NeuroEng 2019

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12th Australasian Workshop on Computational Neuroscience and Neural Engineering

Bringing together computational neuroscientists and researchers at the interface between neuroscience and engineering

The University of Adelaide
29-30 November, 2019

NeuroEng 2019 is a satellite of ANS 2019 to be held at the Adelaide Convention Centre

ARC Centre of Excellence for Integrative Brain Function

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Australasian Neuroscience Society

Welcome to NeuroEng 2019, The 12th Australasian Workshop on Computational Neuroscience and Neural Engineering

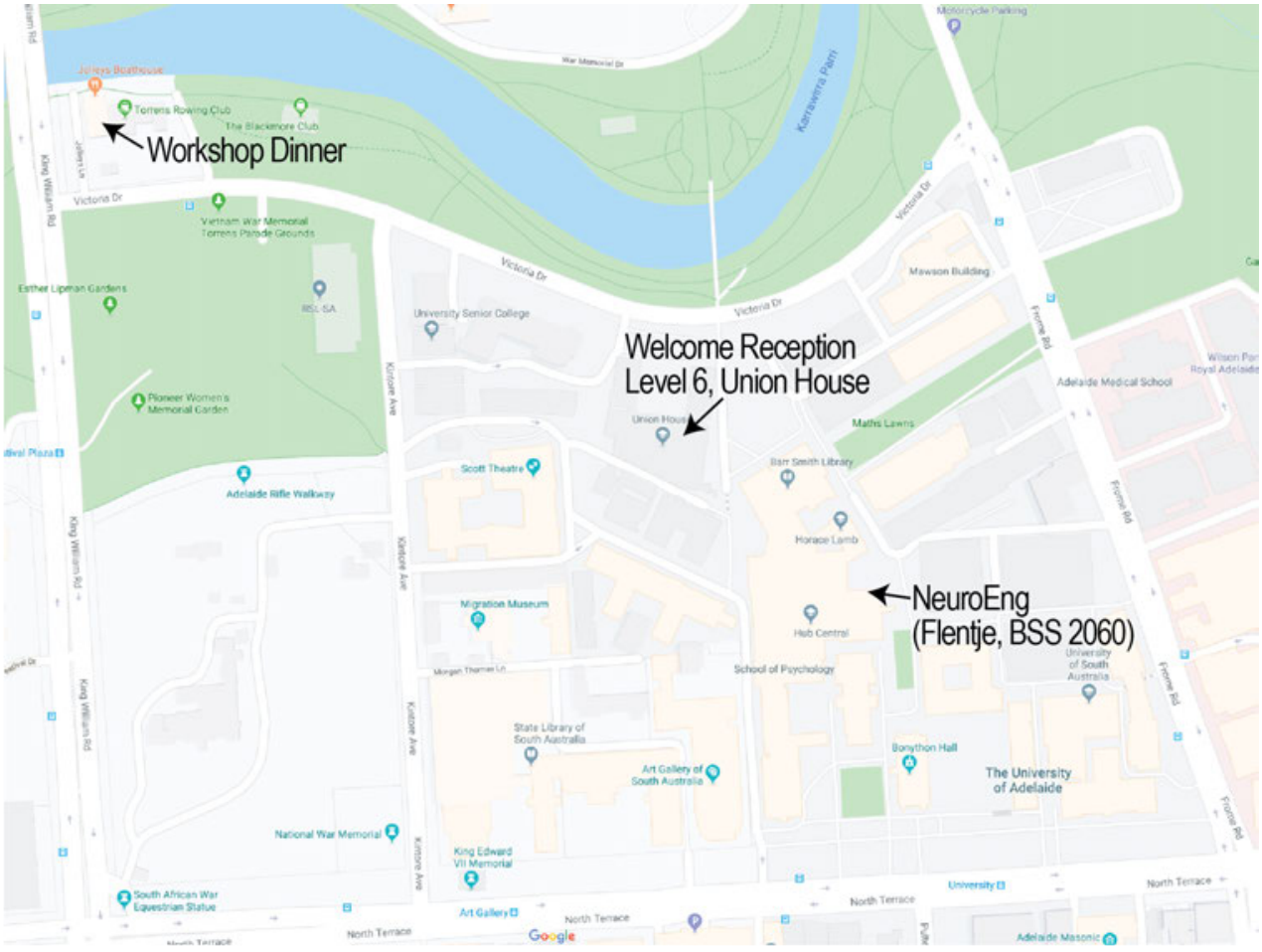
Local Organizing Committee
Steven Wiederman (The University of Adelaide)
Bernard Evans (The University of Adelaide)

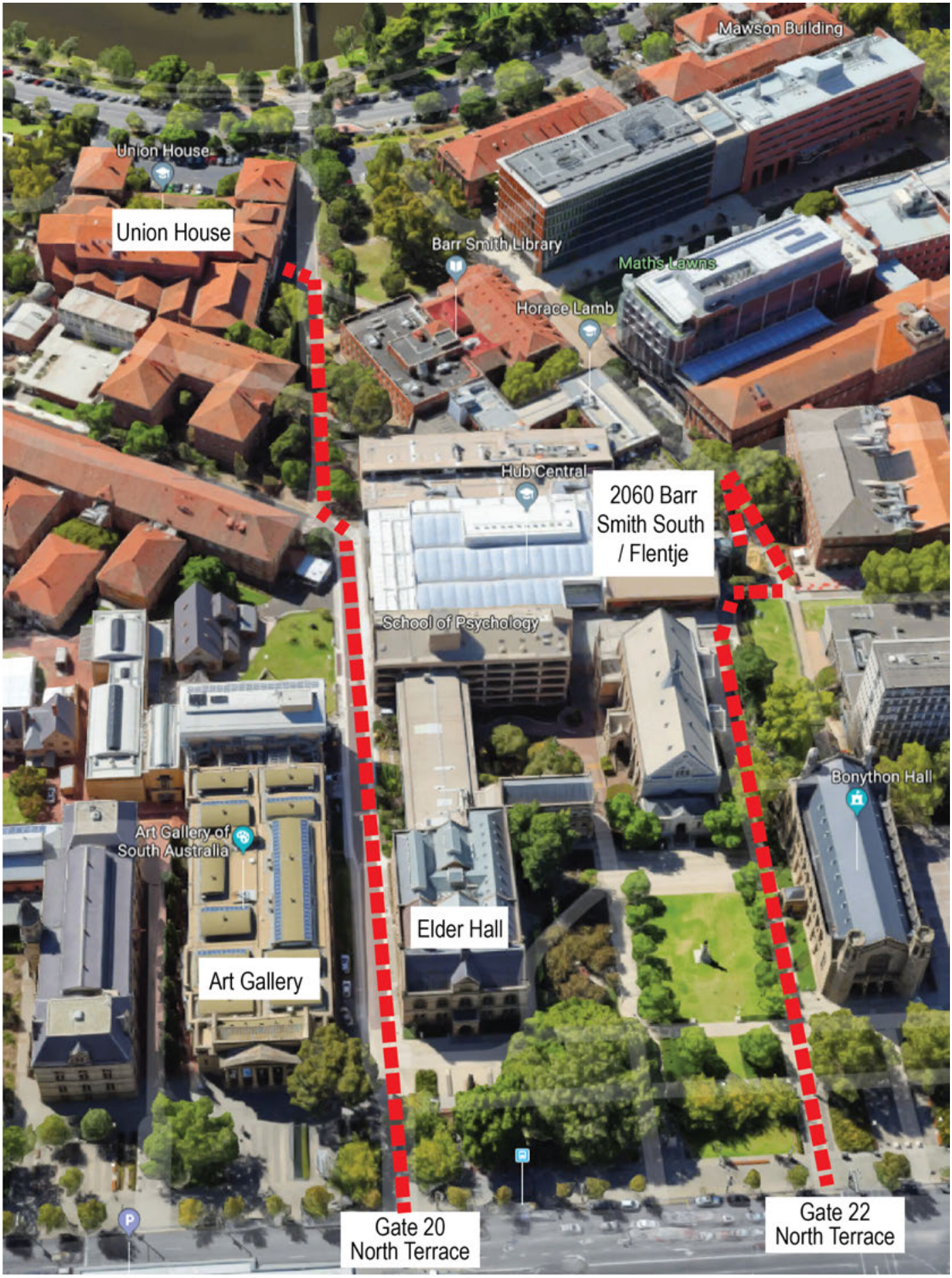
The Venues:

Welcome Reception: 6:30 pm, Thursday 28th November
Rumours, Level 6, Union House

NeuroEng 2019: Friday 29th & Saturday 30th November
Foyer, Level 2, Barr Smith South
Seminars: Flentje Lecture Theatre
Poster Room: 2060 Barr Smith South
North Terrace Campus, The University of Adelaide

Workshop Dinner: 7:00 pm, Friday 29th November,
Jolley's Boathouse Restaurant, 1 Jolleys Lane, Adelaide.

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Maths Lawns
Horace Lamb
Hub Central
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School of Psychology
Bonython Hall
Art Gallery of South Australia
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The Australian Association of Computational Neuroscientists and Neuromorphic Engineers

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Friday Keynote:

Professor Yves De Koninck

Yves De Koninck is professor of Psychiatry & Neuroscience at Laval University, Scientific Director of the CERVO Brain Research Centre and Director of Research of the Quebec Integrated University Health and Social Services Centre. Former President of the Canadian Association for Neuroscience, he holds a Canada Research Chair in Chronic pain and related brain disorders and is a Fellow of the Canadian Academy of Health Sciences and the Royal Society of Canada. He dedicated his career to understanding the mechanisms underlying chronic pain disorders. For this he received the Distinguished Career award from the Canadian Pain Society. He founded the Neurophotonics Centre (*www.neurophotonics.ca*), a unique infrastructure to support the development of novel technologies to probe and manipulate the brain and nervous system. He now leads *Sentinel North* (*www.sentinelnorth.ulaval.ca*) a global initiative to harness the power of light for the benefit of health, environment and sustainable development in the North. For his transdisciplinary efforts at the interface of photonics, computational sciences and neuroscience, he received the Jacques-Rousseau Prize from *Acfas,* the Brockhouse Canada Prize and the Emily Gray Award from the Biophysical Society.

Saturday Keynote:

Professor Barbara Webb

Barbara Webb completed a BSc in Psychology at the University of Sydney then a PhD in Artificial Intelligence at the University of Edinburgh. Her PhD research on building a robot model of cricket sound localization was featured in Scientific American. This established her as a pioneer in the field of biorobotics - using embodied models to evaluation biological hypotheses of behavioural control. She has published influential review articles on this methodology in Behavioural and Brain Sciences, Nature, Trends in Neurosciences and Current Biology. Recently, the focus of her research has moved from basic sensorimotor control towards more complex insect behavioural capabilities, in the areas of associative learning and navigation. She has held lectureships at the University of Nottingham and University of Stirling before returning to a faculty position in the School of Informatics at Edinburgh in 2003. She was appointed to a personal chair as Professor of Biorobotics in 2010.

Friday 29th November

8:30-8:50	**Registration**
8:50-9:00	**Welcome to NeuroEng 2019**
9:00-9:40	**ARC Centre for Nanoscale BioPhotonics Keynote Speaker:** **Professor Yves De Koninck,** Université Laval, Quebec, Canada *How chloride dynamics shape neural computation; challenges in measurements and modeling*
9:40-10:00	**Vincent Daria,** Australian National University *Dendritic spikes in apical oblique dendrites of cortical pyramidal neurons*
10:00-10:20	**Ivan Maksymov**, Swinburne University of Technology *Faraday waves in earthworms: non-invasive tests of the soliton model of nerve impulses*
10:20-10:50	**Morning Tea**
10:50-11:10	**Mark Jenkinson**, Oxford University *Acquisition and analysis of big data for MRI in neuroimaging*
11:10-11:30	**Simon Brown**, University of Canterbury *Avalanches, criticality and correlations in self-organised nanoscale networks*
11:30-11:50	**Demi Gao**, The University of Melbourne *Modeling electrode discrimination in cochlear implants using information theory and machine learning*
11:50-12:10	**Martin Spencer,** The University of Melbourne *Retinal implant vision processing: a global shaping algorithm*
12:10-12:30	**Oliver Cliff**, The University of Sydney *Controlling the increased false positive rate of Granger causality tests in fMRI*
12:30-1:00	**Lunch**
1:00-2:00	**Poster Session (even)**
2:00-2:20	**David Grayden**, The University of Melbourne *Endovascular brain stimulation*
2:20-2:40	**Mandiyam Mahadeeswara**, The University of Queensland *A car racer's way of negotiating sharp turns observed in turning honeybees*
2:40-3:00	**Leonardo Novelli,** The University of Sydney *Relating transfer entropy to network structure and motifs, and implications for brain network inference*
3:00-3:20	**Tara Hamilton**, Macquarie University *Stochastic neuromorphic signal processing*
3:20-3:40	**Brett Schmerl**, University of South Australia *Using deep convolutional neural networks to visualise receptive fields of high level visual cortical neurons*
3:40:4:00	**Afternoon Tea**
4:00-4:20	**André van Schaik**, Western Sydney University *The International Centre for Neuromorphic Systems at Western Sydney University*
4:20-4:40	**Timothy Allison-Walker**, Monash University *Cortical vision prosthesis evoked spiking exhibits phase-dependency*
4:40-5:00	**Saeed Afshar,** Western Sydney University *Seeing through bushes with an event-based camera*
7:00-10:00	**Conference Dinner (Jolley's Boathouse)**

Saturday 30th November

8:30-9:00	**Registration**
9:00-9:40	**ARC Centre for Integrative Brian Function Keynote Speaker:** **Professor Barbara Webb**, University of Edinburgh, Scotland, UK. *The neural basis of insect navigation*
9:40-10:00	**Geoffrey Goodhill,** The University of Queensland *Generative models for extracting latent structure from calcium imaging data*
10:00-10:20	**Michael Ibbotson**, the University of Melbourne *Orientation maps in the primary visual cortex of the Tammar wallaby*
10:20-10:50	**Morning Tea**
10:50-11:10	**Guozhang Chen**, The University of Sydney *Dynamical circuit mechanisms of attentional sampling*
11:10-11:30	**Alan Freeman**, The University of Sydney *A model of the origin of motion sensitivity in primary visual cortex*
11:30-11:50	**Tatiana Kameneva,** Swinburne University of Technology *Acute effects of resonance frequency breathing on muscle sympathetic nervous activity*
11:50-12:10	**Agus Hartoyo,** Swinburne University of Technology *Inference of the parsimonious mechanism underlying the emergence of alpha blocking*
12:10-12:30	**Massoud Yajadda**, The University of Sydney *Neural field theory of the formation of ocular dominance columns in the primary visual cortex*
12:30-1:00	**Lunch**
1:00-2:00	**Poster Session (odd)**
2:00-2:20	**Alon Loeffler**, The University of Sydney *Topological properties of neuromorphic nanowire networks*
2:20-2:40	**Svetlana Postnova**, The University of Sydney *Model-based prediction of sleep, circadian phase and alertness in real-world shiftwork*
2:40-3:00	**Jasmine Walter,** Monash University *Unsupervised analysis of sleep data detects periods of lucid dreaming*
3:00-3:20	**Hamish Meffin**, The University of Melbourne *Nonlinear receptive field estimation reveals novel forms of feature invariance in primary visual cortex*
3:20-3:40	**Ben Fulcher**, The University of Sydney *Spatial embedding of gene transcriptional gradients through brain development*
3:40:4:00	**Afternoon Tea**
4:00-5:00	**Panel Discussion: The Interface Between Wet and Dry Neuroscience** *Michael Ibbotson, Geoff Goodhill, Tony Burkitt, Mark Hutchinson*
5:00-6:00	***Wrap up social mixer – NeuroEng, CIBF and CNBP***

DENDRITIC SPIKES IN APICAL OBLIQUE DENDRITES OF CORTICAL PYRAMIDAL NEURONS

Michael Lawrence Castanares[1] and Vincent Daria[1,2]
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One of the fundamental challenges to crack the neurons' computing power is the understand the functional role of its dendrites. Aside from the fact that dendrites receive synaptic inputs, they can also initiate local regenerative events called dendritic spikes, which can either be driven via a surge synaptic inputs or a train of back-propagating action potentials (bAPs)[1-3]. Dendritic spikes are long lasting depolarisations (~20-50ms) that can boost the efficacy of distal synapses to drive neurons to fire, or can interact with coincident synapses and consequently influence synaptic plasticity. *In vitro* and *in vivo* studies have shown that cortical pyramidal neurons are able to recruit certain types of dendritic spikes in different regions such as: the main apical trunk[1,2], apical tuft dendrites[4,5], and basal dendrites[3]. Here, we investigate the generation and properties of a novel dendritic spike evoked in apical oblique dendrites of Layer 5 pyramidal neurons (L5PNs). Using a multi-compartment model of a L5PN[6], we show that a train of bAPs with critical frequency f_c = 35Hz elicits a dendritic spike in select oblique branches. By numerically blocking voltage-gated ion channels, we characterise the spike as a fast sodium spike followed by a broad (~20 ms) depolarization due to activation of voltage-gated calcium channels. To verify experimentally, we performed *in vitro* two-photon (2P) calcium imaging on cortical L5PNs using our 2P multi-site holographic microscope[7]. Stimulating a 2-bAP train with $f_c = 56 \pm 4$Hz sets up a non-linear increase in the amplitude of the calcium transients in select oblique dendrites of L5PNs. In summary, we report a new type of dendritic spike occurring in oblique branches of cortical L5PNs. Compared to other types of dendritic spikes, the oblique branch spike is evoked using a train of bAPs with lower frequencies. The unique conditions required for bAP bursts to recruit dendritic spikes in specific regions of L5PNs can provide novel insights into branch-specific plasticity of coincident synapses and can therefore advance our understanding of the different functional roles of dendrites in learning and memory.

