
Convergent Science of Mind and Brain. Woods Hole 2015



Woods Hole, Boston, USA, 10-22 August 2015

<http://csnetwork.eu/activities/woodshole2015>

Organizers: John Lisman, Brandeis University, MA, USA; Paul Verschure, ICREA, University Pompeu Fabra, Barcelona Spain

In collaboration with: Dr. **Anna Mura** (UPF, SPECS) and, **Cesar Renno-Costa** (Univ. Federal Rio Grande Norte, Brasil), **Giovanni Maffei** (UPF SPECS), **Diogo Pata** (UPF SPECS).

We are coming to an era where one of the most urgent challenges in neuroscience is the problem of large-scale integration. We need to know how the brain as a whole functions together.

Program:

- Mon. Aug 10** **Morning** lecture at MB L by Fiete on grid cells
Afternoon John Lisman ----- New model of hippocampal place system
- Tues. Aug 11** **Morning** Cesar Renno-Costa ----- Mechanism of rate mapping
----- Honi Sanders
Afternoon: Paul Vershure: DAC -----multi-level control of behavior
- Wed. Aug 12** Matt Van der Meer ----- Coordinate function of hippocampus and
Basal ganglia
- Thur. Aug 13** Adrian Haith ----- Organization of Motor Control
- Frid. Aug 14** Bjorn Merker----- Subcortical control of behavior by the colliculus
- Sat. Aug 15** 2:30 **Discussion on consciousness** with Jean Paul Changeux & others.
5:00 **Cocktail party on roof**
- Sun. Aug 16** 3:30 **View of the Movie “HER”**
5:30 **Discussion on consciousness** and **Pizza dinner**
- Mon. Aug 17** Nicholas Hatsopoulos ----- Motor Cortex
After dinner: Adam Johnson of the “Johnson and Redish experiment”
- Tues. Aug 18** **Morning** Tony Prescott-----Coordination of a sensory-motor
system
Afternoon discussion with Michael Frank

Wed. Aug 19 NOTE: Michael Frank and Josh Tenenbaum are presenting from 9 to 12 in the Computational Neuro course.

Tomoki Fukai----- Coordination of motor cortex

Thur. Aug 20 NOTE: J. Lisman is presenting from 9 to 10:30 to the Computational Neuro. Course his work on Schizophrenia.

David Redish-----Hippocampus and orbitofrontal cortex

Frid. Aug 21 Morning: David Redish discusses path integration

Afternoon --- ALL ---- wrap up

Meeting format

The format of the meeting is organized so as to construct a collective notion of brain architecture by carefully analyzing the work we have done individually and extract main principles and questions from that for our discussion. We will dedicate 1 day to the work and ideas of each one of us. The day starts with a formal presentation (~ 1hr) that articulates the main principles of brain function and organization that the presenter would like to be the basis for the detailed discussion over the day. The goal of this presentation is not to justify the ideas with data, but to articulate the overall vision (speculative or proven) of the presenter. We hope that specific hypotheses and open question might become clear by this point. Indeed, it would be helpful if presenters would send us a list of these hypotheses and questions before the meeting; we'll then share these with the group.

The rest of the day will then be dedicated to investigating and discussing these in detail.

Our goal is to make our dialogue as concrete as possible by defining computational principles that could be included in computational model. If possible new principles might be immediately incorporated into a working model by the resident computational neuroscience team.

We will collect questions and observations in a shared document for which you will receive an invitation. Similarly you can access a repository with core papers from the participants in a shared directory that will be shared with you. In this directory you will find a dedicated folder that contains a few papers that document the computational models that we will have available during the workshop.

Key concepts:

Goal-directed behavior: sensitivity to current value; generate action sequences to produce desired action and use simulator to do so even for novel situations. Consequences of action can be predicted.

Habit system behavior: stimulus/response; involves dorsolateral striatum, its afferent sensorimotor cortex and infralimbic cortex.

Simulator: The one concrete example we have of a simulator is the grid cell network. It contains an x-y coordinate system on which position is represented by a bump of activity. This bump can be moved by an artificial velocity vector (AAV), thereby producing linear mind-travel by integration (Fiete). The system can be used to evaluate potential movement directions by

computing whether a given novel movement direction will intersect with a known goal site. Generation of AAVs requires a **cognitively driven controller (CDC)**.

