第6回新潟大学脳研究所共同研究拠点国際シンポジウム(プログラム)
6th BRI Symposium in Niigata (Program)

「意識を必要とする脳機能の神経メカニズム」
“Neural mechanisms of brain functions that require awareness”

25th PM - 27th AM, July, 2015

Center for integrated human brain science (6F)

Brain Research Institute (BRI), Niigata University

25th PM

13:00-13:05 Masatoyo Nishizawa Openning remarks by the director of BRI

Session 1: Cellular/Molecular mechanisms (chaired by Ryota Kanai & Yutaka Komura)

13:05-13:50 Katsuei Shibuki (BRI, Niigata Univ)

Bottom-up approach to visual awareness in mice

13:50-14:35 Takeshi Yagi (Osaka Univ)

Genetic bases for generating the complex neural networks in the brain

14:35-14:45 (Coffee break)

14:45-15:30 Takahiro Furuta (Kyoto Univ)

Introduction of morphological techniques for integrative brain science

15:30-16:15 Haruo Hosoya (ATR)

Understanding representations in visual cortex with hierarchical statistical models of natural images

16:15-16:25 (Coffee break)

Special lecture 1 (chaired by Toshiyuki Hirabayashi & Shinji Nishimoto)

16:25-17:25 Biyu Jade He (NIH, USA)

Slow cortical potentials in conscious perception and volition

17:30- Reception

Free discussion with speakers

26th AM

Session 2: Basic studies (chaired by Makiko Yamada & Shinji Nishimoto)

9:00-9:45 Ryota Kanai (Univ Sussex/ATR)

Roles of top-down prediction in visual awareness

9:45-10:30 Yutaka Komura (AIST)

Linking metacognitive signals to vision in monkeys and humans

10:30-10:40 (Coffee break)

10:40-11:25 Toshiyuki Hirabayashi (Univ Tokyo/NIRS)

Towards understanding the circuit mechanisms underpinning conscious retrieval of object memory in macaques

11:25-12:10 Atsushi Iriki (RIKEN)

Neurobiological mechanisms for emergence of the objective-self during primate brain evolution

12:10-13:10 (Lunch)

26th PM

Session 3: Applied studies (chaired by Takeshi Yagi & Katsuei Shibuki)

13:10-13:55 Makiko Yamada (NIRS)

Molecular mechanism of conscious self-perception

13:55:-14:40 Jun Miyata (Kyoto Univ)

Psychosis as a disorder of consciousness integration

14:40-14:50 (Coffee break)

Special lecture 2 & 3 (chaired by Takahiro Furuta & Masafumi Oizumi)

14:50-15:50 Naotsugu Tsuchiya (Monash Univ, Australia)

The no-report paradigm: an avenue for distilling the neural correlates of phenomenal consciousness

15:50-16:50 Jakob Hohwy (Monash Univ, Australia)

Better believe the free energy principle

17:00-18:30 Poster Session

27th AM

Session 4: Analytical studies (chaired by Ryota Kanai & Katsuei Shibuki)

9:00-9:45　Shinji Nishimoto (CiNet)

Modeling and decoding of human perceptual experiences

9:45-10:30　Masafumi Oizumi (RIKEN)

The integrated information theory of consciousness - theory and practice

10:30-10:40　(Coffee break)

Special lecture 4 (chaired by Haruo Hosoya & Jun Miyata)

10:40-11:40　Andrew Haun (Univ Wisconsin, USA)

Contents of consciousness and the structure of integrated information

11:40-11:45　Katsuei Shibuki　Closing remarks by the organizer

(問い合わせ先)

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Bottom-up approach to visual awareness in mice

Katsuei Shibuki

Department of Neurophysiology, Brain Research Institute, Niigata University, Japan

If a mouse model is established for investigating awareness/consciousness, it will be useful because of many experimental techniques available for mice. We found that mice have short-term memory of visual objects. In a memory-dependent task, a cue object was presented at center of the display in front of mice, and two choice objects were presented with a delay interval of 20 s. Mice could select the choice object, which was the same as the cue object, based on short-term memory. After the visual short-term memory sessions were finished, we confirmed that mice could differentiate a pair of alphabets, which they had never seen before, similarly based on short-term memory. These results indicate that mice can recognize and memorize visual objects as complex as alphabets.