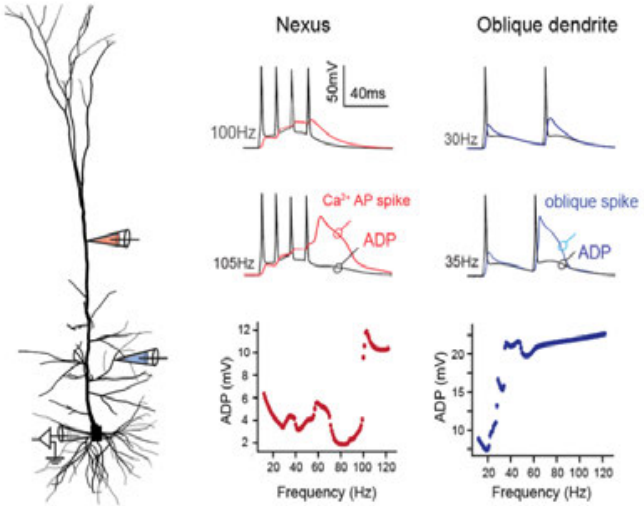

Figure 1. Critical frequency responses at different dendritic regions. Previous works showed a critical frequency response at the basal and nexus of the apical tuft dendrites. The critical frequency protocol showed that a f_{c4} ~100 Hz train of 4-bAPs recruits a dendritic calcium spikes at the **nexus** of the apical tuft[2]. Our work shows that oblique branch spikes are evoked at lower frequencies of train of 2-bAPs: f_{c2} ~35 Hz (from model) and *fc2* ~56Hz (from 2P calcium imaging).

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FARADAY WAVES IN EARTHWORMS: NON-INVASIVE TESTS OF THE SOLITON MODEL OF NERVE IMPULSES

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We aim to conduct rigorous numerical simulations and proof-of-concept experiments to verify the hypothesis that nerve signals can be sound-voltage impulses (solitons) that propagate with little change of form [1-3]. Solitons exist when dispersion (spreading of the impulse) and nonlinearity in the medium are balanced. (Nonlinear effects are those where twice the input signal intensity does not result in twice the output intensity.) Solitons are well-known in the context of water waves in canals and laser light in optical fibres.

We will verify the soliton hypothesis by switching the nonlinearity of the nerve on and off. Modern methods of nerve stimulation, including those using focused high-frequency ultrasound [4], cannot be used to achieve this goal because they are invasive and/or they alter the balance between dispersion and nonlinearity in an uncontrollable way. Therefore, we will develop a non-invasive method of nerve stimulation with low-frequency mechanical vibrations and Faraday waves (ripples on the surface of liquids) that are closely associated with soliton-like phenomena [5].

We will use earthworms because the glial cell wrapping of their giant axons resembles the myelin sheath of vertebrate nerve fibres. Therefore, earthworms serve as an excellent platform for tests of the soliton hypothesis. Earthworms are also cheap and using them does not require ethics approval.

Earthworms have a hydrostatic (supported by fluid pressure) skeleton with a flexible skin and a water-filled body cavity (coelom). The physical principles of hydrostatics also determine the behaviour of drops of water on a glass. When a liquid drop vibrates in the vertical direction with frequency f, nonlinear standing Faraday waves appear because the hydrostatic surface of the drop becomes unstable. The frequency of such waves equals $f/2$ and their nonlinearity can induce solitons. The same effect should be observable in earthworms.

Nerve impulses are observed at acoustic frequencies of up to 300 Hz. In contrast to the recent attempts to control nerve impulses with high-frequency ultrasound (~10,000 times the frequency of nerve impulses) [4], we will vertically vibrate earthworms at low frequencies (20...300 Hz) to excite soliton-like waves of high amplitude. We will controllably create the condition of constructive interference between these waves and the natural nerve impulse (the waves add together) or destructive interference (the waves cancel each other; negative solitons are allowed in the soliton model). This will open up avenues for unambiguous non-invasive tests of the soliton model.

We will build a more precise version of the laser vibrometry setup developed and used by us to investigate Faraday waves in liquid drops [6]. To calibrate the setup, we will employ a simple to use commercial device [7] capable of exciting and measuring nerve impulses with voltage pulses sent through needle electrodes, which do not damage the body of the earthworm and allow to return it to the soil after the experiment.

Apart from the main proof-of-principle experiment, we will also verify another closely related hypothesis. In our experiments, worms will be immobilised by briefly submerging them into a weak alcohol solution. This will also allow us to test whether the interference between the Faraday waves and nerve impulses changes when the worm is given more anaesthesia. There should be an observable change if the soliton model is correct.

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AVALANCHES, CRITICALITY AND CORRELATIONS IN SELF-ORGANISED NANOSCALE NETWORKS

Joshua Brian Mallinson[1], Shota Shirai[1], Susant K. Acharya[1], Saurabh K. Bose[1], Matthew D. Pike[2], Edoardo Galli[1], Matthew D. Arnold[3], and Simon A. Brown[1]

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Neuronal avalanches are one of the key characteristic features of signal propagation in the brain[1]. These avalanches originate from the complexity of the network of neurons and synapses, which are widely believed to form a self-organised critical system. Criticality is hypothesised to be intimately linked to the brain's computational power[2,3] but efforts to achieve neuromorphic computation have so far focused on highly organised architectures, such as integrated circuits[4] and regular arrays of memristor[5]. To date, little attention has been given to developing complex network architectures that exhibit criticality and thereby maximise[6] computational performance. We show here, using methods developed by the neuroscience community[7], that electrical signals from self-organised percolating networks of nanoparticles[8] exhibit brain-like correlations and criticality.[9] Specifically, the sizes and durations of avalanches of switching events are power-law distributed, and the power-law exponents satisfy rigorous criteria for criticality. Additionally we show that both the networks and their dynamics are scale-free. These networks provide a low-cost platform for computational approaches that rely on spatiotemporal correlations, such as reservoir computing, and are a significant step towards creating neuromorphic device architectures.

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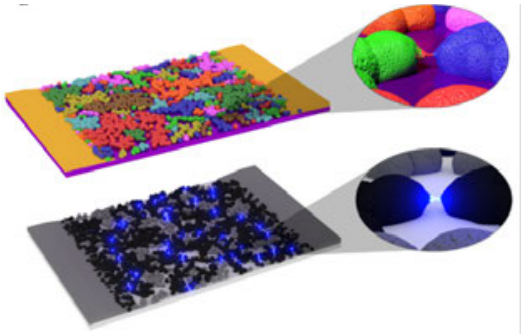

The percolating network of nanoparticles in a simple two-terminal contact geometry. The different colours represent groups of particles that are in contact with one another. The zoomed region shows a schematic of the growth of an atomic filament within a tunnel gap (a switching event, that can be seen as synapse-like) when a voltage is applied. Bottom: The same network schematic presented so as to show the conducting pathways (black) which result from atomic filament formation within the gaps between groups. When the applied potential causes one tunnel gap between groups to be bridged by a conducting filament, the electric field across other tunnel gaps is intensified, leading to avalanches of switching events.

MODELING ELECTRODE DISCRIMINATION IN COCHLEAR IMPLANTS USING INFORMATION THEORY AND MACHINE LEARNING

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Despite the success of cochlear implants (CIs) over more than three decades, wide inter-subject variability in speech perception is reported [1]. The key factors that cause variability between individuals are unclear. We previously developed an information theoretic modelling framework that enables estimation of the optimal number of electrodes and quantification of electrode discrimination ability [2, 3]. However, the optimal number of electrodes was estimated based only on statistical correlations between channel outputs and inputs, and the model did not quantitatively model psychophysical measurements and study inter-subject variability.

Here, we unified information theoretic and machine learning techniques to investigate the key factors that may limit the performance of CIs. The framework used a neural network classifier to predict which electrode was stimulated for a given simulated activation pattern of the auditory nerve, and mutual information was then estimated between the actual stimulated electrode and the predicted one.

Using the framework, electrode discrimination was quantified with a range of parameter choices, as shown in Fig. 1. The columns from left to right show how the distance between electrodes and auditory nerve fibres, r, the number of surviving fibres, N, the maximum current level (modelled as the percentage of surviving fibres N that generate action potentials for a given stimulated electrode), and the attenuation in electrode current, A, affect the model performance, respectively. The parameters were chosen to reflect the key factors that are believed to limit the performance of CIs. The model shows sensitivity to parameter choices, where smaller r, larger N and higher attenuation in current lead to higher mutual information and improved classification.

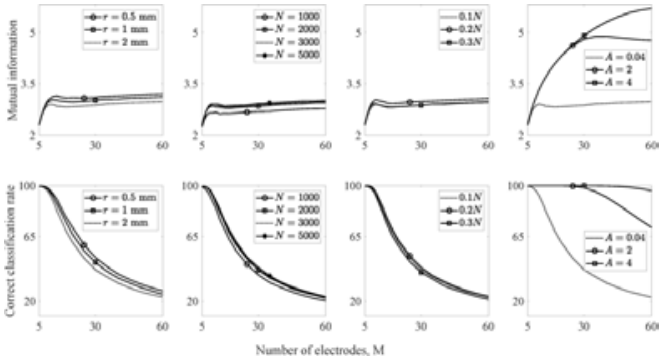

Figure 1. Model performance with a range of parameter choices.

This approach provides a flexible framework that may be used to investigate the key factors that limit the performance of cochlear implants. We aim to investigate its application to personalised configurations of CIs.

This work is supported by a McKenzie Fellowship, The University of Melbourne.

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RETINAL IMPLANT VISION PROCESSING: A GLOBAL SHAPING ALGORITHM

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Retinal implants use an array of electrodes to stimulate the neural tissue of the retina and restore some visual perception. Each electrode induces a local visual percept referred to as a phosphene. In the presence of large overlapping phosphenes the conventional stimulation strategy leads to blurring of the perceived visual scene [1].

To mitigate this effects, our proposed global activity shaping strategy uses a push-pull effect to manipulate the overall pattern of electrical current [2]. The approach uses a forward model for the calculation of the set of neural activations in the retina, $\tilde{r}$, given a set of electrode amplitudes, $\tilde{s}$. Under reasonable assumptions this forward model can be assumed to be linear,

$$\tilde{r} = \mathbf{W}\tilde{s}, \tag{1}$$

where the columns of the matrix $\mathbf{W}$ contain the phosphenes that result from the activation of each individual electrode. Given a target set of neural activations, $\tilde{r}^*$, the electrode amplitudes required to induce this pattern can be calculated using the inverse model:

$$\tilde{s} = \mathbf{W}^+\tilde{r}^*, \tag{2}$$

where $\mathbf{W}^+$ is the pseudoinverse of $\mathbf{W}$ calculated using singular value decomposition. The predicted results for different electrode densities is shown in figure 1. As the number of electrodes in the region is increased from 25 to 529, the phosphene size is assumed to remain constant. It can be seen that the inverse model led to lower errors than the conventional model. This result was confirmed across 32 natural images.

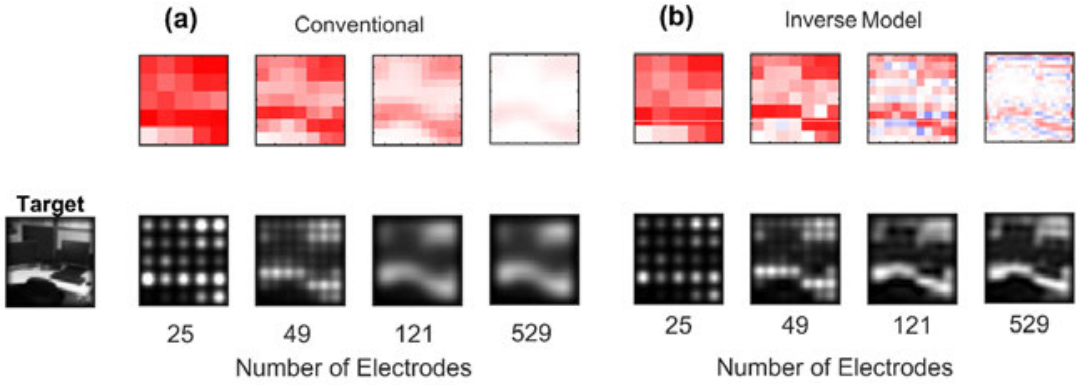

Figure 1: The electrode patterns and retinal activation patterns for (a) the conventional strategy and (b) the inverse model.

The final visual stimulus depends on the selection of eigenvalues used when calculating $\mathbf{W}^+$. It might be expected that a high number of eigenvalues should be used, because this would create the most accurate pseudoinverse, and therefore the optimum electrode pattern. However, in practice this resulted in unrealistically high push-pull electrode amplitudes that indicate overfitting and susceptibility to noise. A model including noise showed that a lower number of eigenvalues could be chosen to limit these effects while still providing lower error than the conventional strategy.

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[2] Spencer M.J, Kameneva T, Grayden D.B, Meffin H, and Burkitt A.N. (2019) "Global activity shaping strategies for a retinal implant." *Journal of Neural Engineering* 16, no. 2

CONTROLLING THE INCREASED FALSE POSITIVE RATE OF GRANGER CAUSALITY TESTS IN FMRI

Oliver M. Cliff[1#], Leonardo Novelli[1], Ben D. Fulcher[2], James M. Shine[3], and Joseph T. Lizier[1]
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The ability to quantify information processing in neural circuits is fundamental to various areas of clinical and theoretical neuroscience. This often involves studying the relationship between different brain regions via connectivity measures such as Granger causality and transfer entropy. These approaches capture how much the signal from one region covaries with another, after taking into account the past of each signal. As such, they are often used for brain mapping where multivariate time series data are obtained through techniques such as functional magnetic resonance imaging (fMRI). However, Bartlett's well-known formula stipulates that sample correlations are overestimated for any two datasets that exhibit a dependence on the past (referred to as autocorrelation). This issue becomes worse as autocorrelation increases and consequently inflates the false positive rate when using standard significance tests. As it is currently presented in literature, Granger causality does not correctly account for this inherent bias and is thus statistically unsound for a finite sample size. An application that is particularly affected is fMRI research, which translates blood oxygen level dependent data into a slowly varying (and thus highly autocorrelated) multivariate time series that traces the haemodynamic response of different regions of the brain. Moreover, digital filtering is commonly used as a preprocessing step to reduce line noise and other artefacts in neuroimaging data; however, this induces an (either finite or infinite) impulse response that can increase autocorrelation in an otherwise serially uncorrelated signal. In this study, we use signals obtained from unconnected regions of multiple subjects in the Human Connectome Project to show that the connections inferred by Granger causality can yield type I errors of up to four times the nominal value of 5\%. These errors are particularly pronounced in less myelinated regions such as the frontoparietal and default mode networks. We then provide a simple fix to the typical procedure that removes the autocorrelation from a signal in order to correctly rescale these measures before significance testing. This is achieved by iteratively performing least squares and testing the residuals for covariance between processes, rather than the signals themselves. Using this new procedure, we can ensure that the false positive rate remains at the nominal value and the discriminatory power of the procedure is not affected.