Simulator provides cue for sequence recall: According to this new concept (Lisman), linear mind-travel provided by the grid cells may intersect with a memory path stored in the hippocampus. When this happens, subsequent positions along the non-linear path, as encoded by hippocampal synapses, may dominate the sequence output of the hippocampus (as in Johnson and Redish).

Vicarious Trial and Error: A very slow type of non-habit behavior that appears to involve deliberative consideration of different alternatives: at the choice point of the maze, the animal stops, rears, and sequentially turns to different arms of the maze (see Johnson and Redish).

Affordance Map/Cognitive Map: According to this concept, there are fundamental cognitive coordinates (e.g., approach/avoid; love/hate) that can be mapped. A further possibility is that position in this map can be moved by a process of integration of motivational signals in a manner akin to the way velocity moves position representation in the grid cell system.

Sequence Representation: According to this concept, we should move away from the idea of hierarchical states and entertain the possibility of hierarchical sequences.

Consciousness: that which is not habit. Characterized by sensory awareness of thought (action goals).

Abstract of works to be presented

New model of place system: Sanders, Renno-costa, Idiart, Lisman

The hippocampal/entorhinal place system has many cell types, but how they function together remains unclear. Here we propose that the fundamental function of grid cells is to produce mind-travel, a process that allows access to associations with potential upcoming positions. To account for properties of phase precession, we propose that mind travel occurs selectively during the second half of each theta cycle (driven by head-direction cells); in the first half, current place is computed by combining sensory information from the lateral entorhinal cortex with path integration information from the medial entorhinal cortex. Because the computations that produce mind-travel and path integration are difficult to

combine, we suggest that path integration is computed in a separate network.

[Trends Cogn Sci](#). 2014 Dec;18(12):647-57. doi: 10.1016/j.tics.2014.06.011. Epub 2014 Aug 23.

Internally generated sequences in learning and executing goal-directed behavior.

[Pezzulo G](#)¹, [van der Meer MA](#)², [Lansink CS](#)³, [Pennartz CM](#)⁴.

A network of brain structures including hippocampus (HC), prefrontal cortex, and striatum controls goal-directed behavior and decision making. However, the neural mechanisms underlying these functions are unknown. Here, we review the role of 'internally generated sequences': structured, multi-neuron firing patterns in the network that are not confined to signaling the current state or location of an agent, but are generated on the basis of internal brain dynamics. Neurophysiological studies suggest that such sequences fulfill functions in memory consolidation, augmentation of representations, internal simulation, and recombination of acquired information. Using computational modeling, we propose that internally generated sequences may be productively considered a component of goal-directed decision systems, implementing a sampling-based inference engine that optimizes goal acquisition at multiple timescales of on-line choice, action control, and learning.

Hippocampal Projections to the Ventral Striatum: From Spatial Memory to Motivated Behavior

(in: "Space, Time & Memory in the Hippocampal Formation" (Knierim JJ and Derdikman D, eds., Springer. E-mail author at mvdm@dartmouth.edu if you'd like a PDF of the chapter.)

Matthijs A.A. van der Meer, Rutsuko Ito, Carien S. Lansink,
and Cyriel M.A. Pennartz

Multiple regions of the hippocampal formation project to the ventral striatum, a central node in brain circuits that subserve aspects of motivation. These projections emphasize information flow from the ventral (temporal) pole of the hippocampus and interact with converging projections and neuromodulatory inputs upon arrival in the ventral striatum. Simultaneous neural recordings in the rat show that ventral striatal activity displays intricate timing relationships with the hippocampus, spanning multiple timescales and behavioral states, such as theta phase precession during reward approach and reactivation of place-reward associations during sleep. Disconnection of the hippocampus and ventral striatum results in impairments in the use of spatial information for place preference, as well as in location-appropriate responding to reward-predictive cues. Together, these findings indicate that spatial and contextual information from the hippocampus shapes reward-predictive activity in the ventral striatum, which in turn contributes to the learning and expression of place-reward associations.

[Biol Cybern](#). 2013 Dec;107(6):711-9. doi: 10.1007/s00422-013-0571-5. Epub 2013 Oct 2.

Adaptive properties of differential learning rates for positive and negative outcomes.

[Cazé RD](#)¹, [van der Meer MA](#).