Higher visual areas responsible for object recognition are unknown in mice. To identify the responsible area, we used an association memory paradigm. After mice were exposed a combination of an object and a sound, they could choose the object based on the associated sound cue only. We further investigated cortical responses to the sound cue using flavoprotein fluorescence imaging. The cortical responses to the sound cue were observed in the auditory cortex and a higher visual area located dorsally to the auditory cortex, suggesting that the activated higher visual area may play an important role in objects recognition. As expected, we found object-specific neuronal activity in the area using two-photon microscopy. Interestingly, the short-term memory, associative memory, and the memory based-cortical activities were not found in mice with reduced gene clusters of protocadherin α, suggesting that the diversity of the clustered cell-adhesion molecules plays an essential role in short-term memory.

The present results suggest that visual short-term memory may be embodied by sustained neural activities in the higher visual area. A logical consequence of the sustained activities is provocation of neural activities in numerous areas connected to the higher visual area. Analysis of these neural activities related to visual short-term memory may open a bottom-up approach to visual awareness in mice.

Genetic bases for generating the complex neural networks in the brain

Takeshi YAGI, Osaka University

Consciousness arises in the complex neural networks in the brain. To address the consciousness, we need to realize how to generate the complex neural networks in the brain during development. Recent physiological approaches reveal that the neural networks in the brain are complex small-world networks between regular and random, and also possess high clustered neuron groups. However, we have not yet understood mechanisms how to generate the complex small-world neural networks in the brain. In 1998, we discovered diverse genes encoding cadherin related-neuronal receptors (*CNR*s) from the mouse brains. The *CNR*s belong to clustered protocadherins (*Pcdh*s) that are constituted by 58 members in mice (53 in humans). Approximately 50 members of the clustered Pcdhs are stochastically expressed in individual neurons in distinct combinations, and induces cell-adhesion between the cellular membranes. Namely distinct combination Pcdhs provide distinct cell-adhesion activities in individual neurons. In simulation analyses, when their cell-adhesion activities make specific neural networks between individual neurons, the complex small-world neural networks spontaneously generate. Recent physiological approaches also revealed that the high clustered neural networks prepare during development. In this talk, I would like to discuss the complex neural networks and approaches for consciousness by using genetic codes.

Ref.

1. Diversity revealed by a novel family of cadherins expressed in neurons at a synaptic complex. Kohmura et al. ***Neuron*** 20, 1137-1151, (1998)
2. Monoallelic yet combinatorial expression of variable exons of the protocadherin-alpha gene cluster in single neurons. Esumi et al. ***Nature Genetics*** 37, 171-176, (2005)
3. Molecular codes for neuronal individuality and cell assembly in the brain. Yagi T ***Front. Mol. Neurosci.*** 5, 45. (2012)
4. Developmental epigenetic modification regulates stochastic expression of clustered Protocadherin genes, generating single neuron diversity. Toyoda et al. ***Neuron*** 82, 94-108 (2014)

Introduction of morphological techniques for integrative brain science

Takahiro Furuta
Morphological Brain Science, Graduate school of Medicine, Kyoto University