A CAR RACER'S WAY OF NEGOTIATING SHARP TURNS OBSERVED IN TURNING HONEYBEES

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We have recently found that bees flying in a semi-outdoor arena keep their centripetal acceleration (CA) nearly constant when executing turns[1]. This strategy might assist them in performing coordinated turns, without deviating from the intended flight trajectory. Do bees always keep their CA constant while executing turns in different environments? To examine this question, we conducted an experiment in which bees were trained to fly through a tunnel comprising two straight sections, connected by a curved section. The flight trajectories of 21 different bees were analysed to investigate their turning behaviour while flying through the curved part of the tunnel. Interestingly, the bees flying in the curved section of the tunnel exhibited a different turning behaviour from that displayed by bees flying in a cloud. For the bees flying in the tunnel, there was an absence of a linear relationship between speed^2 and the radius of curvature, implying that the bees did not hold their CA constant when flying in the curved part of the tunnel. The second part of our study, described below, investigated how the bees orchestrated their turning flights in the tunnel to overcome the centrifugal force that they experienced.

In general, a flying insect will make a coordinated turn if it generates a centripetal force to balance the centrifugal force that it experiences during the turn. The centripetal force is generated by rolling about the longitudinal axis, to convert part of the lift force into a centripetal force. This can be achieved in one of two ways: (i) If the insect rolls without changing the total dorsally-directed force that it generates, the roll can counter the centrifugal force, but will not compensate for the attendant loss of lift. If the insect follows this strategy, it will lose altitude during the turn; (ii) If the insect increases the dorsally-directed force that it generates during the turn to compensate for the loss of lift, it can counter the centrifugal force without losing altitude. We mathematically modelled these predictions to investigate the nature of the turning behaviour of bees flying in the curved tunnel. The modelling revealed that the turning bees adopt strategy (i) That is, they compensate for the centrifugal force by rolling into the turn, but do not compensate for the accompanying loss of lift.

Analysis of the turning behaviour also revealed that the bees often pointed into the turn. This 'side-slipping' or 'skid-based' turning strategy directs a certain component of the bee's forward thrust in the centripetal direction, thus increasing the CA and permitting a tighter turn, similar, in some respects, to the way in which a 'Supercar' race driver negotiates a sharp turn.

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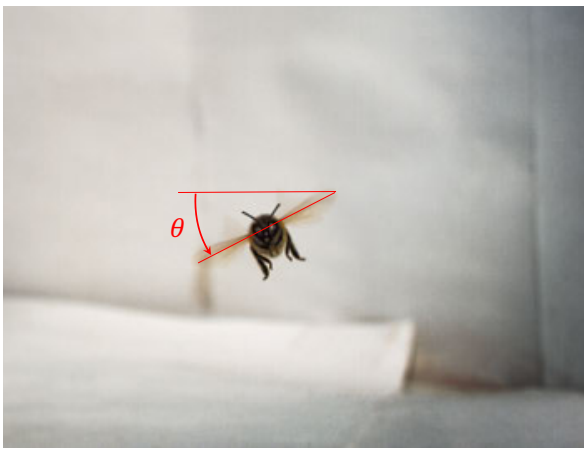

Head-on view of a bee making a turn in the tunnel. The roll angle (θ) of the bee was measured by measuring the orientation of the line connecting the two wingtips with respect to the horizontal axis.

RELATING TRANSFER ENTROPY TO NETWORK STRUCTURE AND MOTIFS, AND IMPLICATIONS FOR BRAIN NETWORK INFERENCE

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Transfer entropy is an established method for the analysis of directed relationships in neuroimaging data. In its original formulation, transfer entropy is a bivariate measure, i.e., a measure between a pair of elements or nodes.[1] However, when two nodes are embedded in a network, the strength of their direct coupling is not sufficient to fully characterize the transfer entropy between them. This is because transfer entropy results from network effects due to interactions between all the nodes.

In this theoretical work, we study the bivariate transfer entropy as a function of network structure, when the link weights are known. In particular, we use a discrete-time linear Gaussian model to investigate the contribution of small motifs, i.e., small subnetwork configurations comprising two to four nodes. Although the linear model is simplistic, it is widely used and has the advantage of being analytically tractable. Moreover, using this model means that our results extend to Granger causality, which is equivalent to transfer entropy for Gaussian variables.

We show analytically that the dependence of transfer entropy on the direct link weight is only a first approximation, valid for weak coupling. More generally, it is affected both by the indegree of the source and the target nodes, which suggests an asymmetry of information transfer between hubs and peripheral nodes. In the case of positive link weights, the transfer entropy increases with the indegree of the source and decreases with the indegree of the target. Importantly, these results also have implications for directed functional network inference from time series, which is one of the main applications of transfer entropy in neuroscience. The asymmetry of information transfer suggests that links from hubs to peripheral nodes would generally be easier to infer than links between hubs, as well as links from peripheral nodes to hubs. This could bias the estimation of network properties such as the degree distribution and the rich-club coefficient.

In addition to the dependence on the indegree, the transfer entropy is directly proportional to the weighted motifs involving common parents or multiple walks from the source to the target (see Figure 1). These motifs are more abundant in clustered or modular networks than in random networks, suggesting a higher transfer in the former case. Further, if the network has only positive edge weights, we have a positive correlation to the number of such motifs. This applies in the mammalian cortex (on average, since the majority of connections are thought to be excitatory) – implying that directed functional network inference with transfer entropy is better able to infer links within brain modules (where such motifs enhance transfer entropy values) in comparison to links across modules.

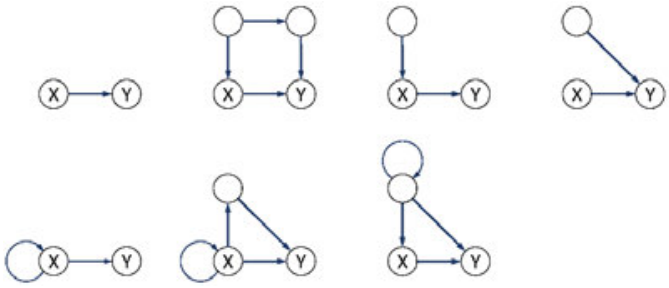

Figure 1. Network motifs involved in the bivariate transfer entropy from node X to node Y.

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STOCHASTIC NEUROMORPHIC SIGNAL PROCESSING

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In this paper we present a noise-robust, low-power signal processing technique that is based on population coding in neural systems [1]. The technique takes advantage of heterogeneous properties of the physical substrate (i.e. silicon or other hardware materials) and makes use of the system noise, in order to sample the input signal. This technique leverages the ideas of stochastic electronics [2] and combines it with the statistical signal processing known to spiking neural networks (SNN). We have shown that this kind of signal processing can provide more information about intermediate signal levels without requiring extra bits (Fig. 1) and we discuss its role in edge, internet-of-things (IoT) applications including audio processing and biomedical applications.

Neuromorphic systems have become popular in recent years for their claimed inspiration from biology, robustness to noise and inherent low-power. The literature, however, often does not support these claims due to issues with interfacing spike-based (and often event-based) systems with conventional computing. Our approach here, overcomes many of these issues and promises to improve the utility of neuromorphic approaches in the future.

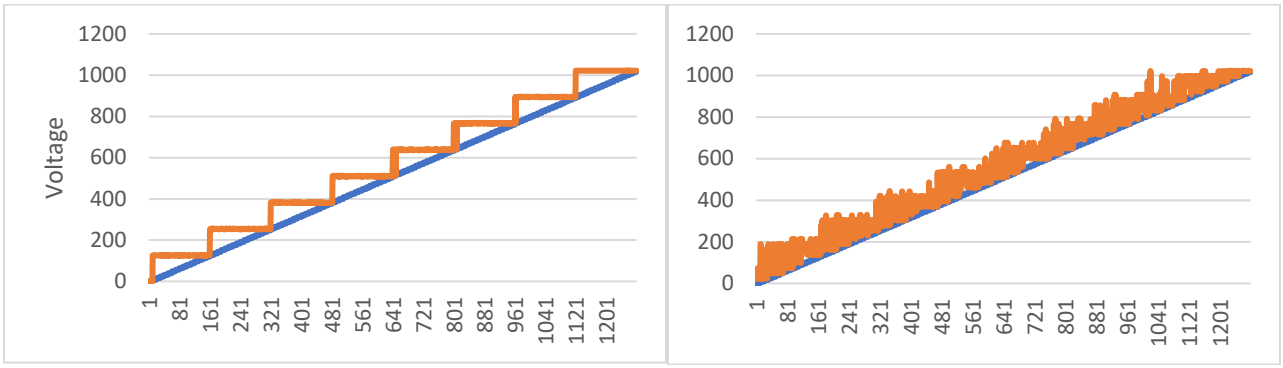

Fig. 1: (left) Output of a 3-bit analog-to-digital converter (ADC) – orange, input signal – blue. (Right) Output of a 3-bit equivalent analog-to-stochastic converter (ASC) – orange, input signal – blue. The noise in right gives more variance but greater bit-precision – up to 6 bits.

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USING DEEP CONVOLUTIONAL NEURAL NETWORKS TO VISUALISE RECEPTIVE FIELDS OF HIGH LEVEL VISUAL CORTICAL NEURONS.

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Understanding the image features that are encoded by neurons throughout the hierarchy of visual cortical areas, particularly in areas higher in the hierarchy that have more complex response properties than in V1, is a challenging yet fundamental goal in visual neuroscience that is often achieved by visualising their pattern of responses [1]. Visualising image features responsible for driving activity of individual units in a hierarchical system used for visual processing for the purposes of understanding the system's functioning and information representation is also encountered in the study of deep convolutional neural networks.

In this study we train deep convolutional neural networks on spiking data recorded from individual neurons in a mid-tier visual area (the dorsomedial area, DM) of the anaesthetised marmoset monkey whilst the animal is presented with changing patterns of spatiotemporally white noise [2]. We show that convolutional neural networks are capable of learning statistically significant input-output relationships of these neurons and are thus able to perform classification of the spiking behaviour of the neuron given the stimuli. Furthermore, we applied deconvolutional techniques [3] used to visualise image features encoded by the convolutional, thus allowing visualisation of input image features that are significant to determining spiking behaviour, by proxy, of the neuron. A comparison between the features recovered using this technique and those recovered by traditional methods of analysis is presented.

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CORTICAL VISION PROSTHESIS EVOKED SPIKING EXHIBITS PHASE-DEPENDENCY

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Cortical vision prostheses offer the potential to restore vision, however, large amounts of charge delivered to the cortex can cause unwanted effects such as seizures [1]. The local field potential (LFP) – a low frequency brain signal – has been implicated in neural excitability via phase-coding [2], wherein the phase of the low-frequency oscillations is intermittently coherent with spiking activity. Electrical stimulation timed to the LFP phase might constitute a control signal to reduce charge requirements, decrease the chance of seizure, and improve cortical visual prosthesis efficacy.

Cells were recorded and electrically stimulated simultaneously in V1 of 6 Wistar rats using a 32-channel probe (NeuroNexus), and an Intan Stimulation/Recording system (Intan). Both spiking activity and the local field potential were recorded in response to stimulation at varying current levels. The phase of the LFP at the time of stimulation was calculated for each trial, and responses were grouped into six phase-bins of equal width (60deg) such that the mean phase vector [3] across all trials was centered in the first phase bin. Stimulation-Recording pairs were defined as all unique combinations of stimulation and recording channels that a) respond significantly, and above 50 spikes/second to electrical stimulation, and b) demonstrate a significant difference in response to stimulation delivered at different phases.

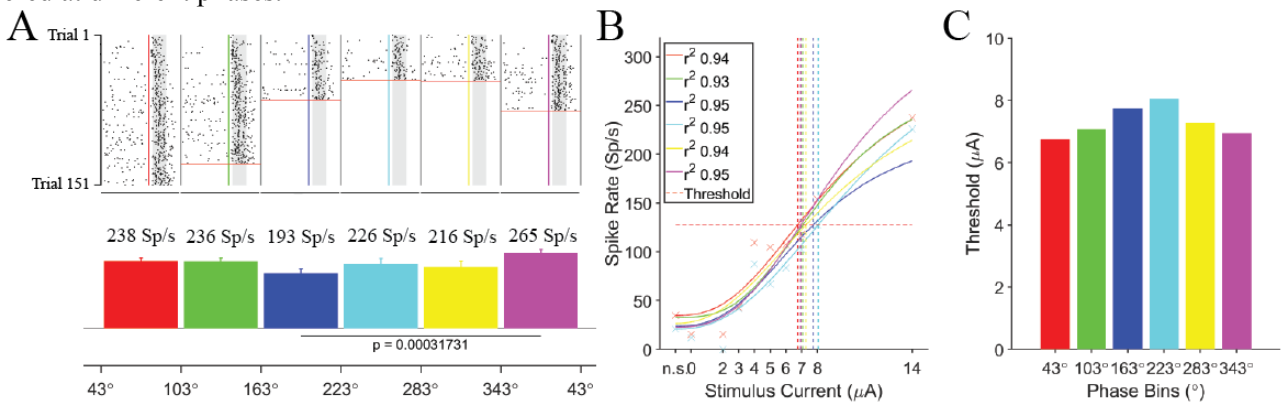

Figure 1: A) Raster and mean spike rates, single stimulation-recording pair. Phase was analysed at 6 ± 2 Hz. Centre phase (73°) calculated from the mean phase vector. Firing rates depended on phase - rank-sum test between the largest firing rate and the phase-bin 180° opposed, $p < 0.001$. B) Response curves for each of the six phase-bins in A. r^2 values indicated in legend. C) Response threshold is found to be the current at which the neuron reaches 50% the global maximum firing rate. Phase-bins closest to the mean phase vector [3] (73°) had a lower threshold (~1 μA).

The data presented shows that there is a relationship between the timing of stimulation to the LFP in V1 and the threshold neural response, in this example representing a difference of ~1 μA. Exploitation of this relationship has the potential to reduce charge requirements, thereby improving efficacy and reducing risk of seizure. Further work to characterize this relationship is ongoing.

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SEEING THROUGH BUSHES WITH AN EVENT-BASED CAMERA

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Dynamic Vision Sensors or silicon retinas are neuromorphic event-based sensors which differ from conventional cameras by generating events in response to changes in illumination at each pixel, rather than through synchronous frames. The generated events streams enable new visual processing techniques such as event-based image segregation of complex natural scenery. In this work, we present such an event-based method where motion information from a robotic sensor platform is used to see through an obscuring garden fence. Using an unsupervised feature extraction network and an event-based motion estimation algorithm the observed scenery is segregated into competing feature-velocity surfaces. A simple event-based competition rule directs each event to one of the many feature-velocity surfaces. The resulting segregated surfaces accurately image the obscured scene in an efficient real-time manner.

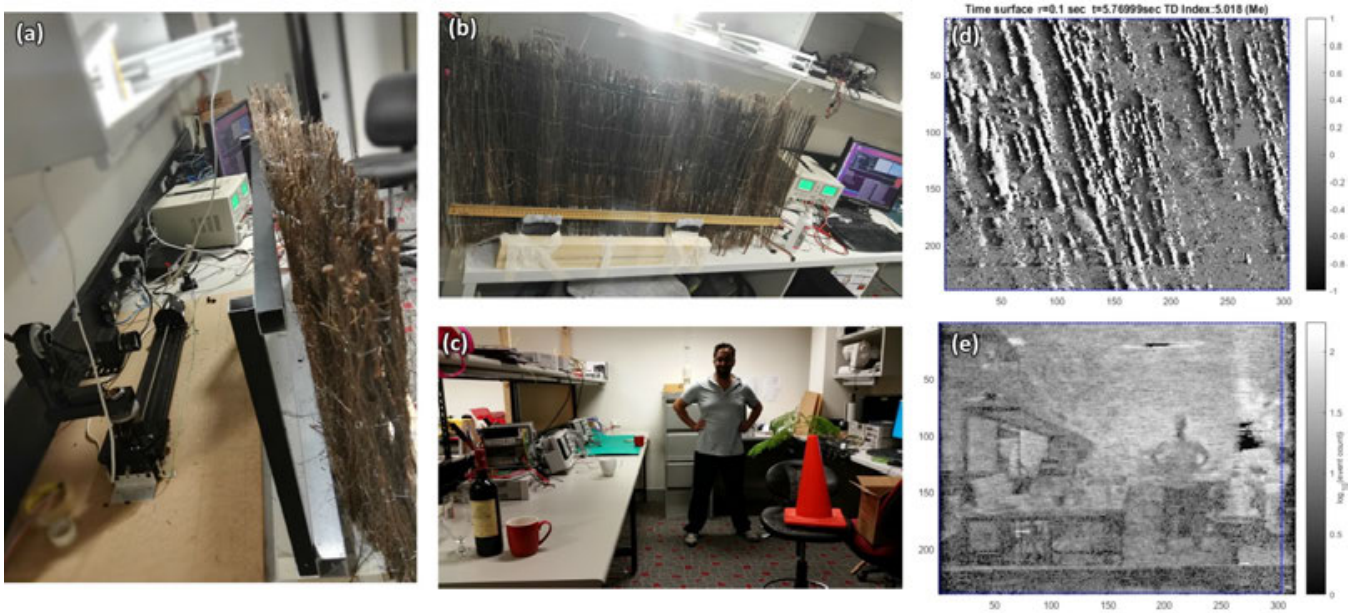

Figure 1. Event-based dynamic scene segregation. Panels (a) and (b) show the experimental set-up where the event-based sensor automatically manoeuvres behind a section of commercial garden screening. (c) Shows the unobscured scene behind the screen. (d) Shows the raw event-based data as the camera moves behind the screen. The raw data stream is dominated by events generated from the irregular structure of the natural screen. (e) Using event-based image segregation, the obscured scene can be resolved in real-time.