The concept of the reward prediction error—the difference between reward obtained and reward predicted—continues to be a focal point for much theoretical and experimental work in psychology, cognitive science, and neuroscience. Models that rely on reward prediction errors typically assume a single learning rate for positive and negative prediction errors. However, behavioral data indicate that better-than-expected and worse-than-expected outcomes often do not have symmetric impacts on learning and decision-making. Furthermore, distinct circuits within cortico-striatal loops appear to support learning from positive and negative prediction errors, respectively. Such differential learning rates would be expected to lead to biased reward predictions and therefore suboptimal choice performance. Contrary to this intuition, we show that on static "bandit" choice tasks, differential learning rates can be adaptive. This occurs because asymmetric learning enables a better separation of learned reward probabilities. We show analytically how the optimal learning rate asymmetry depends on the reward distribution and implement a biologically plausible algorithm that adapts the balance of positive and negative learning rates from experience. These results suggest specific adaptive advantages for separate, differential learning rates in simple reinforcement learning settings and provide a novel, normative perspective on the interpretation of associated neural data

On the brain's global task structure

Woods Hole contribution by Bjorn Merker

To understand large-scale integration in the brain - how the different parts of the brain work together to orchestrate coherent behavior - involves getting our analytic categories to match the way the brain has divided up its functional task among its different parts and pathways. The brain's own functional division of labor need not conform to the way our language has divided up the function space for us. We hardly expect, for example, to see the intuitive concept of a "memory function" neurally implemented in a unique structure dedicated to that function, and it alone, in an operational brain.

Nor should we expect the functional organization of the neocortex to mirror that of the brain as a whole. The neocortex is but one brain component among many, and its organization presumably reflects the demands of whatever function it performs as part of the brain's over-all division of labor. Its relative structural redundancy suggests that it performs a rather unitary function for the many modalities that make use of it. Do we know what that function is? If not, how can we hope to know the place of neocortex in the brain's global task structure?

If there is any part of the brain whose organization might tell us something fundamental about the brain's own operational categories, it is that of the brainstem. There was a time when something much like what we call the brainstem was the entire brain of sensing and behaving mobile creatures. The basic circuitry that served all their behavioral needs is still with us. It was the new parts added on top of it (at its rostral end) that underwent spectacular change in the course of vertebrate evolution. The conserved nature of the complex sensory, motor, and motivational brainstem circuitry means that it served the needs of the front end additions - including those of an expanding neocortex - well, and accordingly is likely to exhibit organizational principles that bear directly on the brain's global division of labor.

I will draw on the functional organization of the brainstem pathways descending to the primary motoneurons themselves to make several points about global operational principles that are essential for our understanding of large-scale integration in the brain. There is, for example, a brainstem system for "orienting" that is anatomically distinct from the system for "engagement". The orienting system (responsible for gaze control) invariably *leads* the engagement system (responsible for a wide range of manipulative activities) in the overt execution of behavior, and does so down to the fine details of those manipulative activities (to

be illustrated by a video demo).

This bears directly on our conception of large-scale integration in the brain, all the more so since it is emerging that the final decisions of the orienting system are not made at the cortical level, but in the roof of the midbrain. That is where priority for triggering the very next gaze movement (the "saccadic command") is determined, on the basis of integrating a staggeringly diverse set of afferents. Among these, cortical ones are prominent, either by direct projection or indirectly, via the basal ganglia, but they are far from alone. I am looking forward to discussing these matters and more when we meet in Woods Hole before long.

[Front Psychol.](#) 2013 Aug 9;4:501. doi: 10.3389/fpsyg.2013.00501. eCollection 2013.

The efference cascade, consciousness, and its self: naturalizing the first person pivot of action control.

[Merker B](#)¹.