Higher brain functions which require awareness, attention and memory are considered to be yielded by the neural circuits which consist of complicated connections of numerous neurons. To understand the mechanisms of the brain functions, we need to analyze relationship between firing pattern of the neurons and structure of the circuits (, which include distribution of functional molecules). Here, I would like to introduce morphological techniques for analysis of neural circuit structures: 1) visualization of neurons by virus vectors, 2) plasmid injection into recorded neurons, and 3) three-dimensional analysis of ultrastructures. Since the fundamental element of the neural circuits is single neuron, we first aimed to develop a method for visualizing single neurons. When we used virus which express membrane-targeted GFP (palGFP), not only the thick dendrites but also the long-projecting axons of infected neurons were labeled nicely. On the other hand, it is also possible to label only dendrites with virus expressing dendrite-targeted GFP. Separating dendrites from axons is important to analyze neural connections in the complicated circuits. Secondly, we tried to transfect plasmids encoding such the useful reporter proteins into single recorded neurons in awake animals. Technique of plasmid transfection into single neurons in vivo was developed by Oyama et al. (2013). We applied this technique to awake animals performing a task. We succeeded in visualizing morphology of long projecting axons derived from neurons whose firing properties were analyzed in awake animals. Finally, ultrastructure of the labeled axons were analyzed by electron microscopy. Synaptic connection is one of essential factors in neural networks and is so small that we have to use electron microscopy to observe the synaptic structure. Using a electron microscope which was equipped with a focused ion beam, we obtained three-dimensional data of ultrastructures which contained the labeled axons. Overall, combining these techniques, we can plan an experiment where morphology of single neurons recorded in an awake animal performing a task is analyzed at a level of three-dimensional data of ultrastructures.

Understanding representations in visual cortex with hierarchical statistical models of natural images

Haruo Hosoya, ATR, Japan
(joint work with Aapo Hyvärinen)

How does our visual system achieve the remarkable ability to recognize and understand our surrounding visual scenes? In traditional visual neuroscience, numerous experimental studies have revealed various response properties of single cells in lower to higher visual areas. Although these studies made tremendous contributions to the understanding of overall functions in those visual areas, precisely how the visual system represents and processes visual information remains to be a mystery.

In this situation, theoretical studies might provide valuable insights. One direction has been suggested in the seminal study of a sparse coding model of natural images (Olshausen and Field, 1996), which well explained receptive field characteristics in V1. In this talk, I propose to extend this approach to the understanding of properties in visual areas beyond V1, using multi-layered models that assume sparse-coding-like computation to be performed in each stage of visual hierarchy. Specifically, I first present that a three-layered hierarchical sparse coding model can qualitatively and quantitatively reproduce three relatively complex properties of local orientation organization that has been found in past experiments of macaque V2. Then, I show that an extended model with four layers also explains two further complex properties related to shape representations in V4. In these, I will expose the internals of the models and discuss potential neural representations in these visual areas. Lastly, I touch on potential roles of feedback processing in the visual system in learning and inference of complex visual representations in connection to visual consciousness.

Slow cortical potentials in conscious perception and volition

Biyu Jade He

NIH, USA

I will discuss recent work from my laboratory on the functional roles of slow cortical potential in conscious perception and volition. Despite intense recent research, the neural correlates of conscious visual perception remain elusive. The most established paradigm for studying brain mechanisms underlying conscious perception is to keep the physical sensory inputs constant and identify brain activities that correlate with the changing content of conscious awareness. However, such a contrast based on conscious content alone would not only reveal brain activities directly contributing to conscious perception, but also include brain activities that precede or follow it. To address this issue, we devised a paradigm whereby we collected, trial-by-trial, measures of objective performance, subjective awareness, and the confidence level of subjective awareness. Using magnetoencephalography recordings in healthy human volunteers, we dissociated brain activities underlying these different cognitive phenomena. Our results provide strong evidence that widely distributed slow cortical potentials (SCPs) correlate with subjective awareness, even after the effects of objective performance and confidence were both removed. The SCP correlate of conscious perception manifests strongly in its waveform, phase, and power. In contrast, objective performance and confidence were both contributed by relatively transient brain activity. These results shed new light on the brain mechanisms of conscious, unconscious, and metacognitive processing.

