

# CONTROL PROCESSES 2017

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**Organizers: Adam Aron, David Badre, Roshan Cools**

## ABSTRACTS

### **Symposium 1: Control Processes in Working Memory**

Control processes and working memory play inter-related roles in executive function. Working memory supports the implementation of control processes by helping to maintain goals and objectives. Conversely, control processes act on the contents of working memory in the service of higher-order goals. The current symposium will examine the interrelationship between control processes and working memory from both of these perspectives. The first two speakers will discuss how the selection of items in working memory can serve to support goal-related behaviors and attentional selection. The latter two talks will focus more on specific control mechanisms that act on the contents of working: refreshing and clearing, respectively. Across the symposium, evidence on the relationship between control processes and working memory will be provided from investigations using a range of techniques including behavioral, neuroimaging, electrophysiology, and brain stimulation approaches.

#### **Tobias Egner**

*Duke University, USA*

#### **Christian N.L. Olivers**

*Vrije Universiteit Amsterdam, Netherlands*

#### **Evie Vergauwe**

*University of Geneva, Switzerland*

#### **Marie Banich**

*University of Colorado Boulder, US*

### **Mechanisms of controlling inputs to and outputs from WM**

*Tobias Egner*

Cognitive control and working memory (WM) are intimately related: in order to process and respond to external information in line with our internal goals (cognitive control), we need to select, maintain, and update temporary representations of goal-relevant stimuli and task rules (WM). The exact mechanisms of how WM content is selected, and how its influence over ongoing processing is controlled, remain poorly understood, however. Here, I will present recent data showing that the selection of items in WM involves a center-surround inhibition mechanism, and that WM contents impose an obligatory bias over attention to sensory stimuli, but that the latter can be modulated by strategic control processes. I will then present fMRI and fMRI-guided TMS results that delineate the neural substrates of control over WM output gating.

## **Current versus prospective memories and how they influence visual attention**

*Christian N.L. Olivers*

Visual attention is driven by top-down control processes reflecting the current goals of the observer. Working memory has been regarded as the mechanism by which such top-down control is implemented, through the activation and maintenance of task-relevant perceptual representations, which then bias sensory input. However, although memory can be used to bias the current perceptual task, it should also serve future tasks. Such prospective memories ought to be shielded from, rather than influence the current perceptual input. I will present behavioural and neurophysiological work using paradigms in which observers perform sequences of visual search tasks that allowed us to dissociate current from future goals in working memory. Behavioural and electrophysiological measures show that working memory distinguishes between what is currently relevant and what is prospectively relevant, with different consequences for attention and the representations it relies on.

## **Behavioral examination of attention-based maintenance in working memory**

*Evie Vergauwe*

Working Memory (WM) keeps information temporarily accessible for ongoing cognition. Our main question is concerned with how information is kept active in WM. One proposed mechanism to keep information active in WM is *refreshing*. Refreshing is similar in many aspects to verbal rehearsal but is assumed to be more domain-general, not related to speech, and attention-based. The idea is that, when possible, attention is used to reactivate WM representations, leading to increased accessibility and less short-term forgetting. Although many studies on refreshing have been published over the last years, there is not much direct evidence for the existence of the process and its characteristics are still poorly understood. I propose a novel approach to advance our understanding of refreshing and will present a series of experiments in which behavioral indices were used to examine how refreshing affects the status of the different representations held in WM.

## **Clearing the contents of working memory**

*Marie Banich*

Generally, it is impossible to know behaviorally whether someone has indeed cleared their mind of a thought. I will discuss work that leverages neuroimaging to provide evidence that information can indeed be cleared from working memory(WM). Moreover, I will differentiate between two types of clearing processes: one focusing specifically on clearing the item currently held in WM, and another that clears the mind of all thought. I will discuss neuroimaging work demonstrating that the neural systems supporting these two types of clearing processes are distinct, and that clearing the contents of WM can be differentiated from either maintaining an item or replacing it with something else. Data to support these distinctions will be drawn from both GLM and MVPA approaches in neuroimaging, as well as from comparing patterns of brain activation in neurologically-normal individuals to with a history of trauma who have difficulty controlling aspects of their thoughts.