The 20 billion neurons of the neocortex have a mere hundred thousand motor neurons by which to express cortical contents in overt behavior. Implemented through a staggered cortical "efference cascade" originating in the descending axons of layer five pyramidal cells throughout the neocortical expanse, this steep convergence accomplishes final integration for action of cortical information through a system of interconnected subcortical way stations. Coherent and effective action control requires the inclusion of a continually updated joint "global best estimate" of current sensory, motivational, and motor circumstances in this process. I have previously proposed that this running best estimate is extracted from cortical probabilistic preliminaries by a subcortical neural "reality model" implementing our conscious sensory phenomenology. As such it must exhibit first person perspectival organization, suggested to derive from forming requirements of the brain's subsystem for gaze control, with the superior colliculus at its base. Gaze movements provide the leading edge of behavior by capturing targets of engagement prior to contact. The rotation-based geometry of directional gaze movements places their implicit origin inside the head, a location recoverable by cortical probabilistic source reconstruction from the rampant primary sensory variance generated by the incessant play of collicularly triggered gaze movements. At the interface between cortex and colliculus lies the dorsal pulvinar. Its unique long-range inhibitory circuitry may precipitate the brain's global best estimate of its momentary circumstances through multiple constraint satisfaction across its afferents from numerous cortical areas and colliculus. As phenomenal content of our sensory awareness, such a global best estimate would exhibit perspectival organization centered on a purely implicit first person origin, inherently incapable of appearing as a phenomenal content of the sensory space it serves.

[Neuroimage.](#) 2014 Sep;98:147-58. doi: 10.1016/j.neuroimage.2014.04.076. Epub 2014 May 9.

Contributions of the cerebellum and the motor cortex to acquisition and retention of motor memories.

[Herzfeld DJ](#)¹, [Pastor D](#)², [Haith AM](#)¹, [Rossetti Y](#)³, [Shadmehr R](#)¹, [O'Shea J](#)⁴.

We investigated the contributions of the cerebellum and the motor cortex (M1) to acquisition and retention of human motor memories in a force field reaching task. We found that anodal transcranial direct current stimulation (tDCS) of the cerebellum, a technique that is thought to increase neuronal excitability, increased the ability to learn from error and form an internal

model of the field, while cathodal cerebellar stimulation reduced this error-dependent learning. In addition, cathodal cerebellar stimulation disrupted the ability to respond to error within a reaching movement, reducing the gain of the sensory-motor feedback loop. By contrast, anodal M1 stimulation had no significant effects on these variables. During sham stimulation, early in training the acquired motor memory exhibited rapid decay in error-clamp trials. With further training the rate of decay decreased, suggesting that with training the motor memory was transformed from a labile to a more stable state. Surprisingly, neither cerebellar nor M1 stimulation altered these decay patterns. Participants returned 24 hours later and were re-tested in error-clamp trials without stimulation. The cerebellar group that had learned the task with cathodal stimulation exhibited significantly impaired retention, and retention was not improved by M1 anodal stimulation. In summary, non-invasive cerebellar stimulation resulted in polarity-dependent up- or down-regulation of error-dependent motor learning. In addition, cathodal cerebellar stimulation during acquisition impaired the ability to retain the motor memory overnight. Thus, in the force field task we found a critical role for the cerebellum in both formation of motor memory and its retention.

[Curr Opin Neurobiol](#). 2015 Aug;33:71-7. doi: 10.1016/j.conb.2015.03.003. Epub 2015 Mar 28.

[Neuroscientist](#). 2015 Aug;21(4):385-98. doi: 10.1177/1073858414541484. Epub 2014 Jun 30.

Motor Planning.

[Wong AL](#)¹, [Haith AM](#)², [Krakauer JW](#)³.

Motor planning colloquially refers to any process related to the preparation of a movement that occurs during the reaction time prior to movement onset. However, this broad definition encompasses processes that are not strictly motor-related, such as decision-making about the identity of task-relevant stimuli in the environment. Furthermore, the assumption that all motor-planning processes require processing time, and can therefore be studied behaviorally by measuring changes in the reaction time, needs to be reexamined. In this review, we take a critical look at the processes leading from perception to action and suggest a definition of motor planning that encompasses only those processes necessary for a movement to be executed—that is, processes that are strictly movement related. These processes resolve the ambiguity inherent in an abstract goal by defining a specific movement to achieve it. We propose that the majority of processes that meet this definition can be completed nearly instantaneously, which means that motor planning itself in fact consumes only a small fraction of the reaction time.

[Nat Commun](#). 2015 May 21;6:7169. doi: 10.1038/ncomms8169.

Large-scale spatiotemporal spike patterning consistent with wave propagation in motor cortex.

[Takahashi K](#)¹, [Kim S](#)², [Coleman TP](#)², [Brown KA](#)³, [Suminski AJ](#)⁴, [Best MD](#)⁵, [Hatsopoulos NG](#)⁶.

