlated with the fMRI signal in different conditions, all of these studies have only assessed power modulations of the LFP because only the power of these frequency ranges has a comparable temporal scale to that of the fMRI signal (<0.5 Hz). Recently, it was found that the raw fluctuations of the low-frequency end of field potentials (<4 Hz), with a temporal scale overlapping that of the fMRI signal, also correlates with the fMRI signal (He and Raichle, 2009; He et al., 2008; Khader et al., 2008; Nagai et al., 2004). This signal, termed the “slow cortical potential” (SCP) by us and others (Birbaumer et al., 1990; He and Raichle, 2009; Khader et al., 2008), appears optimally positioned for carrying out large-scale information integration in the brain. Because conscious awareness (see Glossary) is always experienced as a unitary and undivided whole, rather than components that are experienced independently (in the case of split-brain patients, there are two conscious experiences each located in a separate brain hemisphere, rather than one single conscious experience), segregated information processing in the brain cannot contribute directly to conscious awareness. We propose that the neuronal activities reflected by the SCP may contribute to the emergence of consciousness and review existing empirical evidence supporting this idea. As the current hypothesis is based on a well-defined, well-characterized physiological process, it is entirely amenable to empirical testing.

The SCP and the fMRI signal

The SCP is the slow end (mainly <1 Hz, can extend up to ~4 Hz) of brain field potentials that can be recorded using either depth or surface electrodes. A negative shift in surface-recorded SCP indexes increased cortical excitability (for detailed physiology see the following section). Since the SCP frequency range is subject to artifacts due to sweating (in scalp-electroencephalography (EEG) recordings), movement and electrode drift (if polarizable electrodes are used), it has been eliminated in most animal physiology as well as human EEG studies by online high-pass filtering. This is unfortunate because, as was recognized in the 1970’s, “If DC [i.e., direct-current] recording is used, virtually every stimulus-bound cortical activity is seen to be accompanied by a change in cortical steady potentials” (Goldring, 1974).

Recently a number of studies have revealed a close relationship between the SCP and the fMRI signal. Nagai et al. (2004) demonstrated covariation of simultaneously recorded SCP and fMRI signals during task stimulation using simultaneously recorded EEG and fMRI (Nagai et al., 2004). These authors found a trial-by-trial correlation between the amplitude of a negative SCP response indexing expectancy (“contingent negative variation”, CNV) and the fMRI signal amplitude in anterior cingulate cortex. The anterior cingulate has previously been determined as a generator region of CNV (Nagai et al., 2004). Jones et al. (2007) showed that spontaneously fluctuating total haemoglobin concentration (a signal tightly linked to the fMRI signal) and low-pass filtered LFP (i.e., depth recorded SCP) are temporally correlated (Jones et al., 2007). Our own data using invasive EEG (i.e., electrocorticography, ECoG) and fMRI in neurosurgical patients showed that large-scale (2–10 cm on cortical surface) correlation patterns in the spontaneous SCP and fMRI signals were similar (He et al., 2008). This finding has since been extended to inter-hemispheric correlations as well (unpublished data). Beyond these approaches, there is an extensive literature showing similar modulation patterns of the SCP and the fMRI signal in a wide range of cognitive tasks (for reviews see (Birbaumer et al., 1990; He and Raichle, 2009; Khader et al., 2008; Rosler et al., 1997)). Hence, convergent results suggest that the SCP has a close correspondence to the fMRI signal in different experimental conditions. Next, we consider the physiological mechanisms underlying the SCP.

The physiological basis of the SCP

Simultaneous recordings of surface potentials, field potentials in different cortical layers, and intracellular membrane potentials have clearly demonstrated that synaptic activities at apical dendrites in superficial layers are the main factor contributing to the SCP. Specifically, long-lasting excitatory postsynaptic potentials (EPSPs) at these apical dendrites underlie negative-going surface-recorded SCPs (Birbaumer et al., 1990; Goldring, 1974; Mitzdorf, 1985). As an example, we consider the effect of visual stimulation in V1 – a standard model for the investigation of fMRI-electrophysiology correspondence. Specific thalamic inputs terminate first on the soma of layer-IV stellate cells and layer-III pyramidal cells, and then follow one of two pathways to depolarize the apical dendrites of superficial- or deep-layer pyramidal cells (Mitzdorf, 1985) (Figure 1a).