GENERATIVE MODELS FOR EXTRACTING LATENT STRUCTURE FROM CALCIUM IMAGING DATA

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The brain constructs representations of incoming sensory information and integrates these with internal factors that govern an animal's behavioural or cognitive state. However, such internal factors are usually not observable, and give rise to neural activity that cannot be directly related to sensory stimuli (referred to as spontaneous activity). Here we develop statistical models for calcium imaging data that simultaneously account for activity evoked by sensory stimuli as well as spontaneous activity governed by these latent internal factors. We first develop a linear approach that allows latent sources of spontaneous activity to be identified as the maximum a posteriori estimate under the model and easily decoupled from evoked activity. Interestingly, application of the model to the developing visual system of the larval zebrafish identified populations of neurons that only participated in spontaneous events, with no variance attributable to sensory stimuli [1]. We then develop an approach that combines latent Gaussian processes that govern fluctuations in excitability, spike-and-slab non-negative sparse priors that more tightly control latent factor activity, and nonlinear interactions between evoked and spontaneous activity. We learn an approximate posterior over the latent variables using the stochastic gradient variational Bayes estimator which, due to the spike-and-slab component of the model, requires reparameterised gradients with Concrete relaxations of discrete latent variables. Together, our modelling allows for the decomposition of calcium imaging data into its evoked and spontaneous components, and the extraction of smooth and interpretable fluctuations in excitation.

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ORIENTATION MAPS IN THE PRIMARY VISUAL CORTEX OF THE TAMMAR WALLABY

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Orientation selectivity (OS) is a prominent feature of neurons in the mammalian primary visual cortex, but the spatial organization of these neurons varies across species. In carnivores and primates, orientation-selective neurons are organized into structured orientation columns, which are vertical arrays of neurons with the same orientation preference. These columns are organized into two-dimensional orientation maps in which the different orientations are arranged radially around singular, pinwheel centers. However, rodents and lagomorphs - despite having robust orientation selectivity in individual neurons - do not have orientation columns, but instead the neurons are randomly distributed throughout the cortex, in what is termed a salt-and-pepper organization. We do not know why some mammals have structured pinwheel maps while others have salt-and-pepper maps. We investigated whether the development of orientation maps is influenced by a genetic factor related to phylogeny. The entire mammalian line might have originated with the genetic capacity to develop orientation columns, but perhaps rodents and lagomorphs lost this organization due to a lack of environmental or behavioral drivers. We studied a highly visual marsupial, the Tammar wallaby (*Macropus Eugenii*), which represents a phylogenetically distinct branch of mammals for which the orientation map structure is unknown. If orientation columns are the mammalian norm, we should identify orientation columns in marsupial cortex. We used intrinsic optical imaging and multi-channel electrophysiology methods to examine the functional organization of the wallaby cortex. We found robust OS in a high proportion of cells in the primary visual cortex. Moreover, we found clear orientation columns similar to those found in primates and carnivores but with bias towards vertical and horizontal preferences, suggesting lifestyle-driven variations. The findings suggest that orientation columns are the norm and it might be that the rodents and lagomorphs are unusual in terms of mammalian cortical architecture.

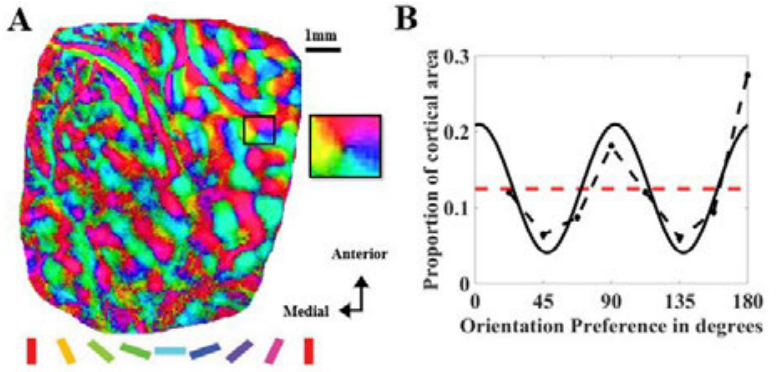

Figure 1. Orientation Preference map. (A) Orientation map showing the orientation preference for every region of the imaged wallaby visual cortex. The angle is color-coded according to the scheme at the bottom of the figure. We zoom in on a pinwheel location. (B) Distribution of orientation preferences. Proportion of cortical area representing different orientations from right eye stimulation (red line ± 1 SEM, thick line: least-squares sine curve fit). The best fitting sine curve with period 90° had peaks at 90° and 180°.

DYNAMICAL CIRCUIT MECHANISMS OF ATTENTIONAL SAMPLING

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Recent physiological studies have demonstrated that distributed attention involving multiple objects is a theta-rhythmic sampling process, with each sampling cycle being implemented through gamma-band oscillations. To elucidate the dynamical circuit mechanisms of such attentional sampling processes, we investigate a biophysically realistic cortical circuit model for distributed attention tasks. We show that in the working regime of the circuit model near the critical transition between asynchronous to localized wave states, localized activity patterns with complex spatiotemporal dynamics emerge. The spatiotemporal dynamics of these patterns provide a mechanistic explanation for a great variety of neurophysiological data. These include the reduction of correlated neural fluctuations, the modulation of on-off transitions in spiking activity and the theta modulation of gamma oscillations. For attention tasks with natural scenes, we find that such dynamical activity pattern-based sampling gives rise to attention maps and sampling paths that are quantitatively comparable to those found in psychophysical studies.

A model for the origin of motion sensitivity in primary visual cortex

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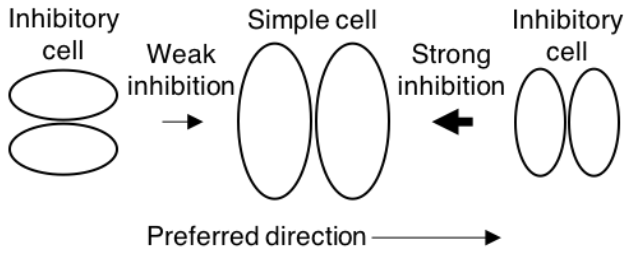
Introduction. Motion-sensitive neurons are prevalent in primate and carnivore primary visual cortex: these cells respond well to stimulus motion in one direction and poorly to motion in the opposite direction. Direction-selective neurons were discovered sixty years ago but the mechanisms underlying this selectivity are still obscure. One possible contributor is intracortical inhibition: inhibitory neurons are orientation-selective (Cardin, Palmer, Contreras, 2007) and their preferred orientation on one side of an excitatory cell may differ from that on the opposite side. This heterogeneity could, in turn, result in asymmetries of the excitatory response for a grating moving in one or the other direction. Our aim was to test computationally whether heterogeneous inhibition could lead to direction selectivity. **Methods.** Each simple cell in the model received converging input from on- and off-centre subcortical neurons, producing orientation selectivity. The preferred orientation varied across the cortical surface because each cell received a unique pattern of inputs. Each inhibitory cortical neuron received the same inputs as its nearest simple cell and therefore had the same orientation preference. **Results.** Simple cells displayed varying degrees of direction selectivity, from none to maximal (no response in the antipreferred direction). To test the hypothesis, we computed the difference in orientation preference between a simple cell and inhibitory cells in its neighbourhood. In a significant majority of cases a grating moving in the antipreferred direction passed through a region in which the preferred orientation was similar to that of the simple cell, evoking strong inhibition. Conversely, as shown in the figure, responses were strong in the preferred direction because the grating passed through a region containing inhibitory neurons with differing orientation preference. **Conclusion.** The model predicts that the preferred motion direction of a simple cell is from heterogeneous areas in the orientation preference map (such as pinwheels) to iso-orientation domains.



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ACUTE EFFECTS OF RESONANCE FREQUENCY BREATHING ON MUSCLE SYMPATHETIC NERVOUS ACTIVITY

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Acute slow breathing may have beneficial effects on cardiovascular regulation by affecting hemodynamics and the autonomic nervous system. Whether breathing at the resonance frequency (RF), a breathing rate that maximizes heart rate oscillations, induces differential effects to that of slow breathing is unknown.

The aim of this study was to compare the acute effects of breathing at either RF and RF+1 breaths per minute on muscle sympathetic nervous activity (MSNA).

Ten healthy men underwent MSNA, blood pressure (BP) and heart rate (HR) recordings while breathing for 10 minutes at their spontaneous breathing (SB) rate followed by 10 minutes at both RF and RF+1 randomly assigned and separated by a 10-minute recovery. Recording of multiunit postganglionic MSNA was made with participants resting in a supine position. A tungsten microelectrode (FHC, Bowdoin, USA) was inserted directly into the right peroneal nerve just below the fibular head. A subcutaneous reference electrode was positioned 2 to 3 cm away from the recording site.

Sympathetic bursts were visually identified and the number of bursts was averaged over the 10-minute period during SB, RF and RF+1. The MSNA was expressed as burst frequency (burst/min) and burst incidence (bursts/100 heartbeats).

The inter-burst interval was used to measure dynamic patterns of MSNA activity. The inter-burst interval was used as a measure of burst-suppression, when a cluster of bursts is followed by a silence period. The difference in inter-burst intervals during each condition was calculated for individual participants and then averaged for the whole cohort.

To calculate the phase of the respiration signal, a Hilbert transform was applied to the signal. A histogram of MSNA burst occurrence was plotted as a function of an instantaneous phase of the respiration signal. The MSNA bursts histograms were normalised to the maximum value for each breathing period and compared between SB, RF, and RF+1 breathing schemes.

Compared to SB, breathing at either RF or RF+1 respiration rates decreased MSNA (-5.6 and -7.3 bursts per min for RF and RF+1), with the sympathetic bursts occurring more often during mid-inspiration to early expiration (+57% and +80%) and longer periods of silence between bursts were seen ($p<0.05$ for RF+1).

Breathing exercises remain an attractive non-invasive strategy to modulate autonomic nervous system function. While breathing at the specific RF is suggested to maximise the effect we found that breathing at RF or 1 breath above RF induced the same acute changes on the sympathetic nervous system and BP, with both breathing paradigms inducing similar changes in the pattern of sympathetic firing.

INFERENCE OF THE PARSIMONIOUS MECHANISM UNDERLYING THE EMERGENCE OF ALPHA BLOCKING

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Alpha blocking, a phenomenon where the alpha rhythm is attenuated by attention to a visual, auditory, tactile or cognitive stimulus, is one of the most prominent features of human electroencephalography (EEG) signals. Here we demonstrate a method to infer the physiological mechanism that is likely responsible. We fit a neural population model to the eyes-open and eyes-closed EEG spectra from 82 subjects, each showing different degrees of alpha blocking. By jointly fitting the model to both eyes-open and eyes-closed states, and regularizing parameter differences between the two states, we were able to constrain the parameter uncertainties inherent to nonlinear model fitting. This revealed a surprisingly parsimonious explanation for the spectral changes between states and across subjects. Just a single parameter – the increase in excitatory input to the inhibitory population – is sufficient to explain the reduction in alpha rhythm upon opening of the eyes. By ordering the 82 subjects according to the degree of alpha blocking observed, we show how the magnitude of the increase in the excitatory input to the inhibitory population closely tracks the magnitude of the alpha blocking, with essentially no changes in the other parameters. We note that this universal trend is detected despite significant differences in the form of EEG spectra across subjects.

Neural field theory of the formation of ocular dominance columns in the primary visual cortex

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Neural field theory (NFT) is used to investigate the plasticity-driven evolution of the connectivity of stimuli to neuronal populations in the primary visual cortex (V1) and the resulting formation of ocular dominance columns (ODCs) in which either left or right eye stimuli dominate in their local connectivity. Stimuli from both eyes reach the excitatory (e) and the inhibitory (i) neuronal populations in V1, and are approximated here as white noise. Resulting synaptic plasticity causes strengths of connections to change on timescales much longer than those of neuronal activity. In NFT these changes are described in terms of the slow evolution of connectivity gains. Differing ranges of known spatial projections of excitatory and inhibitory neurons lead to competition between stimuli for available connectivity, breaking of spatial symmetry at a characteristic scale, and development of ODCs. The evolution of connectivity strengths is calculated in wavenumber (k) space. This yields the least stable mode, k_c, which allows us to determine the width of ODC. The results accord with experiment and they are based directly on the observed multiple neuronal populations and their connections, and the neuronal activity they support, within a unified formalism. Furthermore, we show ODCs are not formed when input stimuli are fully correlated. This analysis forms the basis for the next stage of physiologically based modelling of effects such as strabismus (squint) on ODC formation, and formation of orientation preference columns in V1.

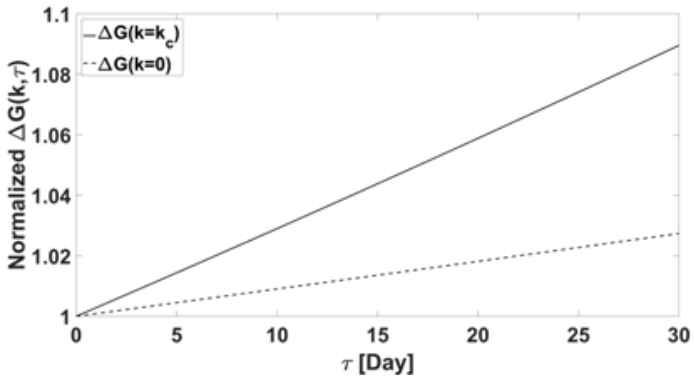

Fig. 1. Evolution of normalized difference between connectivity strengths of neurons in V1 to the left and the right eye $[\Delta G(k;\tau) = (G_{eR}+G_{iR}-G_{eL}-G_{iL})/(G_{eR}+G_{iR}-G_{eL}-G_{iL})_{\tau=0}]$. The solid line is $\Delta G(k_c;\tau)$ and the dashed line is $\Delta G(0;\tau)$. Input stimuli are uncorrelated $c_{LL} = c_{RR} = 1$ and $c_{LR} = c_{RL} = 0$.

TOPOLOGICAL PROPERTIES OF NEUROMORPHIC NANOWIRE NETWORKS.

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Graph theory has been extensively applied to the topological mapping of complex networks, ranging from social networks[1] to biological systems[2]. Only recently, particularly with the commencement of the Human Connectome Project[3], has graph theory been applied to neuroscience as a method to explore the fundamental structural and functional components of human neural networks[4]. Here, we apply graph theory to a novel neuromorphic system, Atomic-Switch Nanowire (ASNs) networks, whose structure and function mimic that of human neural networks[5][6][7]. We explore the topology and associated functionality of ASN networks prior to and during electrical activation. We apply network cartographic approaches detailed by Watts and Strogatz[1] and by Guimera and Amaral[8], to compare our ASN networks with random networks, grid-like networks, the neural networks of *C. Elegans*[9], and artificial neural networks (ANNs). We show that ASN networks exhibit a small-world architecture that is more complex than *C. Elegans,* and significantly different from random and grid-like networks, as well as ANNs. Our findings suggest that the topology of ASN networks resembles biological neural networks, and is a determinant of the network's dynamical response to electrical stimuli.

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Model-Based Prediction of Sleep, Circadian Phase and Alertness in Real-World Shiftwork

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Modern 24-hour society and irregular work schedules put stress on our natural sleep-wake dynamics leading to disrupted and inadequate sleep, misalignment of circadian clocks, and reduced alertness. These lead to accidents and have numerous health implications, including increased risk of obesity, diabetes, and cancer. As such, a detailed, quantitative, understanding of sleep-wake dynamics and its impact on alertness and circadian rhythms would be invaluable. We have developed a biophysical model that captures the dynamics of the key neurobiological processes underlying the human sleep-wake cycle and the effects that these disruptions have on alertness. The model has been calibrated and validated against experimental in-laboratory studies and successfully predicts sleep propensity [1], cognitive performance and subjective sleepiness [2], and melatonin dynamics in response to changes in lighting and wake/work hours [3]. The real challenge, however, is to enable predictions under real-world shiftwork conditions, where physiological outputs are not only governed by endogenous processes and irregular work schedules but also by environmental factors and human choices.