Aggregate signals in cortex are known to be spatiotemporally organized as propagating waves across the cortical surface, but it remains unclear whether the same is true for spiking activity in individual neurons. Furthermore, the functional interactions between cortical neurons are well documented but their spatial arrangement on the cortical surface has been largely ignored. Here we use a functional network analysis to demonstrate that a subset of motor cortical neurons in

non-human primates spatially coordinate their spiking activity in a manner that closely matches wave propagation measured in the beta oscillatory band of the local field potential. We also demonstrate that sequential spiking of pairs of neuron contains task-relevant information that peaks when the neurons are spatially oriented along the wave axis. We hypothesize that the spatial anisotropy of spike patterning may reflect the underlying organization of motor cortex and may be a general property shared by other cortical areas.

[J Neurophysiol](#). 2015 Apr 1;113(7):2812-23. doi: 10.1152/jn.00486.2014. Epub 2015 Feb 11.

Temporal evolution of both premotor and motor cortical tuning properties reflect changes in limb biomechanics.

[Suminski AJ](#)¹, [Mardoum P](#)², [Lillicrap TP](#)³, [Hatsopoulos NG](#)⁴.

A prevailing theory in the cortical control of limb movement posits that premotor cortex initiates a high-level motor plan that is transformed by the primary motor cortex (MI) into a low-level motor command to be executed. This theory implies that the premotor cortex is shielded from the motor periphery, and therefore, its activity should not represent the low-level features of movement. Contrary to this theory, we show that both dorsal (PMd) and ventral premotor (PMv) cortexes exhibit population-level tuning properties that reflect the biomechanical properties of the periphery similar to those observed in M1. We recorded single-unit activity from M1, PMd, and PMv and characterized their tuning properties while six rhesus macaques performed a reaching task in the horizontal plane. Each area exhibited a bimodal distribution of preferred directions during execution consistent with the known biomechanical anisotropies of the muscles and limb segments. Moreover, these distributions varied in orientation or shape from planning to execution. A network model shows that such population dynamics are linked to a change in biomechanics of the limb as the monkey begins to move, specifically to the state-dependent properties of muscles. We suggest that, like M1, neural populations in PMd and PMv are more directly linked with the motor periphery than previously thought.

[Neuron](#). 2014 Dec 3;84(5):1034-48. doi: 10.1016/j.neuron.2014.10.035. Epub 2014 Nov 20.

The habenulo-raphe serotonergic circuit encodes an aversive expectation value essential for adaptive active avoidance of danger.

[Amo R](#)¹, [Fredes F](#)², [Kinoshita M](#)², [Aoki R](#)³, [Aizawa H](#)², [Agetsuma M](#)², [Aoki T](#)², [Shiraki T](#)², [Kakinuma H](#)², [Matsuda M](#)⁴, [Yamazaki M](#)², [Takahoko M](#)², [Tsuboi T](#)⁵, [Higashijima S](#)⁶, [Miyasaka N](#)⁷, [Koide T](#)⁷, [Yabuki Y](#)⁷, [Yoshihara Y](#)⁷, [Fukai T](#)⁸, [Okamoto H](#)⁹.

Anticipation of danger at first elicits panic in animals, but later it helps them to avoid the real threat adaptively. In zebrafish, as fish experience more and more danger, neurons in the ventral habenula (vHb) showed tonic increase in the activity to the presented cue and activated serotonergic neurons in the median raphe (MR). This neuronal activity could represent the expectation of a dangerous outcome and be used for comparison with a real outcome when the fish is learning how to escape from a dangerous to a safer environment. Indeed, inhibiting synaptic transmission from vHb to MR impaired adaptive avoidance learning, while panic behavior induced by classical fear conditioning remained intact. Furthermore, artificially triggering this negative outcome expectation signal by optogenetic stimulation of vHb neurons evoked place avoidance behavior. Thus, vHb-MR circuit is essential for representing the level of expected danger and behavioral programming to adaptively avoid potential hazard.

[J Neurosci](#). 2013 Nov 20;33(47):18515-30. doi: 10.1523/JNEUROSCI.2126-13.2013.

A θ - γ oscillation code for neuronal coordination during motor behavior.

[Igarashi J](#)¹, [Isomura Y](#), [Arai K](#), [Harukuni R](#), [Fukai T](#).