Given the geometry of cortical fields, the earlier processes – excitations of pyramidal cells at their soma, produce positive-going surface potentials (Figure 1b i). The later processes, excitations of pyramidal cells at their apical dendrites, produce surface negative potentials (Figure 1b ii and iii). However, EPSPs at apical

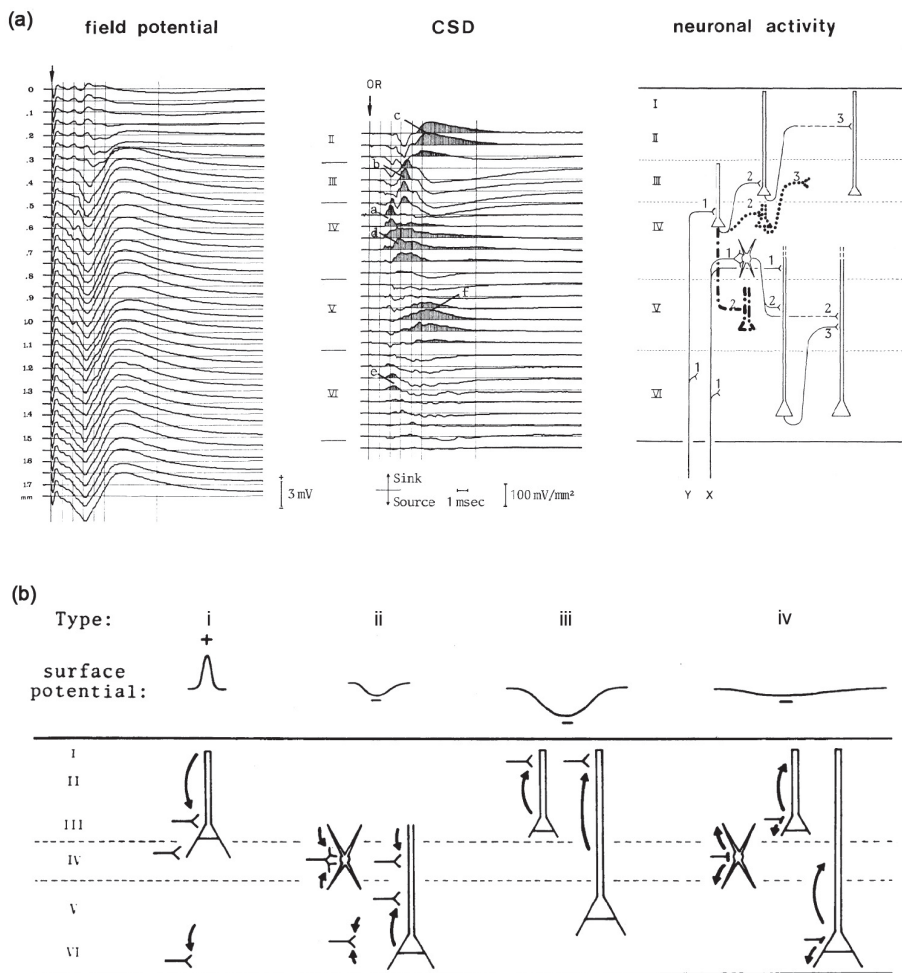


Figure 1. The physiological basis of the SCP. (a) *Left:* field potential in primary visual cortex of the cat evoked by electrical stimulation of optical radiation. Each trace is the average of 20 responses. Distance between adjacent recordings is 50 μm . *Middle:* current source-density (CSD) distribution obtained from the potential profile on the left. Sinks, corresponding to active EPSPs, are shaded. Cortical laminae are indicated. Sinks a, b, and c reflect mono-, di-, and trisynaptic Y-type activity as shown in the right panel; sinks d and f reflect mono-, di-, and trisynaptic X-type activity shown in the right panel; sink e reflects Y-type and X-type monosynaptic activity. Sinks a, b, and e contribute to type *i* activity in (b); sinks d and f contribute to type *ii* activity in (b); sink c contributes to type *iii* activity in (b). *Right:* schematic diagram of successive intracortical excitatory relay stations as well as cell types involved. Long-range feedback connections and nonspecific thalamic inputs are not depicted. Numbers 1, 2, 3 denotes mono-, di-, and tri-synaptic activity respectively. (b) Schematic diagram of

dendrites of deep layer pyramidal cells create closed fields and thus have rather small influence on surface potentials (Figure 1b ii). By contrast, depolarizations of superficial layer apical dendrites contribute greatly to negative SCPs (Figure 1b iii). The contribution of inhibitory interneurons to SCP or field potentials in general is also small because of the low amplitude of membrane current flow during inhibitory activity and a lack of laminar specificity (Figure 1b iv) (Birbaumer et al., 1990; Mitzdorf, 1985). In summary, the later component of sensory evoked potentials in EEG or ECoG recordings – a negative slow-potential shift – is primarily due to long-lasting depolarizations of superficial layer apical dendrites.