In this study we test how our biophysical model of arousal dynamics performs when tested against real-world data collected from a cohort of intensive-care-unit (ICU) nurses engaged in shiftwork (N=22). The data were collected over 2-3 weeks of daytime and night work. Participants wore wrist-borne activity and light monitors, completed daily sleep logs, and completed a battery of cognitive performance tests. Circadian phase was measured from urinary 6-sulphatoxymelatonin rhythms over 48 hours during the daytime work block and at the end of the night work block. The model was evaluated in the context of six different constraint configurations having input of either (i) shift times only, (ii) shift times and commute to/from work, (iii) shift times and actiwatch light, (iv) shift, commute and light, (v) sleep times, and (vi) sleep times and light. We find that in all six constraint cases the model performs well in predicting distributions of sleep times (sleep-wake state overlaps range from 79 to 98%), mean circadian phase (mean error range -1.9 to 0.1 h), and subjective sleepiness on Karolinska Sleepiness Scale (error between 0.33 and 1.1). Discrepancies between the data and the model were observed where sleep-wake dynamics were determined by behavioural choices rather than physiology and providing more information as an input led to a smaller prediction error. The evaluation constraint of *shift+commute+light* provided robust predictions across all measures while not requiring active input from the participant (e.g., no self-reported sleep data) and may therefore be more practical in future real-world applications.

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UNSUPERVISED ANALYSIS OF SLEEP DATA DETECTS PERIODS OF LUCID DREAMING

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The scoring guidelines developed by the American Academy of Sleep Medicine for sleep polysomnographic recordings consist of rules made for the human eye that lack precision and objectivity. Here, we aim to provide a novel approach to clustering sleep data that is independent from visual scoring conventions and instead implements unsupervised analysis techniques which identify patterns in unlabeled data. Our method clusters unlabeled sleep polysomnographic (PSG) data based on a diverse range of features selected by a generalised time-series feature extraction tool, *hctsa* (highly comparative time-series analysis). We aimed to determine whether our unsupervised, data-driven approach could detect periods of lucid dreaming (during which sleepers become aware that they are dreaming). Although lucid dreaming is not reflected in current sleep scoring rules and was not distinguishable to trained human scorers based on EEG alone, our clustering approach was able to identify periods of lucid dreaming at a rate that was significantly above chance. These results suggest that our data-driven approach could fill a clear clinical need for more meaningful sleep classification by objectively detecting the electrophysiological activity associated with significant physiological and subjective changes during sleep. Overall, our method has the potential to address some of the limitations of existing visual sleep scoring methodology in order to develop a system that can be effectively tailored to a wide range of individuals, populations, and sleep states, better exploit rich physiological data to objectively reflect underlying states, and to consider changes in conscious experience during sleep.

NONLINEAR RECEPTIVE FIELD ESTIMATION REVEALS NOVEL FORMS OF FEATURE INVARIANCE IN PRIMARY VISUAL CORTEX

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Object recognition in scenes develops across a hierarchy of visual areas. Robust recognition requires fine selectivity for particular features of relevance and invariance to irrelevant features. Deep convolutional neural networks have achieved near-human levels of performance in object recognition by iteratively applying filters that select features, followed by pooling of their outputs to generate invariance.

We applied a "filter-then-pool" model (Fig.1) to recordings from neurons in cat primary visual cortex (V1) to investigate visual feature selectivity and invariance in the brain. Many neurons pooled the outputs of multiple filters, resulting in selectivity for feature characteristics that were preserved across filters, and invariance to feature characteristics that differed across filters. We found cells corresponding to the well-known "energy model" of V1 complex cells that were invariant to spatial phase but selective to a combination of other feature characteristics. We also frequently found cells that showed only partial invariance to spatial phase, while exhibiting invariance to perturbations in peak orientation and spatial frequency, and orientation and spatial frequency bandwidth. This type of invariance has not been reported previously. For each of these feature characteristics, some cells were more selective for the characteristic and others that were more invariant.

To quantify the "selective-to-invariant" spectrum we used a bandwidth measuring the range of a characteristic over which a cell responded equally allowing for modest changes in contrast (< 2×). Peak orientation had the greatest portion of selective cells, followed by peak spatial frequency and then spatial phase, the latter showing the greatest portion of invariance. The bandwidth measure also allowed us to quantify how much the nonlinear pooling operation contributed to invariance by comparing it to the bandwidth expected from a linear operation. This showed that spatial phase invariance benefited the most from nonlinear pooling over multiple features, with the bandwidth frequently greater than expected in the linear case, and sometimes reaching the maximum possible (360 deg). In contrast, orientation and spatial frequency had bandwidths that did not increase much with nonlinear pooling over that of linear pooling.

Thus, in V1 there is a diversity of cells that combine selectivity for some feature characteristics with invariance to perturbations in others. This diversity encompasses a variety of feature characteristics beyond spatial phase.

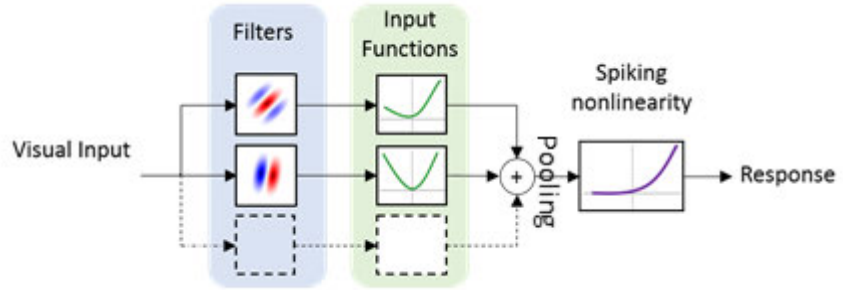

Figure 1: Block diagram of the filter-the-pool model used in this study

SPATIAL EMBEDDING OF GENE TRANSCRIPTIONAL GRADIENTS THROUGH BRAIN DEVELOPMENT

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The structure of the adult brain is the result of complex physical mechanisms acting through development. A well-known example is the exponential distance rule which describes the exponential decay in connection probability with physical separation distance. Recent work has shown that spatial proximity also plays a strong role in gene-expression gradients, with nearby areas exhibiting more similar gene-expression profiles than more distant areas in the head neurons of *C. elegans* [1], mouse brain areas [2], and regions of the human cortex [3]. As gene expression reflects the structural underpinning of functional specialization [4], characterizing its spatial embedding allows us to understand the physical constraints shaping the brain's functional organization. While the exponential distance rule for connectivity has been well studied across species—it obeys allometric scaling with brain size [5]—we don't know whether a similar relationship applies to the brain's molecular gradients through development within a species.

In this work we investigate the spatial embedding of transcriptional patterns of over 1800 genes across seven time points through mouse brain development [6], shown schematically in Fig. 1. Fitting an exponential relationship to correlated gene expression (CGE) at each developmental time point, allows us to estimate the spatial correlation length, λ, as the characteristic spatial scale on which gene-expression gradients are embedded (Fig. 1C). We find that CGE is well described by an exponential across all time periods, and with a striking linear scaling of λ with brain size, reflecting a new allometric scaling rule for gene expression. These empirical observations are reproduced using a simple physical growth model of spatially embedded transcriptional gradients, yielding new understanding of the key physical processes shaping brain development.

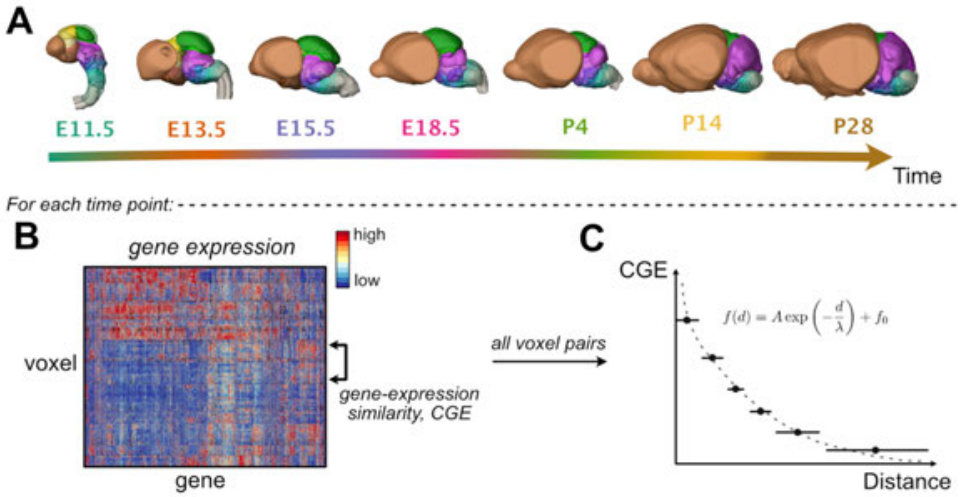

Figure 1: Schematic of our approach. Across each developmental time point (A), we compute the correlated gene expression (CGE) for each pair of voxels (B) and analyse how transcriptional similarity is spatially embedded through an exponential fit of CGE as a function of physical separation distance (C).

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A NEUROPHYSIOLOGICAL APPROACH TO SPATIAL FILTER SELECTION FOR BRAIN-COMPUTER INTERFACES

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Introduction: Electroencephalography (EEG) recordings have the potential to be interpreted by a brain-computer interface (BCI) to restore communication and control to people with severe motor disabilities. The popular common spatial patterns (CSP) algorithm is an effective method to overcome the poor spatial resolution of EEG and extract discriminatory features. Informed selection of CSP filters typically requires oversight from a BCI expert to accept or reject filters based on the neurophysiological plausibility of their time-invariant source patterns [1]. Participants can learn to adjust their brain activity patterns within a single session, so adapting the spatial filters may offer a solution to improve BCI performance [2]. However, the dependence on expert knowledge to select filters impedes the automatic application of this algorithm and, therefore, there is a need to develop a method to perform this task autonomously.

Methods: Two offline datasets consisting of 52 (Dataset 1) and 10 (Dataset 2) participants performing left and right hand motor imagery were used to extract CSP source patterns [3, 4]. An unsupervised clustering technique was used to identify the most common patterns and to establish classes of prototypical spatial patterns. All extracted patterns were visualised and manually assigned to either an 'established' class or an 'other' class. A convolutional neural network (CNN) was trained on 80% of the patterns from Dataset 1. The remaining 20% of Dataset 1 and all of Dataset 2 were used to evaluate the performance of the CNN.

Results: The nine types of prototypical spatial patterns are displayed topographically in Figure 1. The test accuracy across all participants for the CNN was 93% and 89% for Datasets 1 and 2, respectively. Cohen's kappa coefficient was 0.83 and 0.77, respectively, with $p<0.01$.

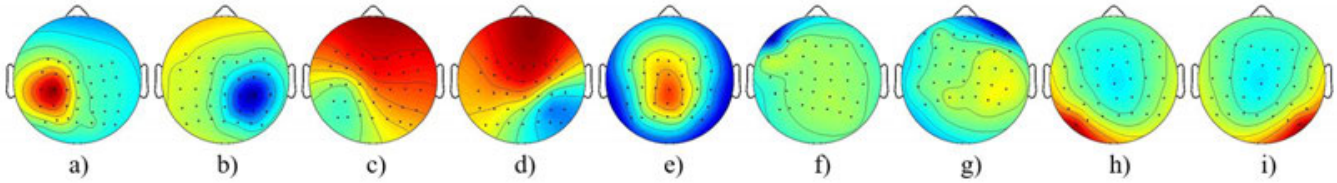

***Figure 1**. Nine classes of prototypical spatial patterns. Described as: a) left motor cortex, b) right motor cortex, c) frontal/left parietal, d) frontal/right parietal, e) central, f) left eye artifact, g) right eye artifact, h) left parietal artifact, i) right parietal artifact*

Discussion & Conclusion: The classes of spatial patterns consist of neurophysiologically plausible (a-e) and artifactual (f-i) sources. The results show that a small CNN trained with relatively few samples can classify topographical source patterns into a large number of classes with high accuracy. Although the performance on Dataset 2 was lower, the results show that this technique can generalise to new, unseen data generated under slightly different experimental conditions. The ability to distinguish between brain, artifactual and other source patterns means this classifier may be used to explore adaptive spatial filtering techniques that autonomously apply the CSP algorithm.

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PREFERENTIAL ATTACHMENT AMONGST NEURONS

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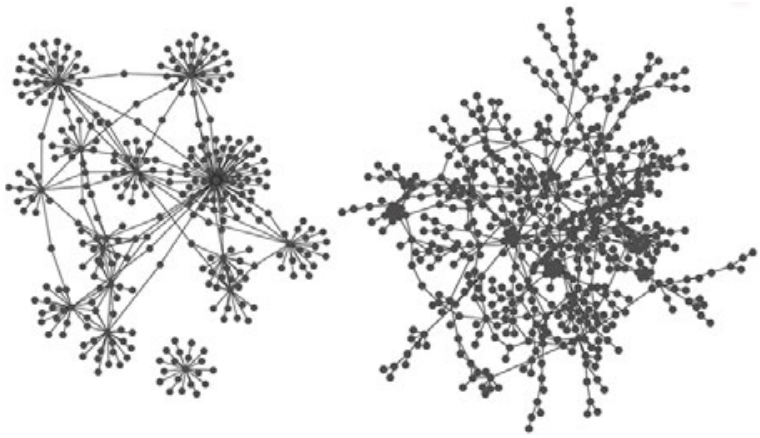
We study large scale networks of model neurons and their dynamical behaviour. Each network has numerous structural properties, which may or may not affect the overall dynamics of those neurons. Our current project focuses on the property called "assortativity", also known as "preferential attachment". Previous studies give reason to believe that it does have an effect[1].

Modelling a neuronal network at a relevant scale one is quickly faced with a rather large set of equations. A feasible approach is using the Theta Neuron model[2] and the Ott/Antonsen ansatz[3,4] to translate the system into a mean field theory, which subsequently can be reduced drastically. Further we worked on algorithms to introduce assortativity in the “adjacency matrix” and on how to utilise it in the mean field description.

With this framwork we have been able to get first results showing to what extent assortativity matters.



Example networks with negative and positive assortativity. (Image taken from [5])

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COGNITIVE STATE ALTERS THE GRADIENT OF WHOLE-BRAIN INFORMATION FLOW

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Cognition involves the dynamic adaptation of information processing resources as a function of task demands. To date, the neural mechanisms responsible for mediating this process remain poorly understood. In this study, we integrated cognitive neuroscience with information theory, network topology and neuropharmacology to advance our understanding of the fundamental computational processes that give rise to cognitive function in the human brain. In order to understand the affect of task load on neural processing, we obtained time series functional magnetic resonance imaging (fMRI) data by translating whole-brain blood oxygen level dependent signals from both the resting state and a cognitively-challenging N-back task from the Human Connectome Project (N = 457). We then compute the pairwise information transfer between all voxels using transfer entropy, a non-linear and model-free approach to connectivity analysis. By directly comparing this connection strength to the myelination gradient and the relative number of cells in distinct cortical layers, we were able to compare the direction of information flow during resting and task states. Our results show that cognitive task performance alters the whole-brain information processing landscape in a low-dimensional manner: during rest, information flowed from granular to agranular cortices, whereas this pattern was reversed during the performance of the cognitive task. Together, our results provide a conceptual bridge between cognitive function and neural information processing.

LEARNING VISUAL MOTION IN NEURAL NETWORKS

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Convolutional neural networks have had renewed success in recent years due to the higher computational power available and access to more data. Breakthroughs started with image classification on the ImageNet dataset [1] and then moved to tasks such as object detection, object tracking and image segmentation. While most of these neural networks would only process single images at a time, more recently have networks used optical flow inputs to help give context of motion [2]. Despite this, the ability for the networks to independently understand motion has not been well studied. We trained neural networks on a series of motion tasks to determine if they process motion analogously to the brain. We examined how the neural networks tuned their responses to speed and direction based on the training data. We compared the networks against human psychophysics experiments to observe the conditions under which the networks struggled to detect unique motion and how these conditions varied to humans. The networks and humans generally detected unique motion in the same scenarios.