Sequential motor behavior requires a progression of discrete preparation and execution states. However, the organization of state-dependent activity in neuronal ensembles of motor cortex is poorly understood. Here, we recorded neuronal spiking and local field potential activity from rat motor cortex during reward-motivated movement and observed robust behavioral state-dependent coordination between neuronal spiking, γ oscillations, and θ oscillations. Slow and fast γ oscillations appeared during distinct movement states and entrained neuronal firing. γ oscillations, in turn, were coupled to θ oscillations, and neurons encoding different behavioral states fired at distinct phases of θ in a highly layer-dependent manner. These findings indicate that θ and nested dual band γ oscillations serve as the temporal structure for the selection of a conserved set of functional channels in motor cortical layer activity during animal movement. Furthermore, these results also suggest that cross-frequency couplings between oscillatory neuronal ensemble activities are part of the general coding mechanism in cortex.

Fukai paper on secondary motor cortex under review.

[Nat Neurosci](#). 2015 Feb;18(2):289-94. doi: 10.1038/nn.3909. Epub 2015 Jan 5.

Hippocampal theta sequences reflect current goals.

[Wikenheiser AM](#)¹, [Redish AD](#)².

Hippocampal information processing is discretized by oscillations, and the ensemble activity of place cells is organized into temporal sequences bounded by theta cycles. Theta sequences represent time-compressed trajectories through space. Their forward-directed nature makes them an intuitive candidate mechanism for planning future trajectories, but their connection to goal-directed behavior remains unclear. As rats performed a value-guided decision-making task, the extent to which theta sequences projected ahead of the animal's current location varied on a moment-by-moment basis depending on the rat's goals. Look-ahead extended farther on journeys to distant goals than on journeys to more proximal goals and was predictive of the animal's destination. On arrival at goals, however, look-ahead was similar regardless of where the animal began its journey from. Together, these results provide evidence that hippocampal theta sequences contain information related to goals or intentions, pointing toward a potential spatial basis for planning.

[Cogn Affect Behav Neurosci](#). 2012 Sep;12(3):513-26. doi: 10.3758/s13415-012-0097-7.

Interactions between deliberation and delay-discounting in rats.

[Papale AE](#)¹, [Stott JJ](#), [Powell NJ](#), [Regier PS](#), [Redish AD](#).

When faced with decisions, rats sometimes pause and look back and forth between possible alternatives, a phenomenon termed vicarious trial and error (VTE). When it was first observed in the 1930s, VTE was theorized to be a mechanism for exploration. Later theories suggested that VTE aided the resolution of sensory or neuroeconomic conflict. In contrast, recent neurophysiological data suggest that VTE reflects a dynamic search and evaluation process.

These theories make unique predictions about the timing of VTE on behavioral tasks. We tested these theories of VTE on a T-maze with return rails, where rats were given a choice between a smaller reward available after one delay or a larger reward available after an adjustable delay. Rats showed three clear phases of behavior on this task: investigation, characterized by discovery of task parameters; titration, characterized by iterative adjustment of the delay to a preferred interval; and exploitation, characterized by alternation to hold the delay at the preferred interval. We found that VTE events occurred during adjustment laps more often than during alternation laps. Results were incompatible with theories of VTE as an exploratory behavior, as reflecting sensory conflict, or as a simple neuroeconomic valuation process. Instead, our results were most consistent with VTE as reflecting a search process during deliberative decision making. This pattern of VTE that we observed is reminiscent of current navigational theories proposing a transition from a deliberative to a habitual decision-making mechanism.

[Learn Mem.](#) 2013 Feb 15;20(3):130-8. doi: 10.1101/lm.028753.112.

Conflict between place and response navigation strategies: effects on vicarious trial and error(VTE) behaviors.

[Schmidt B](#)¹, [Papale A](#), [Redish AD](#), [Markus EJ](#).