Roles of top-down prediction in visual awareness

Ryota Kanai

Sackler Centre for Consciousness Science, University of Sussex, UK

There is an increasing interest in the roles of top-down predictions in shaping sensory experiences. We have previously shown psychophysically that metacognitive insight into perceptual experience is enhanced by prior expectations (Sherman et al., 2015). Recent work suggests that ongoing alpha oscillations rhythmically modulate perception and reflect the readiness of the perceptual system. Here, we asked whether this modulation reflects rhythmic top-down influences of perceptual prior expectations. To address this question, we collected scalp EEG while participants performed a detection task which orthogonally manipulated prior expectations of target presence or absence, and the availability of full attention. Critically, our design enabled us to time-lock to both target present and absent trials, allowing us to calculate independent measures of detection sensitivity and decision threshold. Results showed that the top-down influence of expectations on decision threshold underwent rhythmic modulation that followed the phase of spontaneous occipital alpha oscillations. Trial-by-trial retrospective confidence ratings were modulated by alpha phase, such that they reflected cycles in top-down and bottom-up influences on perception. Collectively, our data provide evidence for a rapid, periodic alternation between top-down and bottom-up influences on decision at early stages of perceptual processing, and before target appearance. These results extend recent work implicating a causal influence of alpha/beta oscillations in communicating top-down and have implications for predictive coding theories of perception and consciousness by indicating that prior expectations impose their influence at specific phases of neuronal oscillations.

Linking metacognitive signals to vision in monkeys and humans

Yutaka Komura
National Institute of Advanced Industrial Science and Technology, Japan

When we are aware of a sensory event, our subjective experience has two aspects: one involves perceptual content (e.g., an upward moving red ball) and the other refers to metacognitive one (e.g., a feeling of knowing that we have actually perceived it). Confidence is regarded as a consequence of metacognition. Previous studies have suggested that sensory awareness emerges from the thalamo-cortical complex.

To address the issue of what the visual thalamus encodes in the visual awareness, we first recorded single-unit activities in the visual thalamus while monkeys performed the two tasks: a perceptual categorization task which was used to evaluate perceptually experienced content, and a metacognitive task which was used to explore the subjects' confidence levels. We found the majority of pulvinar responses decreased when monkeys chose escape options during a metacognitive task, suggesting less confidence in their perceptual categorization. Second, we performed the human psychophysics with subjective reports of confidence in visual discrimination tasks. We found that human's confidence scores as a function of stimulus ambiguity and behavioral outcome showed the same patterns as the modulation of monkey's pulvinar activities. These data indicate the monkeys and humans shared a computation for metacognition, thereby potentially relating the animal data to humans' subjective experiences in vision.

Towards understanding the circuit mechanisms underpinning conscious retrieval of object memory in macaques

Toshiyuki Hirabayashi
Univ Tokyo (NIRS)

Inferior temporal (IT) cortex in monkeys locates at the final stage of visual object processing. Although neuronal responses in this cortical region have been characterized with various task paradigms, it remains largely unknown how individual neurons interact to form functional circuits for implementing cognitive demands. Here, I will discuss microcircuit operations in macaque IT cortex in an object-association memory task, focusing on two different topics. The first topic is the circuit operation for object memory retrieval. We found the directed signal flow between functionally different classes of memory neurons that generates memory retrieval signal of visual objects. The second topic is hierarchical object processing across cortical areas. The representation of a given feature of visual objects has been believed to be constructed in the cortical area where that representation is prevalent. However, another possible scheme is that preparatory codes of a given feature are created in a lower-order area before their increase to become predominant in a higher-order area. In the object association task paradigm, we found the microcircuits that generate and increase the representations of object associations in successive lower- and higher-order areas in the IT cortex, respectively, consistent with the latter hypothesis. Together, these results demonstrate that examinations of microcircuit operations in monkeys performing an object association memory task provides the principles of cortical computations for representation and memory retrieval of visual objects.

Neurobiological mechanisms for emergence of the objective-self during primate brain evolution

Atsushi Iriki
RIKEN Brain Science Institute

Hominin evolution has been a continuous addition of various novel cognitive capacities, including manufacture and usages of tools and establishment of language. Such intelligence has affected on the ecology of their habitat to be modified quite rapidly. Human primate ancestors' dramatically expanded brains to adapt such improved environment resulted in addition of novel brain areas, which subserved further intelligent cognitive capacities to develop. Hence, human primates have constructed novel niche for each of these ecological, neural, and cognitive domains, of which interactions accelerated their evolution – namely, "Triadic Niche Construction". Thus emerged human intelligence should be structured to comprise a part of dynamic patterns of holistic terrestrial ecosystem. Neurobiological mechanisms to acquire novel tool-use skills in non-human primates would shed light on such properties of human intelligence developed through the course of evolutionary processes.