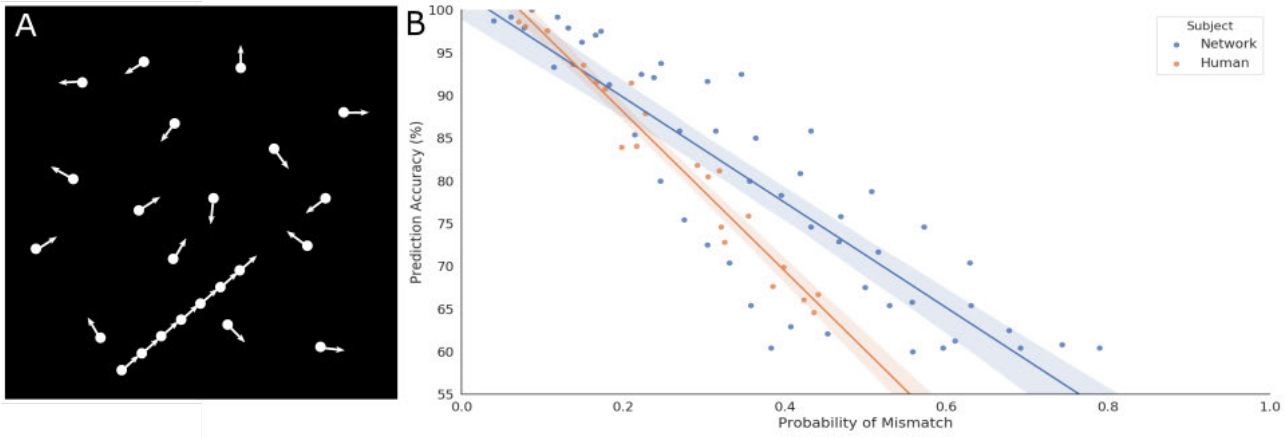

Figure 1 (A) Example of stimulus for detecting a dot moving with constant trajectory (signal dot) in Brownian noise (clutter dots). The signal dot moved with the same trajectory over the duration of the stimulus while the clutter dots chose a random direction every frame. Every dot moved with the same speed. The network was trained on the stimulus shown in A with varying dot densities and speeds. At test time, the network was shown two stimuli – where one video had a constant trajectory signal dot present and one where it was absent and it had to decide in which stimulus the signal dot was present. (B) Accuracy of choosing the video where the signal dot was present, as the speed and density increases. The 'probability of mismatch' represents the probability of nearest neighbours intruding on the path of the signal dot and causing a misdetection. It is dependent on the speed and density of dots and is represented by the equation $1 - e^{-(\pi * speed^2 * density)}$. *Data was collected as the mean from 3 trails of 80 videos where each video was 9 frames in length. The human data was reproduced from experiments by Watamaniuk et al. who tested human subjects on a near identical experiment [3]. These results show that while an increase to the probability of mismatch decreased detection accuracy for the networks, it does not have the same linear effect as it does for humans.*

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TRANSFER FUNCTION SYNTHESIS OF BRAIN STUDIES AT THE MESOSCALE AND ABOVE

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Observing, describing, understanding and controlling the relationship between the anatomical connectivity structure of brains, and the coordinated dynamics of neural tissues is the basis for many of the studies undertaken in neuroscience. The varied challenges involved in this work have driven the development of an ever expanding array of experimental modalities, methods for time series and data analysis, descriptions and models of brain systems, theory to analyze and expand these models, and applications, for example in treating disease. The rapid rate of expansion in neuroscience has sprouted a proliferation of fragmented and isolated subfields. However, ultimately this fragmentation must be synthesized into a systematic, self-consistent description of brain structure and function.

The linear system transfer function encompasses all relevant structural and dynamical information about a system for a given level of system description. Thus, the system transfer function is shown to be a quantity that can act as a conduit between experimental observations, clinical applications, time series and data analysis, models and system description and systematic analysis. The ability to relate all these aspects of neuroscience through the transfer function provides a clear picture of the usefulness of much existing knowledge applicable at the mesoscale and above.

From this transfer function perspective, systematic approaches can be identified and contrasted with ad-hoc and phenomenological ones, highlighting areas where self-consistent, systematic relationships are lacking. An existing, but underappreciated and important step in relating brain function and structure is the recovery of the system transfer function from correlations of system activity using spectral factorization algorithms. The recovery of the transfer function from correlations is demonstrated on synthetic and EEG data.

More generally, a greater focus on the system transfer function allows a wealth of existing ideas in neuroscience to be unified into a systematic description. Systematizing existing ideas will enable greater insight into data, motivate and generate new hypotheses and experimental tests, and strengthen the interaction of modelling and experimental studies in neuroscience. These benefits will increase the scope of neuroscience to identify and attack new problems.

QUALITY VS QUANTITY OF CONSCIOUSNESS: EMPIRICAL EVIDENCE FROM INTEGRATED INFORMATION ANALYSIS OF HUMAN INTRACRANIAL DATA

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Integrated information theory (IIT) gives quantitative predictions about the relationships between consciousness, its informational structure, and its neural basis. Specifically, based on the phenomenological analysis, IIT gives two predictions about the relationships between consciousness and its informational structure. One is that quality of consciousness (e.g. redness of red) correlates with "shape" of "Integrated Information Structure (IIS)" (so-called Maximally Integrated Conceptual Structure [1]). The other is that quantity of consciousness (e.g. awake vs. sleep) correlates with "system-level Integrated Information (system-level II)" (so-called big-phi [1]). In addition, IIT prescribes methods to estimate both IIS and system-level II based on our knowledge of the neural system. Previously, we made a first step towards the empirical testing of an IIT's prediction on quality of consciousness by analysing human Electrocorticographic (ECoG) data derived from visual perception experiments [2]. Here, we resolved several issues in the study, specifically issues that are associated with the computation of IIS and system-level II. In our preliminary analysis with the improved method, we tested the two IIT predictions on the neural data recorded from one patient, finding that IIS correlated with visual perception while system-level II did not. We plan to replicate this result using data obtained from other experiments.

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MODULARITY OF ARTIFICIAL NEURAL NETWORKS DURING TRAINING BY BACKPROPAGATION

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Connectivity within the brain provides the paths along which it processes information. Numerous studies have been conducted using graph theoretic measures to understand the properties of both its structural and functional networks[1]. These show a high level of small-worldness[2], modularity[3] and centrality[1] compared with random graphs. Explanations for the effectiveness of these topological characteristics include increased adaptability and robustness, with decreased wiring cost[3]. Differences in these measures also allow healthy brains to be distinguished from those with disorders such as Alzheimers[2].

These graph theoretical measures can also be used on artificial neural networks (ANN), with the advantage of being able track how they change as the ANN is trained to perform particular tasks. For a simple multi-layer ANN, the untrained network is fully connected between each layer and initialised with random weights, giving it an essentially random topology. As the network is trained, however, the topology changes.

As training epochs progressed, we found an increase in modularity, mean participation and and communicability. Some measures scale relatively linearly with an increase in the accuracy of the network. Modularity, however, does not always increase monotonically. The change depends on which layer of the ANN is observed and where this layer sits within the overall structure. Early layers see a rapid increase in the modularity during the initial epochs of training, followed by a slow decline down to a steady value. Later layers, however, only sees a smooth increase and reaches a larger final value. The decline in modularity in the early layers may be related to ideas of information bottleneck[3], and allow for the network to better generalise to unseen examples as training proceeds.

In addition to observing the training progress, we can also affect the speed of training by modulating the slope of the non linearity (sigmoid function) in each unit – effectively changing the gain within the network[5]. Changing this parameter at a global level has a similar effect to changes in the learning rate, and there is a trade off between speed of the training and the optimality of the final solution.

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CRITICALITY OF CORTICAL STATES: A MODELLING STUDY.

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Recent experimental studies have demonstrated that neural circuits exhibit a diverse repertoire of behavioural regimes - ranging from highly correlated to asynchronous states and often hovering over the critical transition between these states. However, the circuit mechanisms underlying the emergence of this critical transition, which is hypothesised as a working regime for the brain, remain unclear. In this study, we investigate a biophysically realistic circuit model of spiking neurons, which exhibits a rich repertoire of dynamical activity states, ranging from asynchronous to localised and global propagating wave states. We find that around the critical transition between asynchronous and localised propagating wave states, our circuit model exhibits neural avalanches that can be characterised by a set of scaling relations of their size and duration distributions at an intermediate value of spiking variability, consistent with recent empirical observations. This critical transition and its neighbouring cortical states are further analysed and distinguished by applying adapted Renormalisation Group (RG) methods. We find power-law dependences of several static and dynamic quantities on the coarse-graining scale.

GAMMA-BAND CORRELATIONS IN PRIMARY VISUAL CORTEX

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In the primary visual cortex (V1), neurons with similar orientation preference (OP) are preferentially linked by patchy lateral connections [3]. Furthermore, these patchy connections are concentrated toward an axis that corresponds to the OP of the neurons involved, and thus are strongly anisotropic [1]. Experiments [2][4] have shown that V1 neurons with similar feature preference exhibit synchronized gamma band (30 -- 70 Hz) oscillations when the stimulus is optimal, and it has also been showed that the corresponding two-point correlation functions of multi-unit activities (MUA) or local field potentials (LFP) commonly have peaks at zero time-lag. we use neural field theory (NFT) with patchy propagator to quantitatively analyze the two-dimensional spatiotemporal correlation properties of gamma-band oscillations evoked by stimuli arriving at V1, and relates the spatially distributed neural responses to the periodic spatial structure of OP map in V1. We produced 2D correlation maps (Fig. 1), which showed that the positive correlations appear as patches on an axis oriented at the OP of the source, and negative correlations occur where the OPs of the measurement sites are nearly orthogonal to the OP of the source. Moreover, our predictions reproduce a range of published experimental results, including the existence of two-point oscillatory temporal cross-correlations with zero time-lag between neurons with similar OP, the influence of spatial separation of neurons on the strength of the correlations, and the effects of differing stimulus orientations..

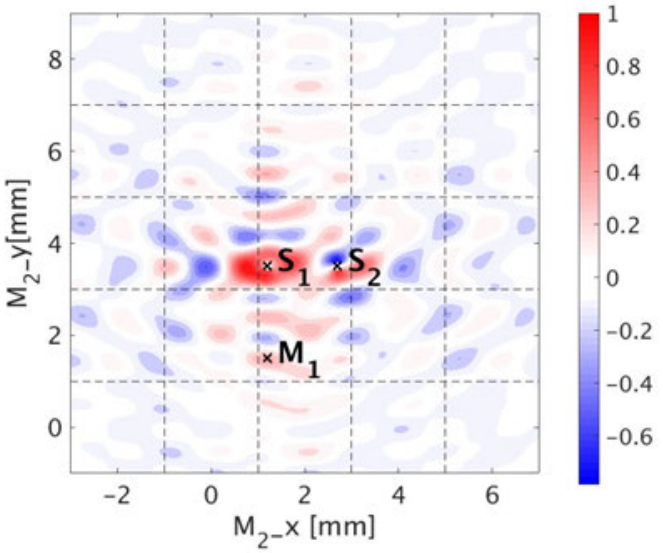

Figure 1. Normalized correlation map with two input points.

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SPATIAL-TEMPORAL ORGANISATION PROPERTIES OF NEURAL OSCILLATIONS IN PRIMATE CEREBRAL CORTEX

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Neural oscillations emerging from cortical circuits exhibit oscillatory bands covering frequencies from a few tenths to hundreds Hz. These oscillations have been widely observed in cortex, but their spatial and temporal organisation properties remain unclear. In this study, we adapt concepts and methods from turbulence physics to analyse neural oscillations in local field potential (LFP) activity recorded from the extrastriate visual cortex of marmosets. We find that rather than being sustained, regular oscillations, neural oscillations at all frequency bands exhibit intermittent, bursting properties with varying peak frequencies, and that these bursts are organised as spatially localized, propagating patterns. We further demonstrate that the higher the frequency bands, the smaller the averaged size of the propagating pat- terns, and find that the averaged sizes of these patterns scale as a power function of their frequencies with an exponent of -0.3. Such a scaling behaviour of the propagating patterns is invariant across different recordings. In addition, we find that there exist rich interactions of these propagating patterns across temporal scales.

MODELLING THE ELECTRICAL IMPEDANCE OF NEURAL TISSUE BASED ON ITS CELLULAR BUILDING BLOCKS

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Knowledge of electrical properties of neural tissue, such as conductivity, is important in various applications such as therapeutic electrical stimulation of the nervous system and electrical impedance tomography. It is also essential for the interpretation of intrinsic electrical signals in neuroscience such as single and multiunit activity, the local field potential and electroencephalogram.

It is usually assumed that neural tissue can be described by a locally homogeneous conductivity that captures the bulk properties of heterogeneous cellular microstructure. However, the cellular structure of tissue creates a complex partition of intra- and extra-cellular spaces that are separated by a high impedance membrane. These microstructure inhomogeneities lead to complicated current paths through the tissue, invalidating assumptions that allow a description based on a simple conductivity.

Starting from the underlying heterogeneous microstructure of neural tissue we use a mean-field theory to derive the tissue's bulk electrical properties in the form of the admittivity, which generalized the usual conductivity. A novel aspect of the admittivity is that it has both spatial and temporal spectral frequency dependence. New expressions are given for the admittivity of several tissue types including isotropic tissues with fibers oriented randomly in all (three-dimensional) directions and laminar tissues types with fibers oriented randomly within planes that are stacked upon each other.

The spatio-temporal spectral frequency dependence of the tissue admittivity leads to non-trivial spatiotemporal electrical filtering properties of neural tissue, which we illustrate here. First, we show how a variation in a temporal parameter, namely applied pulse-width, can affect a spatial property like the profile of the extracellular potential. Second, we showed that, for tissue with a homogeneous structural anisotropy, variation in a spatial variable, namely distance from the electrode, can nonetheless affect the degree of electrical anisotropy.

DIFFUSE NEURAL COUPLING MEDIATES COMPLEX NETWORK DYNAMICS THROUGH THE FORMATION OF QUASI-CRITICAL BRAIN STATES

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A key feature of the human brain is its ability to adapt to a diverse range of tasks and environmental stimuli. In order to facilitate this level of flexibility, the brain has been shown to strike a balance between network-level segregation and integration. How the brain is able to shift between these operational modes, and what physical mechanisms underpin the presence of these states, remains an open question. A potential solution to this mystery may lie in a unique aspect of neurobiology, which is that numerous brain systems contain both targeted and diffuse synaptic connections. In this manuscript, we demonstrate that increasing diffuse cortical coupling within a validated biophysical corticothalamic model traverses the system through a regime in which spatial heterogeneities in input noise support transient critical dynamics in distributed sub-regions. We introduce a novel measure of these quasi-critical states – the distribution of distances to a local bifurcation point across the network – and show this term bounds a zone that supports a broadened range of dynamics. We further demonstrate that the presence of quasi-critical states coincides with known signatures of complex, adaptive brain dynamics: susceptibility, communicability, flexibility and low-dimensionality. Finally, we demonstrate the presence of similar dynamic signatures in empirical whole brain human neuroimaging data. Together, our results establish that the modulation of the balance between local and diffuse synaptic coupling in a thalamocortical network model subtends the emergence of quasi-critical brain states that may have been exploited by the brain in order to flexibly transition between unique modes of information processing.

DUAL SPIKING MODES OF LAYER V PYRAMIDAL CELLS VIA APICAL AMPLIFICATION MEDIATE COMPLEX, ADAPTIVE BRAIN DYNAMICS

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Efficient cognitive function requires the brain to be able to synthesise feed-forward drive and feed-back modulation dynamically, and then accurately convey this synthesised information against the noise of its ongoing activity. A unique and often overlooked property of mature Layer V pyramidal cells in the cerebral cortex is their ability to synthesise these separate streams of information [1]. These cells receive distinct channels of inputs into their apical and basal dendrites, and they have been shown to use the apical input to modulate basal driven spiking response modes [2]. This phenomenon is known as 'apical amplification' [3], and it is integral to cognitive function [4], as evidenced by its absence under anaesthesia [5] and marked increase with arousal [6]. However, how this mechanism relates to macroscopic whole-brain functional modes remains poorly understood. At baseline, the apical tuft is electrically separated from the basal dendrites and unable to generate action potentials in the soma. When the apical and basal dendrites are simultaneously stimulated, a layer V pyramidal cell may shift its response from a regular-spiking to a burst-spiking mode [2]. Input onto basal dendrites is feed-forward, from segregated, 'core' cells of the thalamus and intra-telencephalic projections from pyramidal cells in lower layers of the cerebral cortex. In contrast, input onto apical dendrites consists of integrated and diffuse feed-back from higher cortical regions and non-specific, 'matrix' cells of the thalamus [7]. Furthermore, the threshold to transition from regular spiking to burst spiking is mediated by an HCN [8] channel on the apical dendrite, which can be raised and lowered via adrenergic and cholinergic neurotransmitters, respectively. In this project, we reproduce and explore the fundamental features within this circuit using parameterised quadratic integrate-and-fire neurons (Izhikevich neurons; [9]). Our approach combines the biological plausibility of Hodgkin-Huxley-type dynamics with substantial computational efficiency. This allows us to explore the role of diffuse matrix input, core input, and neuromodulatory effects on the HCN channel, in constraining whole brain function. From the resulting spiking dynamics, we identify various regimes of the system that facilitate known signatures of complex, adaptative brain dynamics. These differing regimes are likely utilised by the brain as it responds to stimuli shifting context-driven attention during the conscious state to efficiently mediate adaptive cognitive behaviour.