Other than activations by specific thalamic inputs described above, the superficial layers are also where long-range intracortical (i.e., intra-areal) and cortico-cortical (i.e., inter-areal) connections preferentially terminate (Braitenberg and Schuz, 1998; Douglas and Martin, 2004; Mitzdorf, 1985). First, only in superficial layers do pyramidal cells make extensive horizontal arborizations (Douglas and Martin, 2004). Thus, EPSPs in superficial layers spread over a considerable spatial extent and manifest themselves as “depolarization fields” (~several mm²) in optical imaging recordings (Roland et al., 2006). Second, long-range inter-areal feedback connections also terminate mainly in superficial layers. Hence, it is not surprising that the SCP and the correlated fMRI signal reveal large-scale brain networks in their spontaneous fluctuations (He et al., 2008). Moreover, superficial-layer apical dendrites are also the main target of nonspecific thalamic inputs that originate from “matrix cells” spread throughout the thalamus (Jones, 1998). Interestingly, the reticular thalamic nucleus, which the nonspecific thalamocortical projections must pass through, exerts a low-pass filter influence that may facilitate the emergence of slow activity (He and Raichle, 2009). In summary, long-range intracortical and feedback cortico-cortical connections, as well as the nonspecific thalamic inputs, all contribute directly and significantly to the SCP.

4 main types of cortical activities and their reflection in surface potential (recorded by ECoG or EEG). *i*: Depolarization of pyramidal cells at their deeper extremities, which generates a surface-positive potential deflection. *ii*: Depolarization of deep-layer pyramidal cells at their apical dendrites or stellate cells. This type of activity generates a sink in the middle layers and a surface-negative potential deflection. But because of the closed-field arrangement of CSD components, its contribution to surface potential is rather small. *iii*: Depolarization of superficial layer pyramidal cells at their apical dendrites. This is the main contributor to long-lasting surface-negative potentials. This type of activity involves long-distance connections and depends greatly on the general state of cortical excitability. *iv*: Inhibitory activity does not usually cause significant CSD contributions, because of the low amplitudes of membrane currents involved and a general lack of lamina specificity. Adapted with permission from Mitzdorf (Mitzdorf, 1985).