## **Symposium 2: (Mal)adaptive decision control.**

In the past decades, the field of decision neuroscience has made huge advances in understanding the neural and computational basis of simple decisions such as choosing between two options or navigate simple mazes. However, humans routinely formulate plans in domains so complex that even the most powerful computers are taxed. To do so, they seem to avail themselves of many strategies and heuristics that efficiently simplify and approximate these difficult decisions<sup>1,2</sup>. This symposium will take a translational approach to understanding how our brain balances heuristic versus controlled responding, to help us to navigate and reduce the computational complexity of the world around us.

Amitai Shenhav will introduce theoretical ideas on cost-benefit principles of cognitive effort, and address how the brain may allocate control between the different decision strategies, based on their relative costs and benefit. Hanneke den Ouden will focus on likely the brain's most economical yet least flexible decision heuristic, namely hardwired Pavlovian affective response tendencies, and our ability to control these when necessary, using a combination of computational modelling psychopharmacology and EEG. Michael Frank will combine computational models and empirical data of adaptive control in decision making. Finally, Oliver Robinson will focus on how the balance between heuristic vs controlled responding can become sub-optimally biased in mood and anxiety disorders. Together, these talks present cutting-edge perspectives on how the brain allocates processing resources in the service of maximizing rewards, across diverse behavioural repertoires and healthy and clinical populations.

### **Amitai Shenhav**

*Brown University, Providence*

### **Hanneke den Ouden (chair)**

*Radboud University, Donders Institute for Brain, Cognition and Behaviour, Nijmegen*

### **Michael J Frank**

*Brown University, Providence*

### **Oliver Robinson**

*University College London, UK*

### **Weighing the costs and benefits of control**

*Amitai Shenhav*

I will describe recent theoretical and empirical work aimed at understanding control allocation through the lens of value-based decision-making, focusing on our proposal that individuals choose how much and what kind of control to allocate based on its Expected Value of Control (EVC), calculated as the predicted benefits minus the costs associated with effort exertion. I will describe a computational implementation of EVC-based control allocation that accounts for dynamic adjustments of control and behaviors with changes in incentives and task demands. I will further describe recent work that bridges the EVC framework with approaches from computer science for deciding how to decide between computationally demanding strategies (referred to as rational metareasoning). This combined computational approach enables us to describe how individuals learn the optimal control allocation based on features of the environment, and to identify situations that may lead to maladaptive allocation of control based on past experience.

## **Motivational biases and how we overcome them**

*Hanneke den Ouden*

In order to navigate our complex and ever-changing world we need to simplify the combinatorial explosion of all choice options and their possible future consequences. Perhaps the most parsimonious mechanism to help reduce this computational load are Pavlovian response tendencies that shape our actions in an evolutionarily hardwired manner. For example, when we tend to approach in the face of reward, while when hold back when threatened by a punishment. Most of the time, following these biases is a good idea, but sometimes they lead us astray, and we need to suppress their influence. I will present work in which we investigate the computational and neurochemical basis of these motivational response biases, looking at particularly the role of catecholamines in motivational biases in learning and choice. Next, I will present EEG work investigating the computational role of mid-frontal theta in overcome their influence when our motivations work against us.

## **Computational tradeoffs in decision making and adaptive cognitive control**

*Michael Frank*

Adaptive decision-making involves optimizing multiple inter-related computational tradeoffs: between speed and accuracy, rapid learning vs. developing structured task representations that afford generalization and transfer, flexibility vs. stability, updating and maintenance, information vs. reward seeking, and between the precision vs. quantity of representations in working memory. Computational models suggest that navigating these tradeoffs involves interactive dynamics in corticostriatal circuits that can be adapted based on reinforcement learning, and disruption of these mechanisms leads to aberrant decision-making in patient populations. It would be silly to attempt to present all of these ideas, but there is also a tradeoff between committing to a particular talk abstract and the possibility of keeping related options open.