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COMPLEX DYNAMICS OF PROPAGATING WAVES IN A TWO-DIMENSIONAL NEURAL FIELD

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Propagating waves with complex dynamics have been widely observed in neural population activity. To understand their formation mechanisms, we investigate a type of two-dimensional neural field model by systematically varying its recurrent excitatory and inhibitory inputs. We show that the neural field model exhibits a rich repertoire of dynamical activity states when the relevant strength of excitation and inhibition is increased, ranging from localized rotating and traveling waves to global waves. Particularly, near the transition between stable states of rotating and traveling waves, the model exhibits a bistable state; that is, both the rotating and the traveling waves can exist, and the inclusion of noise can induce spontaneous transitions between them. Furthermore, we demonstrate that when there are multiple propagating waves, they exhibit rich collective propagation dynamics with variable propagating speeds and trajectories. We use techniques from time series analysis such detrended fluctuation analysis to characterize the effect of the strength of excitation and inhibition on these collective dynamics, which range from purely random motion to motion with long-range spatiotemporal correlations. These results provide insights into the possible contribution of excitation and inhibition toward a range of previously observed spatiotemporal wave phenomena.

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NON-LINEAR ADAPTATION IN EARLY VISUAL PROCESSING MAY SUPPORT COMPETITIVE SELECTION BETWEEN VISIBLE SMALL MOVING TARGETS IN NATURAL CONDITIONS

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In several species of flying insects, neurons have been identified which selectively and robustly respond to small moving targets in natural scenes [1,2]. These small target motion detector (STMD) neurons may play a role in pursuits of prey and conspecifics. Visually guided aerial pursuits in natural scenes present challenges for target discrimination due to both the complex environment, containing diverse spatial features which may be mistaken for small targets, as well as apparent movement of the environment due to ego-motion. Wind and turbulence are examples of environmental conditions which may cause stochastic variations in the position or heading of a flying insect, resulting in unpredictable wide-field motion.

Some STMD neurons in dragonflies have demonstrated selective attention whereby the neuron's response to multiple visible targets strongly matches the response to only one of the targets [3]. The mechanisms behind selective attention are not understood, but one possible explanation for the phenomenon is a competitive selection between targets [4]. Although it is easy to identify potential advantages of focussing on a single target at a time, this nevertheless involves discarding potentially useful information from the visual scene. Moreover, if only one target signature out of many candidates will be selected, it is important to choose the right one; that is, the signature generated by a real moving target as opposed to a moving part of the background. One may speculate that the neuronal machinery underlying target detection has been tuned by evolution to support this selection behaviour.

Elementary small motion detectors (ESTMDs) have been proposed as hypothetical processing units which subserve the characteristic selective responses of STMD neurons [5]. Responses of STMD neurons could be explained by integration of many ESTMDs. The ESTMD model includes a separation of input signals into ON and OFF, representing luminance increments and decrements respectively. These separated signals are then inhibited via a non-linear adaptation mechanism reflecting physiologically observed adaptation in the blowfly lamina and medulla [5,6]. We carried out computer simulations of the responses of an array of ESTMD units to targets moving through natural scenes. Ours simulations featured a wide variety of natural imagery and patterns of background motion. We found that the amount of mutual information between the position of a target in the visual field and the output of an array of ESTMDs was improved by the non-linear adaptation mechanism during repetitive background motion. When comparing non-linear adaptation to other simple mechanisms which could perform a similar role, we found that the non-linear adaptation mechanism had a greater advantage over the tested alternatives if only the maximum ESTMD output at a point in time was available for inferring the target position. These results suggest that non-linear adaptation on separated ON and OFF channels support effective target localisation in a context where competitive selection between ESTMD outputs occurs in higher-order neurons.

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CATEGORICAL AND INVARIANT VISUAL OBJECT CAPABILITIES OF THE SUPERIOR COLLICULUS – A THREAT DETECTION CENTRE OF THE BRAIN.

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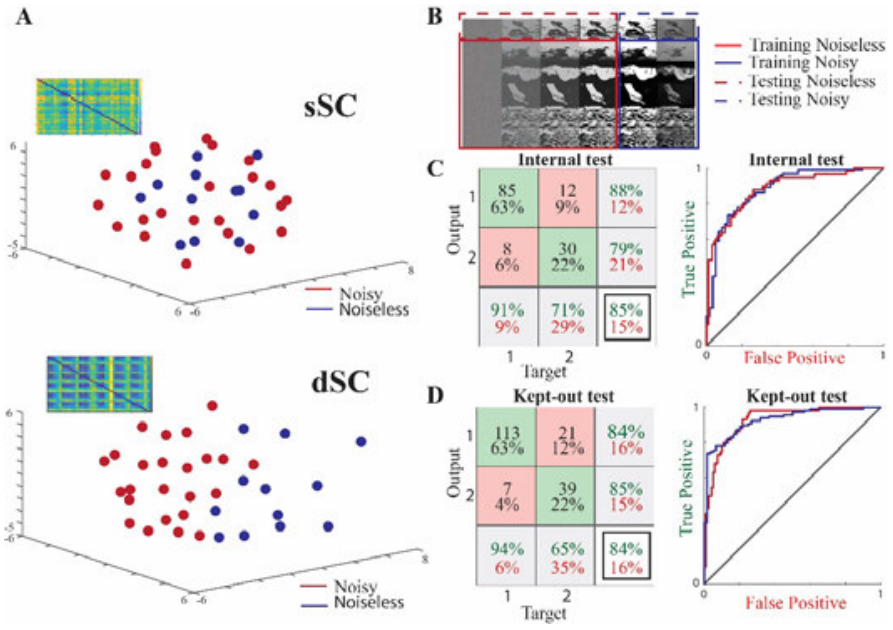
The superior colliculus (SC) is a sensory integration hub in the dorsal brainstem where multimodal information is combined and, depending on the saliency of the competing sensory inputs, appropriate motor commands and supportive autonomic changes initiated. In rodents, the SC is indispensable for initiating behavioural responses to stereotypical visual stimuli that resemble approaching objects, such as looming (an expanding overhead black circle)[1]. In pilot experiments, we found that presentation of overhead looming stimuli drove acute surges in blood pressure in telemetered conscious rats. Surprisingly, equivalent autonomic responses could be driven by more complex visual stimuli (e.g. snakes) but not by control stimulations. We hypothesized that the encoding capabilities of the SC might extend beyond detection of stereotypical approach conventionally attributed to the region, and that complex naturalistic shapes could be detected by SC circuits based on a saliency-map of behaviourally relevant cues important for survival (from appetitive to threatening). To investigate this idea, we made extracellular single-unit recordings from a population of SC neurons (over 800 visually responsive neurons recorded so far) in anaesthetised rats and used machine-learning based approaches to decode the visual cues presented, clustering stimuli according to the similarity of population responses. We report categorical and invariant visual object capabilities of SC microcircuits that differ by subregion and are several orders of magnitude more complex than previously recognised. Furthermore, the addition of granular noise caused a progressive, level-dependant attenuation of these responses. Our data suggest that the SC is capable of nuanced object recognition, suggesting mechanisms through which complex visual cues can initiate defence manoeuvres.



(A) Dissimilarity matrix and 3d scatter plot of response profiles to videos in sub-regions of the SC. Shallow neural network classifiers were trained on the dSC data. (B) Dataset was divided in two classes (noisy/noiseless) and a whole set of stimulations was kept out of training. (C) Internal testing of the training phase achieved 85% accuracy. Bottom: The algorithm achieved 84% accuracy when deployed on the 180 stimulations from video set kept out of training. (note: ***perstimulus time histogram (PSTH) from single stimulations of all responsive cells were used, no averaging/normalising, showing potential for real-time detection.***

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ESTIMATING TRANSFER ENTROPY IN CONTINUOUS TIME FOR SPIKE TRAINS

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Transfer entropy (TE) [1] is a measure of the flow of information between components in a system. It is defined as the mutual information between the past of a source and the present state of a target, conditioned on the past of the target. It has received widespread application in neuroscience [2, 3], both for characterizing information flows as well as inferring effective connectivity from data sources such as MEG, EEG, fMRI and electrode arrays. Previous applications of TE to spike trains have relied on time discretization, where the spike train is divided into time bins and the TE is estimated from the numbers of spikes occurring in each bin. There are, however, several disadvantages to estimating TE from time-discretized data [4]. First and foremost, as time discretization is a lossy transformation of the data, it will result in an underestimate of the TE. Thus, any estimator based on time discretization is not consistent. Secondly, whilst the loss of resolution of the discretization will decrease with decreasing bin size, this requires larger dimensionality of the history embeddings to capture correlations over similar time intervals, resulting in an exponential increase in the state space size being sampled and therefore the data requirements. This increase in the data requirements renders the estimation problem intractable for the typical dataset sizes present in neuroscience.

Recently, a continuous-time framework [4] for transfer entropy was developed. This framework has a distinct advantage in that it demonstrates that, for spike trains, the TE can be calculated solely from contributions occurring at spikes. This presentation reports on a newly developed continuous-time estimator for transfer entropy for spike trains which utilizes this framework. Importantly, this new estimator is a consistent estimator of the TE. As it does not require time discretization, it calculates the TE based on the raw interspike interval timings of the source and target neurons. Similar to the popular KSG estimator [5] for mutual information and TE, it performs estimation using the statistics of K-nearest-neighbour searches in the target and source history spaces. Tests on synthetic datasets of coupled and uncoupled point processes have confirmed that the estimator is consistent. Similar tests of the time-discretized estimator have found it to not be consistent, have a substantially higher variance and require longer spike trains to differentiate coupled from uncoupled processes. The results of further experiments will also be discussed.

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MODELLING MELANOPSIN-DEPENDENT EFFECTS OF LIGHT ON CIRCADIAN PHASE AND ALERTNESS

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Blue light directly increases alertness during exposure and also shifts the circadian phase. Prediction of alertness and circadian phase would prove highly useful under shiftwork and jetlag conditions where reduced alertness and phase shifts in the circadian clock increases the risk of accidents and diseases respectively. Modelling is an essential tool to predict and optimize the effects of external cues on the sleep-wake cycle. So far, however, no model has accounted for the effects of light wavelength on the direct alerting effect of light and circadian phase. Here a recent biophysical model of arousal dynamics is extended to incorporate the effect of melanopsin; a photopigment expressed in photoreceptors in retina, responsible for short wavelength dependent behavior of non-image forming processes.

The model of arousal dynamics simulates the switch between the sleep- and wake-active neuronal populations under the effects of the homeostatic and circadian drives. The model has been successful in prediction of subjective alertness and objective performance under acute sleep deprivation and forced desynchrony in dim light conditions. It is known that short wavelength light dependency in non-image forming processes is due to the contribution of melanopsin which is expressed in intrinsically photosensitive retinal ganglion cells (ipRGCs) or melanopsin-containing cells. These cells are mostly sensitive to short wavelength light (λ_{max} 480 nm) and project directly to suprachiasmatic nucleus (SCN) and other brain regions. Here, the melanopic irradiance of light is introduced as the key input to the SCN to replace the photopic illuminance that was used previously. A new melanopic-dependent, term is added to the homeostatic weight component of subjective sleepiness to account the direct alerting effect of light mediated by melanopsin. The revised model is then tested and calibrated against experimental data with different light conditions.

The revised model's predictions are compared to 15 experimental data sets, including experiments on direct alerting effects of light and effects of light on circadian phase. Compared to older model version, the prediction of circadian phase and subjective sleepiness improved significantly, especially for the monochromatic blue and blue-enriched white light sources. The revised model accounts for any light source using their spectral power distribution and calculating melanopic irradiance as the light input to the model. However, in predicting effects of monochromatic green light, the prediction error is larger than that for blue light, indicating that the contributions of other photoreceptors may need to be considered.

POSITIVE-GOING SPIKES RECORDED EXTRACELLULARLY IN CAT VISUAL CORTEX CORRESPOND TO THALAMIC AXONS

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Extracellular spike waveforms from recordings in the visual cortex have been classified into either regular spiking (RS) or fast spiking (FS) units, which are often associated with excitatory and inhibitory neurons, respectively. While both these types of spikes have waveforms with negative first phases, we show that there are also distinct classes with positive first phases, which are not regularly reported. The spatial receptive fields (RFs) of these different spike waveform types were estimated and we found that each spike type had distinctly different RF structures.

837 single units (SUs) in the cat visual cortex were classified into five categories by the shape of their spike waveforms: RS units (52%, 432/837) which are biphasic, have a dominant negative peak, and a slow declining slope at the end of the waveform; FS units (22%, 185/837) which are biphasic, have a dominant negative peak, and a fast declining slope at the end of the waveform; triphasic spiking units (TS, 9%, 74/837) which have a positive first peak that is >10% of the negative peak, followed by a large negative peak and then a smaller positive peak; compound spiking units (CS, 3%, 27/837) which are also triphasic but with a significantly longer waveform; and positive spiking units (PS, 14%, 118/837) which have a positive peak greater than the negative peak.

Of these 837 SUs, 231 had their spatial RFs estimated as the spatial filters in a general non-linear model of response to white-Gaussian noise (WGN) and classified as either oriented and Gabor-like (orientation bandwidth < 90°) or non-oriented and blob-like (orientation bandwidth > 110°). RS and FS units had mostly oriented RFs (95%, 68/72; 99%, 71/72, respectively), while TS, CS and PS units had mostly non-oriented RFs (56%, 14/25; 75%, 6/8; 78%, 28/36, respectively). These non-oriented RFs are very similar to the centre-surround RFs reported in the lateral geniculate nucleus. We calculated several response properties that are statistically distinguishable between cortical and thalamic neural populations: spike-rate, burstiness, and response latency. On average, PS units had significantly higher spike-rate (t-test, $p < 0.05$), significantly higher proportion of burst spikes ($p < 0.001$), and significantly shorter response latency ($p < 0.05$) to RS and FS units.

To further investigate the origin of the spikes, we recorded from the visual cortex before and after silencing it with the GABA agonist muscimol. None of the RS, FS and CS units remained after cortical silencing (0/39; 0/5; 0/1, respectively), while few TS units remained (25%, 2/8) and the majority of PS units remained (60%, 3/5).

Thus, our results suggest that PS units, which have mostly non-oriented RFs, thalamic-like response properties and remain after cortical silencing, correspond to recordings from thalamic axons projecting to the visual cortex. RS and FS units correspond to cortical neurons, which have mostly oriented RFs and do not remain after cortical silencing. This would allow cortically implanted electrodes to record activity from thalamus and cortex simultaneously.

Figure 1: Spike waveform classification: mean waveforms are shown for the five different categories used in this study (left to right): regular spiking, fast spiking, triphasic spiking, compound spiking and positive spiking

AVOIDING RETINAL GANGLION CELL AXON ACTIVATION WITH ORIENTED RECTANGULAR ELECTRODES

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Retinal prostheses can restore visual sensations in people that have lost their photoreceptors by electrically stimulating surviving retinal ganglion cells (RGCs). The quality of visual perception depends strongly on being able to confine each electrodes activation pattern. For epi-retinal implants where electrodes are placed adjacent to RGCs, the spread of activation is large, partly due to the unintended activation of passing axon bundles.

First, we use simulations of electrical excitation of the retina to show that the activation of axon bundles can be minimized either by using long electrodes oriented parallel to theses axons or with simultaneous stimulation of multiple electrodes that are aligned with the axons [1]. The mechanism underlying the minimal activation of axon bundles depends of the first spatial derivative of the extracellular electric field in the direction of the axon. Stimulation with long electrodes parallel to theses axons minimizes this first spatial derivative.

Second, we use calcium imaging of ex vivo retina to show that rectangular electrodes oriented parallel to the axons can prevent the activation of axon bundles, as predicted through simulation. When using biphasic stimulation as short as 33 μs, the activated RGCs were mostly confined to the region below or very close-to the electrode, as observed using confocal microscopy.