Given that negative SCPs index increased cortical excitability, it should not come as a surprise that during the negative shift of spontaneous SCP fluctuations there are increased multi-unit activity, increased higher-frequency field potentials, and better behavioral performance (see references in (Birbaumer et al., 1990; He and Raichle, 2009; He et al., 2008)). The recently acclaimed phase-coding in the delta frequency range (e.g., (Lakatos et al., 2008)) is likely of the same origin as information carried in the SCP phase. Moreover, the P300 evoked potential, a proposed correlate of conscious neuronal activity (Dehaene et al., 2006), might reflect inhibition of cortical pyramidal neurons and constitutes the flip side of negative SCP shifts (Deecke and Lang, 1988). Since the SCP modulates power of higher-frequency activities, it may be a more fundamental correlate of the fMRI signal than LFP power is, as implicated in a previous study (He et al., 2008).

As mentioned previously, the SCP is one important and substantial contributor to the fMRI signal. In addition to advancing our understanding of the fMRI signal and bridging the neuroimaging and neurophysiology fields, this observation is also of particular interest in the study of consciousness. For example, fMRI experiments and single-unit recordings often show discordant results during manipulations of consciousness; this disagreement has been most dramatic in V1 (Logothetis, 2008; Tononi and Koch, 2008). These puzzling results are at least partially illuminated when we bring the SCP and its underlying physiology into the picture. In what follows we discuss these data and further propose a specific hypothesis on the involvement of the SCP in engendering conscious awareness.

The SCP and consciousness – A neurophysiological hypothesis of consciousness

From a theoretical perspective, information has to be integrated to contribute to conscious awareness, for conscious experience is always a unitary and undivided whole. We suggest that the superficial-layer neuronal activities indexed by the SCP may be an optimal neural substrate to carry such information integration across wide cortical areas because (1) its slow time scale allows synchronization across long distance despite axonal conduction delays (He et al., 2008; von Stein and Sarnthein, 2000); (2) long-range intracortical and corticocortical connections terminate preferentially in superficial layers and thus contribute significantly to the SCP. Furthermore, for each patch of superficial-layer pyramidal neurons (for definition of “patch”, see (Douglas and Martin, 2004)), corresponding deep layer neurons could provide additional information through specialized local processing. These local deep-layer loops might constitute a neural substrate for unconscious processes that can affect and be affected by conscious experience. A rough schematic depicting our hypothesis is shown in Figure 2a.