Navigation can be accomplished through multiple decision-making strategies, using different information-processing computations. A well-studied dichotomy in these decision-making strategies compares hippocampal-dependent "place" and dorsal-lateral striatal-dependent "response" strategies. A place strategy depends on the ability to flexibly respond to environmental cues, while a response strategy depends on the ability to quickly recognize and react to situations with well-learned action-outcome relationships. When rats reach decision points, they sometimes pause and orient toward the potential routes of travel, a process termed vicarious trial and error (VTE). VTE co-occurs with neurophysiological information processing, including sweeps of representation ahead of the animal in the hippocampus and transient representations of reward in the ventral striatum and orbitofrontal cortex. To examine the relationship between VTE and the place/response strategy dichotomy, we analyzed data in which rats were cued to switch between place and response strategies on a plus maze. The configuration of the maze allowed for place and response strategies to work competitively or cooperatively. Animals showed increased VTE on trials entailing competition between navigational systems, linking VTE with deliberative decision-making. Even in a well-learned task, VTE was preferentially exhibited when a spatial selection was required, further linking VTE behavior with decision-making associated with hippocampal processing.

[PLoS One.](#) 2014 Jul 22;9(7):e102708. doi: 10.1371/journal.pone.0102708. eCollection 2014.

A robotic approach to understanding the role and the mechanism of vicarious trial-and-error in a T-maze task.

[Matsuda E](#)¹, [Hubert J](#)², [Ikegami T](#)².

Vicarious trial-and-error (VTE) is a behavior observed in rat experiments that seems to suggest self-conflict. This behavior is seen mainly when the rats are uncertain about making a decision. The presence of VTE is regarded as an indicator of a deliberative decision-making process, that is, searching, predicting, and evaluating outcomes. This process is slower than automated

decision-making processes, such as reflex or habituation, but it allows for flexible and ongoing control of behavior. In this study, we propose for the first time a robotic model of VTE to see if VTE can emerge just from a body-environment interaction and to show the underlying mechanism responsible for the observation of VTE and the advantages provided by it. We tried several robots with different parameters, and we have found that they showed three different types of VTE: high numbers of VTE at the beginning of learning, decreasing numbers afterward (similar VTE pattern to experiments with rats), low during the whole learning period, and high numbers all the time. Therefore, we were able to reproduce the phenomenon of VTE in a model robot using only a simple dynamical neural network with Hebbian learning, which suggests that VTE is an emergent property of a plastic and embodied neural network. From a comparison of the three types of VTE, we demonstrated that 1) VTE is associated with chaotic activity of neurons in our model and 2) VTE-showing robots were robust to environmental perturbations. We suggest that the instability of neuronal activity found in VTE allows ongoing learning to rebuild its strategy continuously, which creates robust behavior. Based on these results, we suggest that VTE is caused by a similar mechanism in biology and leads to robust decision making in an analogous way.

[Philos Trans R Soc Lond B Biol Sci](#). 2014 Nov 5;369(1655). pii: 20130472. doi: 10.1098/rstb.2013.0472.

A functional difference in information processing between orbitofrontal cortex and ventral striatum during decision-making behaviour.

[Stott JJ](#)¹, [Redish AD](#)².

Both orbitofrontal cortex (OFC) and ventral striatum (vStr) have been identified as key structures that represent information about value in decision-making tasks. However, the dynamics of how this information is processed are not yet understood. We recorded ensembles of cells from OFC and vStr in rats engaged in the spatial adjusting delay-discounting task, a decision-making task that involves a trade-off between delay to and magnitude of reward. Ventral striatal neural activity signalled information about reward before the rat's decision, whereas such reward-related signals were absent in OFC until after the animal had committed to its decision. These data support models in which vStr is directly involved in action selection, but OFC processes decision-related information afterwards that can be used to compare the predicted and actual consequences of behaviour.

[PLoS Comput Biol](#). 2013;9(9):e1003236. doi: 10.1371/journal.pcbi.1003236. Epub 2013 Sep 26.

Whisker movements reveal spatial attention: a unified computational model of active sensing control in the rat.

[Mitchinson B](#)¹, [Prescott TJ](#).