An important problem for the tool-using brain to solve is how to 'regard' a tool—as one's own body-part or merely as an external object. This would lead to two important aspects emerging in the mind of the tool-user: first, explicitly realizing that one's own body is composed of multiple parts that are spatially arranged and intentionally controllable; and second, that those body parts could be compatible with external objects, namely tools. This establishment of parity between body parts and tools enables tool users to incorporate tools into their own body schemas. Moreover, tool users can then 'objectify' their own body parts, and eventually should be able to objectify themselves entirely — to observe themselves mentally from a third-person perspective. Finally, we might hypothesize that these 'self-objectification' processes establish equivalence in the mind of the agent between other agents and the self, including understanding that tools are equally compatible for both. The result is an emergence of human mind that possesses the concept of the objective-self.

Molecular mechanism of conscious self-perception

Makiko Yamada
National Institute of Radiological Sciences, Japan

Contrary to our intuition, most of us possess a biased self-perception, called "the superiority illusion". This is a tendency to evaluate oneself as superior to average along various dimensions, such as intelligence, cognitive ability, and possession of desirable traits. A positive outlook of the self is an essential aspect of the human mind. It motivates future goals, and is deep-rooted in the process of human evolution. Possessing this illusion is also important for mental health, as depressed patients appear to have a more realistic perception of themselves, dubbed "depressive realism". Our recent study revealed the interrelationship between functional connectivity and striatal dopaminergic neurotransmission that generate this illusion, using resting-state fMRI and PET. A striatal functional connectivity, regulated by inhibitory dopaminergic neurotransmission, determines inter-individual variations in the superiority illusion. We further revealed that blockage of the dopamine transporter, which enhanced the level of dopamine in striatum, increased the degree of superiority illusion. Similarly, the association between the striatal dopamine release and the superiority illusion was observed in depressed patients after antidepressant treatment. These findings suggest that dopamine acts on striatal dopamine receptors to suppress striatal functional connectivity, leading to disinhibited approaches to positive self-evaluation. These findings help us to understand how this key aspect of conscious human mind is biologically determined, and will point to treatments for depressive symptoms by targeting specific molecules and neural circuits.

Psychosis as a disorder of consciousness integration

Jun Miyata
Department of Psychiatry
Graduate School of Medicine
Kyoto University, Japan

Catatonia is an altered state of consciousness with impairment of volition, perception, and motor function, and clinically expresses such symptoms as catalepsy, echolalia, and stereotypy. Catatonia is treated with benzodiazepines and electro-convulsive therapy (ECT), however it often relapses. Catatonia was traditionally considered as a type of schizophrenia, however nowadays is considered as a psychotic syndrome that occurs during the course of many neuropsychiatric diseases. There is limited number of studies about the neural basis of catatonia, which postulate involvement of brain regions such as the prefrontal cortex, sensorimotor cortex, thalamus and basal ganglia in catatonia (Fink and Taylor, 2003). However, it is unclear what kind of abnormality in the functioning of the neural networks consisting of these brain regions causes catatonia. To elucidate the functional abnormality of neural networks, functional magnetic resonance imaging (fMRI) during cognitive tasks is used, however it is difficult for patients in catatonic state to perform such cognitive tasks because of the nature of disorder. On the other hand, fMRI during at rest (resting state fMRI: rsfMRI) does not require certain cognitive tasks, and is recently widely used to investigate abnormal connectivity of neuropsychiatric disorders. The default mode network (DMN), which is involved in self and preparation for future events, and the sensorimotor network (SMN), which is connecting sensory and motor systems, are known to be intrinsic neural networks that are active at rest. These networks are considered to be deeply relevant to catatonia. In addition, the medial prefrontal lobe and parietal cortex are the core nodes of the DMN, and the SMN involves somatosensory area, both of which consist of basal ganglia-thalamo-cortical circuits. Therefore, the abnormalities of connectivity within and between the DMN, SMN, and basal ganglia-thalamo-cortial circuits might be the neural underpinnings of catatonia, and rsfMRI would be suitable for investigation of such abnormalities. We are collecting rsfMRI data of catatonia patients in pre and post treatment, and will discuss on the preliminary results.