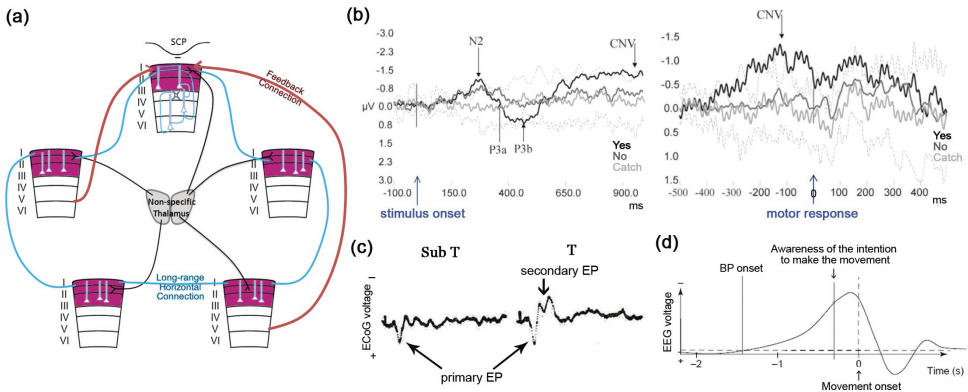


Figure 2. SCP and consciousness. (a) Schematic illustration of our hypothesis. Superficial layers of the cerebral cortex (shown in purple) are the only layers containing extensive long-range horizontal connections (thick blue lines); they are also the main target for nonspecific thalamo-cortical inputs (black lines) as well as long-range inter-areal feedback connections (thick red arrows). We propose that long-lasting synaptic activities in superficial layers, manifesting as SCPs in surface recording or low-frequency current source density (CSD) activity in superficial layers, carry large-scale information integration in the brain and contribute directly to conscious awareness. Neuronal circuits in deep layers (thin blue lines) provide specialized local processing that assist superficial-layer computations and send output to subcortical structures. Two specific predictions made by this hypothesis are provided in Conclusions. (b) Subjects performed a target detection task in which a visual grating stimulus at threshold was briefly presented. Following a variable delay, the subject was prompted by an auditory cue to press one of two buttons to indicate whether they saw the stimulus. A small percentage of catch trials in which no grating was presented were randomly interleaved. EEG potential from the left parietal electrode (P3, using Laplacian derivation, which emphasizes local vertical currents underneath the electrode) was averaged around the onset of grating stimulus (*left panel*), or around the motor response (*right panel*). The evoked potentials for “Yes, I saw”, “No, I did not see”, and catch trials are shown in black, dark grey and light grey respectively. The inter-subject s.d. for catch trials are shown as dotted lines. A negative slow potential builds up between stimulus onset and motor response during “Yes” trials but not catch trials nor the trials during which the stimulus was present but not perceived. Adapted with permission from Pins and ffytche et al. (Pins and ffytche, 2003). (c) Average evoked-potentials (EPs) in response to single stimulus pulses at the skin, recorded from the surface of somatosensory cortex. EPs to 500 stimulus presentations were averaged for each condition. Sub T: subthreshold stimuli, none of the 500 stimuli were felt by the subject. T: threshold stimuli, subject reporting feeling some of the 500 stimuli. Each recording trace is 500 milliseconds long. Primary EP: a transient, surface-positive deflection that occurs ~30 ms after the stimulus, was present in both cases. Secondary EP: a later slower surface-negative component, only occurs when the stimulus was at times felt. Adapted with permission from Libet (2004). (d) The *Bereitschaft potential* (BP) is a negative SCP shift preceding the onset of a voluntary movement. It was shown by Libet (2004) that the onset of the BP also precedes the subject’s subjective awareness of the intention to make the movement by a few hundred milliseconds. Adapted with permission from Haggard (2008).

Interestingly, the cerebellum, generally considered nonessential for consciousness (Tononi and Koch, 2008), is notably weak in its low-frequency activity as compared to the neocortex (Bullock and Basar, 1988). The cerebellar cortex also lacks the “crowning mystery” of the neocortex – layer I, which is one major target for long-range feedback connections and nonspecific thalamic inputs in the cerebrum (Douglas and Martin, 2004; Jones, 1998). From an evolutionary perspective, the superficial layers are endowed with the largest expansion in thickness among cortical layers during mammalian evolution (DeFelipe et al., 2002). Furthermore, the nervous systems of most invertebrates (with the exception of octopus), when compared to the cerebrum of vertebrates, contain much more pronounced fast activity but notably weak slow activity, and in this sense are more similar to the vertebrate cerebellum, brain stem or spinal cord (Bullock and Basar, 1988).

In what follows we review existing empirical data supporting a functional role of the SCP in the emergence of conscious awareness.

Attention

Although attention and consciousness are distinct and dissociable phenomena (Tononi and Koch, 2008), attention clearly affects which information has better access to conscious awareness. The top-down effect of attention in early sensory cortex is largely invisible to spike recordings, but is readily seen in the fMRI signal (Logothetis, 2008). Consistent with a close correspondence between the SCP and the fMRI signal as argued here, top-down influence in V1 can be seen with measurements of the SCP using either optical imaging or field potential recordings (Lakatos et al., 2008; Roland et al., 2006). In the first case, a feedback wave of depolarization was found to traverse the superficial layers from higher-order to lower-order visual areas (Roland et al., 2006). In the second case, top-down attention was found to modulate the phase of delta-frequency activity which further modulated the power of higher frequencies (Lakatos et al., 2008). Importantly, this effect was found only in superficial layers, consistent with the physiology of the SCP and with the laminar preference of feedback connections (Douglas and Martin, 2004).

Perception

Many studies have investigated the neural correlates of conscious perception, however, only a handful presented data including the SCP, which we will focus on here. Pins and ffytche (Pins and Ffytche, 2003) presented visual stimulation