Spatial attention is most often investigated in the visual modality through measurement of eye movements, with primates, including humans, a widely-studied model. Its study in laboratory rodents, such as mice and rats, requires different techniques, owing to the lack of a visual fovea and the particular ethological relevance of orienting movements of the snout and the whiskers in these animals. In recent years, several reliable relationships have been observed between environmental and behavioural variables and movements of the whiskers, but the function of these responses, as well as how they integrate, remains unclear. Here, we propose a unifying

abstract model of whisker movement control that has as its key variable the region of space that is the animal's current focus of attention, and demonstrate, using computer-simulated behavioral experiments, that the model is consistent with a broad range of experimental observations. A core hypothesis is that the rat explicitly decodes the location in space of whisker contacts and that this representation is used to regulate whisker drive signals. This proposition stands in contrast to earlier proposals that the modulation of whisker movement during exploration is mediated primarily by reflex loops. We go on to argue that the superior colliculus is a candidate neural substrate for the siting of a head-centred map guiding whisker movement, in analogy to current models of visual attention. The proposed model has the potential to offer a more complete understanding of whisker control as well as to highlight the potential of the rodent and its whiskers as a tool for the study of mammalian attention.

[Philos Trans R Soc Lond B Biol Sci](#). 2014 Nov 5;369(1655). pii: 20130483. doi: 10.1098/rstb.2013.0483.

The why, what, where, when and how of goal-directed choice: neuronal and computational principles.

[Verschure PF](#)¹, [Pennartz CM](#)², [Pezzulo G](#)³.

The central problems that goal-directed animals must solve are: 'What do I need and Why, Where and When can this be obtained, and How do I get it?' or the H4W problem. Here, we elucidate the principles underlying the neuronal solutions to H4W using a combination of neurobiological and neurorobotic approaches. First, we analyse H4W from a system-level perspective by mapping its objectives onto the Distributed Adaptive Control embodied cognitive architecture which sees the generation of adaptive action in the real world as the primary task of the brain rather than optimally solving abstract problems. We next map this functional decomposition to the architecture of the rodent brain to test its consistency. Following this approach, we propose that the mammalian brain solves the H4W problem on the basis of multiple kinds of outcome predictions, integrating central representations of needs and drives (e.g. hypothalamus), valence (e.g. amygdala), world, self and task state spaces (e.g. neocortex, hippocampus and prefrontal cortex, respectively) combined with multi-modal selection (e.g. basal ganglia). In our analysis, goal-directed behaviour results from a well-structured architecture in which goals are bootstrapped on the basis of predefined needs, valence and multiple learning, memory and planning mechanisms rather than being generated by a singular computation.

[Neuron](#). 2013 Apr 24;78(2):249-55. doi: 10.1016/j.neuron.2013.02.006.

Neural variability in premotor cortex is modulated by trial history and predicts behavioral performance.

[Marcos E](#)¹, [Pani P](#), [Brunamonti E](#), [Deco G](#), [Ferraina S](#), [Verschure P](#).

In the study of decision making, emphasis is placed on different forms of perceptual integration, while the influence of other factors, such as memory, is ignored. In addition, it is believed that the information underlying decision making is carried in the rate of the neuronal response, while its variability is considered unspecific. Here we studied the influence of recent experience

on motor decision making by analyzing the activity of neurons in the dorsal premotor area of two monkeys performing a countermanding arm task. We observe that the across-trial variability of the neural response strongly correlates with trial history-dependent changes in reaction time. Using a theoretical model of decision making, we show that a trial history-monitoring signal can explain the observed behavioral and neural modulation. Our study reveals that, in the neural processes that culminate in motorplan maturation, the evidence provided by perception and memory is reflected in mean rate and variance respectively.

[Neural Netw.](#) 2013 Nov;47:64-71. doi: 10.1016/j.neunet.2013.01.026. Epub 2013 Feb 16.

Nucleo-olivary inhibition balances the interaction between the reactive and adaptive layers in motor control.

[Herreros I](#)¹, [Verschure PF](#).

In the acquisition of adaptive motor reflexes to aversive stimuli, the cerebellar output fulfills a double purpose: it controls a motor response and it relays a sensory prediction. However, the question of how these two apparently incompatible goals might be achieved by the same cerebellar area remains open. Here we propose a solution where the inhibition of the Inferior Olive (IO) by the cerebellar Deep Nuclei (DN) translates the motor command signal into a sensory prediction allowing a single cerebellar area to simultaneously tackle both aspects of the problem: execution and prediction. We demonstrate that having a graded error signal, the gain of the Nucleo-Olivary Inhibition (NOI) balances the generation of the response between the cerebellar and the reflexive controllers or, in other words, between the adaptive and the reactive layers of behavior. Moreover, we show that the resulting system is fully autonomous and can either acquire or erase adaptive responses according to their utility.