The no-report paradigm: an avenue for distilling the neural correlates of phenomenal consciousness

Naotsugu Tsuchiya
School of Psychological Sciences, Faculty of Biomedical and Psychological Sciences, Monash University, VIC, 3800, Australia

The ultimate goal of consciousness research is to reveal the neural basis of phenomenal experience. To study phenomenology, however, third-person experimenters seem obliged to resort to verbal or manual reports from the studied subjects to know about the presence or absence as well as the quality of consciousness. However, here we argue that requirement of reports have biased much of the search for the neural correlate of consciousness (NCC) over the last decades. Have we not confounded the neural causes of consciousness with the consequences of consciousness? Did we not confuse the processes that generate visual experience with the cognitive processes enabling us to decide on the conscious content, attend to it, store it, and report about it? Recently, various studies tried to dissociate neural activity that gives rise to conscious phenomenology from the activity that enables the reports via executive and cognitive functions, including attention and working memory. In particular, a no-report paradigm has been utilized to study conscious experience in the absence of report. We will discuss the advantages and disadvantages of report-based and no-report paradigms and ask how these jointly bring us closer in understanding the neural basis of conscious phenomenology.

Better believe the free energy principle

Jakob Hohwy
Monash University, Australia

Many now believe that key aspects of perception and cognition are characterized by predictive processing. The free energy principle, in contrast, is not very widely believed. Using general considerations from epistemology and philosophy of science, I argue that, if one believes predictive processing characterizes perception and cognition, then one had better also believe the free energy principle. Further, I discuss three separate objections to the free energy principle, concerning the level of evidence for it, its falsifiability, and its wider implications. Even though the free energy principle seems controversial and esoteric, there are thus good reasons for believing it. Finally, I consider what, if anything, believing the free energy principle might tell us about the fundamental nature of consciousness.

Modeling and decoding of human perceptual experiences

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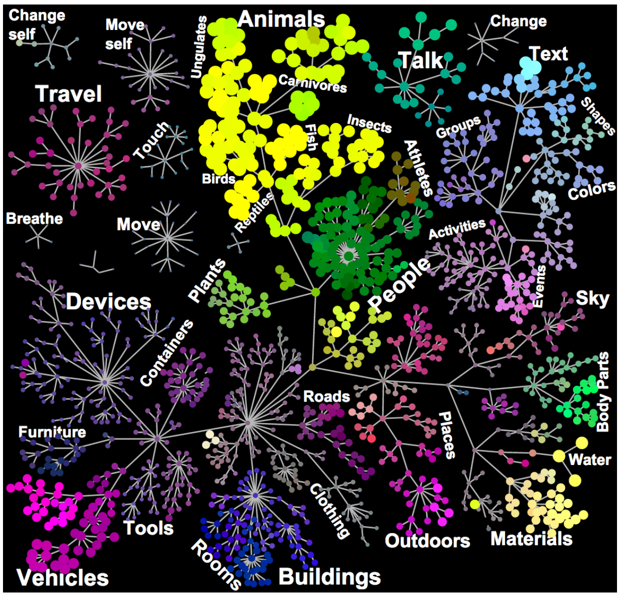
Perceptual experiences

Decoded experiences from human brain activity

A tree representation of human semantic perception



Advancement in measuring and analyzing large-scale bio-imaging data allows us to study brain activity evoked under complex, natural perceptual conditions. Here I present an encoding modeling framework as a powerful tool to decipher brain activity underlying our experiences. The modeling framework aims to build predictive models of brain activity using high-dimensional representations of perceptual and cognitive features. We have used this framework to model data acquired in both neurophysiological and fMRI experiments. These studies have provided new insights about natural visual coding, including spatiotemporal and semantic representation in the visual system and their attentional modulation. The framework can also be used to decode objective and subjective experiences from brain activity. The modeling framework is quite general and has many potential applications for studying our perception and cognition.