These results suggest that it should be possible to greatly improve the performance of future retinal prostheses.

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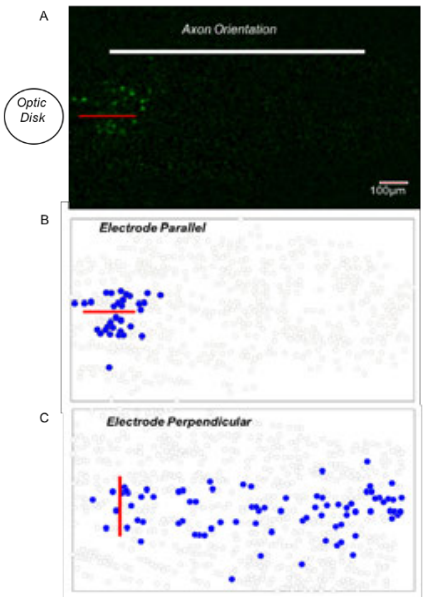

Figure 1: Calcium imaging of ex vivo retina. (A) Calcium indicator fluorescence (green) in relation to the electrode (red line) and axon orientation. (B) Activation (blue) of RGCs is localised to the region around the electrode when the electrode is aligned with the axon orientation. (C) However, activation extends to cell bodies in the direction of passing axons when the stimulation electrode is perpendicular to these axons.

MEAN FIELD MODELLING OF THE EPILEPTOGENIC EFFECTS OF CORTICAL LESIONS

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Brain lesions are represented by a broad variety of pathologies that all produce structural brain changes. Their most broad classifications would include structural abnormalities whose causes include but are not limited to stroke, tumor, brain insult/injury, autoimmune disease (such as multiple sclerosis), radiologically and surgically induced lesions. Brain lesions have long been associated with a variety of pathologies. Epilepsy is seen to occur in a significant portion of patients who have suffered brain lesions, including up to a 10% occurrence for stroke patients.

The EEG has been an important diagnostic and monitoring tool for epilepsy. Acute epileptic seizures show clear presentation as abnormalities in the EEG, and libraries of these exist for comparative diagnosis.

A variety of modelling approaches exist to simulate the genesis of EEG signals. One of these approaches is the mean field approach, focusing on the large-scale electro-dynamics of cortex or the brain as a whole. A well-known mean field model is the Liley model for cortex. The Liley model has been successful in simulating normative EEG features along with features that are commonly observed under anaesthetic conditions.

We present an investigation of the Liley model's ability to simulate EEG abnormalities known to be associated with cortical lesions. We present results demonstrating the model's ability to simulate localized and generalized seizure-like dynamics under parametric conditions that are consistent with the physiological conditions associated with brain lesions. Bifurcation analysis is also presented demonstrating the underlying transition between normative and epileptic states.

A WIRELESS RECORDING MICROCHIP FOR BRAIN MACHINE INTERFACES

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Brain Machine Interfaces (BMIs) aim to restore lost function to amputees and quadriplegics. These devices require monitoring of outputs of the brain (e.g. neural signals from the motor cortex), to extract information to control effectors such as prosthetic limbs. Providing input into the brain by modulating neural activity is also desirable to allow sensory input such as touch to regulate the strength of a grasp. Ideally these interfaces should be wireless – that is, operate through the skin using radio waves, rather than have bulky, inconvenient and potentially leaky connectors penetrating through the skin.

We are developing a wireless BMI system which is able to record and transmit neural activity via an array of microelectrodes implanted directly into the brain.

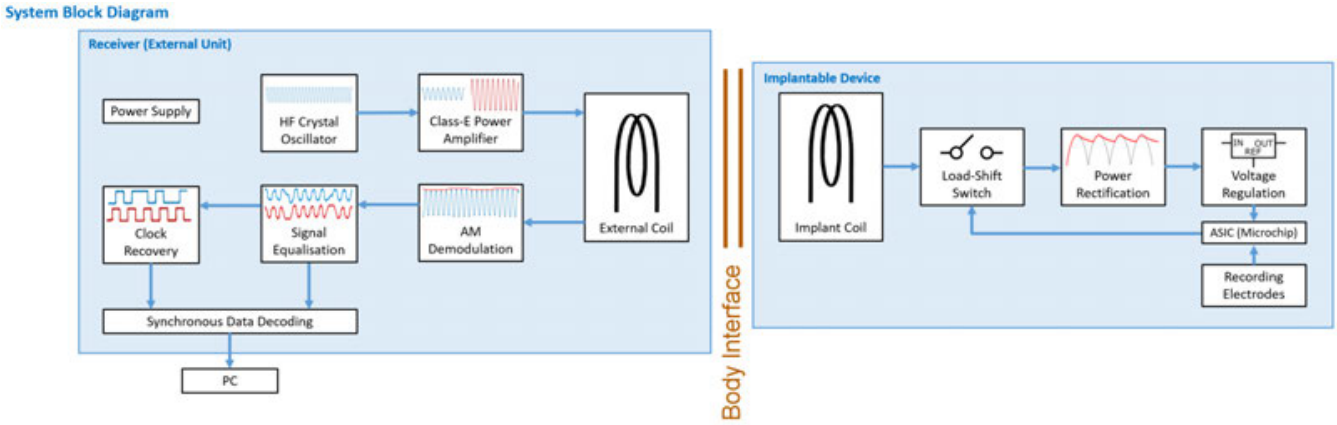

Figure 1. Block diagram of the developed wireless brain machine interface system.

We have designed a custom integrated circuit microchip in 180 nanometre Complementary Metal-Oxide Semiconductor (CMOS) technology. Each microchip die consists of 20 low noise programmable front-ends, a high-speed, high-resolution time division multiplexed (TDM) analog-to-digital converter (ADC) and digital modulation circuitry. Each front-end has a combination of operational transconductance amplifiers with selectable gain from 29 dB to 52 dBV. Bandwidth is from 10 Hz to 20 kHz allowing us to target both local field potentials and action potentials. Front-ends have been designed to have a very low noise floor of <4uVrms (10Hz-10kHz) while ensuring minimum possible power consumption and die area. Analog signals captured by each front-end are multiplexed into a 10-bit Pipeline Analog to Digital Converter, which can sample at rates up to 1.25 MSa/s. TDM is utilised to achieve up to 39 kSa/s per frontend. Digital sample data is processed into serial, parallel stream of binary encoded data that can then be transmitted to the outside world with or without various modulation schemes.

An important feature of this chip is its ability to operate as either a wired or wireless device. As a wired device, a high-bandwidth wired bus supports data from all channels to be sent at the full sampling rate simultaneously to a PC. As a wireless device, due to data bandwidth and power limitations of the inductive link, one channel can be selectively transmitted at a time at the full sampling rate, or multiple channels can be transmitted simultaneously at a reduced sampling rate.

A NORMATIVE MODEL OF NEURAL COMPUTATION BY FRACTIONAL DIFFUSION

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Recent studies have demonstrated that high-frequency neural oscillations such as gamma oscillations (30-100 Hz) are organised as localised patterns with fractional diffusion dynamics. To reveal the fundamental computational roles of such activity patterns, we develop a normative model by constructing the responses of these patterns as spatiotemporal fractional motion modulated by external potential wells. We demonstrate that this model can explain the emergence of slow theta oscillations that are coupled to gamma oscillations as found in experimental studies; this cross-frequency coupling is analysed based on the first-passage between the local minima of the well. In addition, we illustrate that the fractional motion of the patterns enables a scale-free representation of space and time.

A COMPUTATIONAL MODEL OF VISUAL PATTERN MOTION PROCESSING BY MT NEURONS

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A large proportion of neurons in the Middle Temporal (MT) area of the extrastriate primate visual cortex are direction selective. When the MT area of the visual cortex is stimulated with plaid patterns, a range of cell specific responses are observed. Some of the MT neurons are pattern neurons, which respond optimally to the direction of the pattern motion, and some are component neurons, which are selective to the directions of the individual gratings. A current theory on the generation of pattern selectivity of MT neurons is based on a hierarchical relationship between component and pattern MT neurons, where V1 (primary visual cortex) direction selective cells provide input to component MT cells that then combine to drive pattern MT cells [1]. However, the theory is developed largely around the use in experiments of plaid stimuli that do not have terminators on the moving grating. Where the gratings cross in plaids, blobs are formed that move in the pattern direction. In human perceptual experiments, revealing the ends of the moving gratings (terminators) immediately breaks the illusion of the direction of pattern motion: the true direction of motion is perceived.

Here, we propose a computational model of the V1 and area MT for the processing of visual motion information. We developed a model that emphasizes the extraction of terminators by the motion processing system [2]. Based on the response in MT to specific combination of inputs from V1, we propose that some MT cells, labelled pattern cells, are better at extracting the direction of the terminators, while other cells are intermediate or component selective cells. The initial motion and form information are extracted by neurons in V1 by three different types of neurons with distinctive response characteristics: standard complex V1 cells, end-stopped V1 cells, and complex V1 cells with suppressive extra-classical receptive fields (RFs). The resulting visual information is transmitted to the neurons in MT for integration of local motion signals and segregation of overlapping stimuli.

The results show that the responses of the MT neurons are highly dependent on the values of two parameters: the excitatory input that they receive from the complex V1 neurons with extra-classical RFs and the inhibitory effect of the end-stopped neurons. The results also show the contrast dependency of the pattern motion preference of MT neurons; the level of the pattern selectivity of MT neurons drops significantly when the contrast of the bars is reduced. The temporal dynamics of the pattern and component MT neurons are also different; there is a delay in the detection of the pattern motion compared to the component motions of the stimuli.

The model provides an explanation of the mechanism involved in pattern and component motion selectivity of MT neurons. The model demonstrates that the degree of pattern or component selectivity in MT can be explained in terms of the relative strengths of the three V1 input types described above. Dominance of end-stopped V1 neurons in the model leads to pattern selectivity in MT, while dominance of V1 cells with extra-classical RFs results in component selectivity.

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DEPLOYING ITERATIVE TOMOGRAPHY FOR RECEPTIVE FIELD MAPPING

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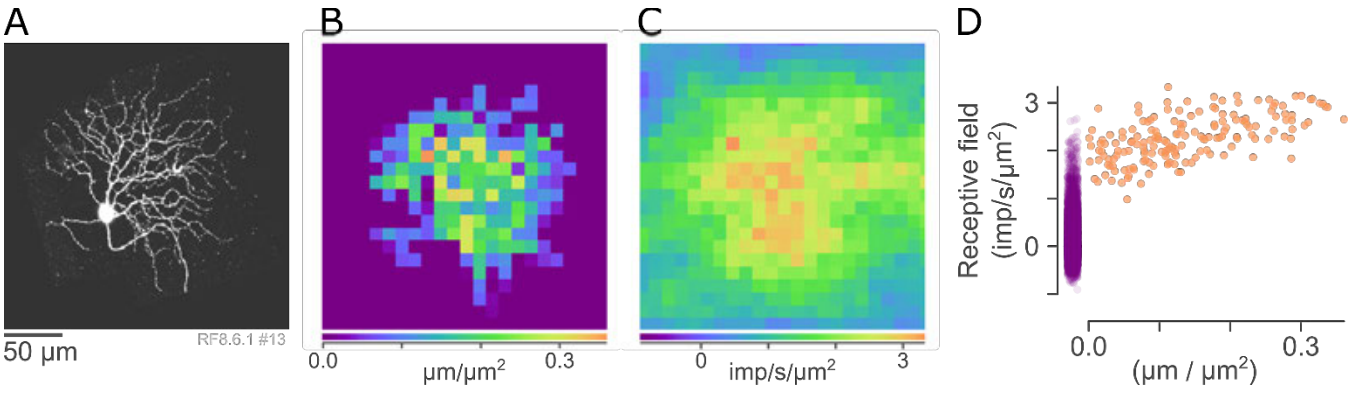
Receptive fields in the retina emerge from the dendritic morphology and synaptic inputs to retinal ganglion cells, the output neurons of the retina. These properties show great variability across the different classes of retinal ganglion cell; such functional diversity is one of the underpinnings of visual function. Receptive field structure has typically been studied using traditional stimuli such as drifting gratings which must be tuned to individual cells, or long exposures (in excess of 1h) to white-noise-type stimuli which are analysed by spike-triggered reverse-correlation. A new approach was recently proposed [1] in which bars are flashed at different orientations and positions and the receptive field is computed using an inverse Radon transform; however, the algorithms used in [1] obscure the fine details of the receptive field structure. Here, we harness recent advances in tomographic image analysis to produce high resolution receptive field maps in the retina using simultaneous algebraic reconstruction tomography. Receptive fields can be mapped for both classical (linear) and non-classical cells in the retina and are closely correlated to the underlying dendritic morphology of the cells. Receptive field mapping using iterative tomographic reconstruction can reproduce both the centre and surround mechanisms of the receptive field, as demonstrated by comparing the receptive fields with observed aperture tuning curves. The graphical abstract shows an example filled cell recorded in the retina (A) and the corresponding local dendritic field density (B), the receptive field as reconstructed from in-vitro patch-clamp recording (C), and the spatial correlation between the morphology and the physiology (D). In summary, iterative tomography is a powerful new technique for visual neuroscience which will permit new insights to the relation between neural structure and function.



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Intracellular delivery of nanoparticles via microelectrophoresis technique

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Nanoparticles with various properties and functions are of growing interest for biomedical research, such as in vivo and in vitro sensors, imaging agents and delivery vehicles of therapeutics. An effective method to deliver nanoparticles into the intracellular environment is still a major challenge and critical to many biological studies. Current techniques, such as intracellular uptake, electroporation and microinjection, have different benefits and limitations (e.g., aggregation and endosomal degradation of nanoparticles, high cell mortality and low throughput). We demonstrate application of the well-established microelectrophoresis technique for the first time to deliver nanoparticles into target cells using fine-tipped micropipettes, which overcomes some of these delivery difficulties. Semiconductive quantum dots were selected as the nanoparticles in this study as they are widely used for biomedical imaging and sensing due to having functionalized surfaces suitable for bioconjugation, adaptable photophysical properties for multiplexed detection, and superior stability for longer investigation times. We developed a method to prepare monodisperse suspensions of quantum dots with average hydrodynamic diameter of ~20nm, which demonstrated sufficient colloidal stability to prevent aggregation and blockages in the tip of micropipettes during ejection while enabling sufficient electrical conductivity for ejection and recording electrical activity of cells. Fine-tipped glass micropipettes with an average tip inner diameter of 206 nm for ejection but less than 500 nm to minimize the cell membrane damage and cell distortion were successfully fabricated. Finally, quantum dots were successfully delivered into living human embryonic kidney cells using small electrical currents through fine-tipped glass micropipettes. The delivered quantum dots were found to stay monodispersed within the cells for 2 hours. We believe that microelectrophoresis technique may serve as a simple and general strategy for delivering a variety of biocompatible nanoparticles intracellularly in various biological systems.

Optimising non-invasive brain-computer interface systems for free communication between naïve human participants

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Free communication is one of the cornerstones of modern civilisation. While manual keyboards currently allow us to interface with computers and manifest our thoughts, a next frontier is communication without manual input. Brain-computer interface (BCI) spellers often achieve this by decoding patterns of neural activity as users attend to flickering keyboard displays. To date, the highest performing spellers report typing rates of ~10.00 words/minute. While impressive, these rates are typically calculated for experienced users repetitively typing single phrases. It is therefore not clear whether naïve users are able to achieve such high rates with the added cognitive load of genuine free communication, which involves continuously generating and spelling novel words and phrases. In two experiments, we developed an open-source, high-performance, non-invasive BCI speller and examined its feasibility for free communication. The BCI speller required users to focus their visual attention on a flickering keyboard display, thereby producing unique cortical activity patterns for each key which were decoded using filter-bank canonical correlation analysis. In Experiment 1, we tested whether seventeen naïve users could maintain rapid typing during prompted free word association. We found that information transfer rates were indeed slower during this free communication task than during typing of a cued character sequence. In Experiment 2, we further evaluated the speller's efficacy for free communication by developing a messaging interface, allowing users to engage in free conversation. The results showed that free communication was possible, but that information transfer was reduced by voluntary textual corrections and turn-taking during conversation. We evaluated a number of factors affecting the suitability of BCI spellers for free communication, and make specific recommendations for improving classification accuracy and usability. Overall, we found that developing a BCI speller for free communication requires a focus on usability over reduced character selection time, and as such, future performance appraisals should be based on genuine free communication scenarios.