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The integrated information theory of consciousness – theory and practice

Masafumi Oizumi

RIKEN, Brain Science Institute

Assessing the level of consciousness based on the activity of the brain is an important issue, yet it is one of the most challenging problems in neuroscience. Brain-based measures of the level of consciousness are most required for assessing the conscious state of those who cannot speak or move (e.g., under anesthesia, in the vegetative state, etc), where behavioral unresponsiveness tends to be confused with unconsciousness. The Integrated Information Theory (IIT) of consciousness has potential importance for this purpose. IIT is an attempt to mathematically characterize consciousness both in quality and quantity by analyzing informational relationships between elements in a system. As for the quantitative aspect of consciousness, IIT predicts that the amount of integrated information, which measures how much information is integrated in a system, corresponds to the level of consciousness. According to IIT, the brain significantly loses the ability to integrate information when consciousness is lost. If the prediction of IIT is correct, the level of consciousness could be measured by quantifying the amount of integrated information in brain activities. There are some supportive evidences for the prediction of IIT. However, there has not been yet direct evidence because it is computationally intractable to exactly compute the integrated information in real neural data.

In this talk, we briefly review the essence of IIT and propose a practical method to quantify integrated information in real neural data. As a proof of concept, we apply the proposed method to electrocorticogram (ECoG) data recorded in monkeys before and after anesthesia. We discuss the implications of our study and future prospects for consciousness studies.

Contents of Consciousness and the Structure of Integrated Information

Andrew Haun, Department of Psychology, University of Wisconsin-Madison, USA

The various aspects of conscious experience are experienced as an integrated whole, a unified phenomenon that is intrinsic to the experiencer. How can understand such an intrinsic, integrated state in terms of neuronal mechanisms? Standard practice in neuroscience is to decompose a system into independent parts, understood in terms of their extrinsic relationships. For example, a current focus in the neuroscience of consciousness is the search for neural correlates of perceptual experience, where perceptual states are psychophysically controlled and correlated neural states – whatever they may be – are observed. However, these studies inevitably yield measures of neural activity that are qualitatively unlike perceptual experience –e.g. mutual information between stimulus and neural state, coherence between neural loci, or certain band-limited oscillations within an area. What can be done to break out of this correlational approach?

In contrast to the standard approach, the *integrated information theory of consciousness* (IIT; Tononi, *BMC Neuroscience*, *5*(1), 42) starts from a phenomenological basis. The theory axiomatizes the fundamental properties of consciousness and the postulates how these properties must manifest in a neural system. A key concept is of integrated information, or *phi*. Defined from the internal perspective of a neural system, phi for a system AB is the information generated by the whole system (AB) above and beyond its parts (A and B, separately). According to the theory, contents of consciousness (e.g. a particular sensory experience) are completely determined by the structure of causal interactions between parts of a system that contribute to the system's phi. This causal structure would be reflected in the integrated information as computed over all the possible parts of a system (e.g., for a system ABC, the possible parts include AB, BC, CA and ABC). We refer to this exhaustive description of system integration as the *integrated information (phi) structure*. The phi structure shares key characteristics with perceptual experiences: it is integrated, intrinsic, and hierarchically structured. There is thus strong *a priori* reason to expect that phi structure should mirror the contents of consciousness.

For our study, we tested whether the phi structure of neural activity correlates with contents of consciousness. We computed phi structures for groups of intracranial electrode (ECoG) recordings obtained from the cerebral cortices of epilepsy patients. When we dissociated the contents of visual consciousness from the physical stimuli by using visual illusions, we found that the phi structure correlates with subjective percept independent of physical stimulus. In contrast to phi, other structural measures of information content (entropy and mutual information) do not correlate closely with the contents of consciousness. We have replicated this result in several patients; in a particularly striking case, phi structures generated in on patient's fusiform cortex map closely to conscious perception of faces, across multiple stimulus paradigms. Our results show that the integrated information theory generates testable predictions about how neural activity corresponds to contents of consciousness, and strongly suggest that such tests will elucidate the neural mechanisms supporting the fundamental properties of conscious experience.