## **Motivational biases in mood and anxiety disorder**

*Oliver Robinson*

Pavlovian decision-making biases can provide a computationally efficient strategy for adapting to a changing environment. In general, it is adaptive to avoid making a response in the face of potential threats (i.e. a Pavlovian punishment avoidance heuristic). However, over-reliance on these biases, or reliance in the wrong context can lead to suboptimal performance. Excessive avoidance behaviour in some psychiatric disorders can, for instance, leave sufferers housebound and socially isolated. I will present work suggesting that avoidances symptoms in mood and anxiety disorders might be a result of excessive reliance on Pavlovian avoidance heuristics. Moreover, I will argue that clinically relevant symptoms can be distilled as components of reinforcement learning models, thereby providing novel targets for interventions.

### **Symposium 3: Interactions Between the Prefrontal Cortex and the Medial-Temporal Lobes Supporting Inhibitory Control of Memory Retrieval**

Although memory retrieval can occur automatically, adaptive behavior often recruits cognitive control processes that guide retrieval in a goal directed manner. For example, cues often activate memories that are not relevant to task goals, causing interference that must be suppressed by inhibitory control. Sometimes this control demand arises when competing memories interfere during selective retrieval and inhibitory control suppresses the distraction they cause; other times, the retrieval process itself may need to be suppressed to support cognitive or emotional goals. Whereas episodic retrieval depends on medial temporal lobe (MTL) systems, control over memory retrieval is known to require the prefrontal cortex (PFC), and it is widely believed that inhibitory control over memory is achieved by PFC-MTL interactions. Despite this, little is known about these interactions or the pathways that support them. Here we examine the nature of PFC-MTL interactions that support inhibitory control over memory, the pathways mediating those interactions, the computations performed, and the mnemonic functions they serve. We draw together research using diverse methods and perspectives, ranging from work with functional imaging in humans, and inactivation, and single unit electrophysiology studies of fronto-hippocampal interactions in rodents. Two broad computational situations will be considered: the role of inhibitory control in retrieval stopping and in selective retrieval.

#### **Michael C. Anderson (chair)**

*MRC Cognition and Brain Sciences Unit, &  
Behavioral and Clinical Neurosciences Unit, University of Cambridge*

#### **Maria Wimber**

*Department of Psychology, University of Birmingham*

#### **Pedro Bekinschtein**

*Instituto de Biología Celular y Neurociencias, Facultad de Medicina, UBA-CONICET, Buenos Aires, Argentina*

#### **Matthew Shapiro**

*Icahn School of Medicine at Mount Sinai*

#### **Parallel regulation of memory and emotion supports the suppression of intrusive memories.**

*Michael Anderson & Pierre Gagnepain*

Intrusive images are detailed mental pictures emerging with highly distressing content, and may frequently initiate psychopathological symptoms. A fundamental goal of clinical neuroscience is to understand the mechanisms by which people may suppress intrusive memories while reducing their distressing impact. Current evidence suggests that intrusion suppression is mediated by a right fronto-parietal top-down influence on hippocampal activity that interrupts episodic retrieval. Here we report that stopping the episodic retrieval process to suppress awareness of an unpleasant memory also triggers in parallel inhibition of emotional content. We found that successful intrusion control was linked to reduced negative affect associated with suppressed traces. Regulation of memory retrieval and emotion was mediated by the same fronto-parietal inhibitory network and were both explained by a common profile of MTL down-regulation involving the anterior hippocampus and largely extending to the amygdala. Critically, effective connectivity analysis revealed that down-regulation of amygdala activity was not an indirect consequence of hippocampal suppression. Both structures were targeted in parallel

by an inhibitory control signal originating from the dorsolateral prefrontal cortex. These findings support the broad principle that inhibitory control targets not only hippocampal memory processes but also other content-specific regions in an activity-dependent fashion.

### **Retrieval induces adaptive forgetting of competing memories via cortical pattern suppression**

*Maria Wimber*

Remembering is an active selection process that adaptively shapes the underlying memory traces such as to optimize them for future retrievals. Surprisingly, remembering not only enhances future access to the retrieved target memories, but can also induce forgetting of other memories that interfere during retrieval. This form of forgetting has been attributed to a cognitive control process that adaptively reduces future interference by suppressing the competing traces. We here use multivariate brain imaging approaches to track the activation state of target and competing memories across repeated retrievals. We demonstrate that two distinct changes emerge in the neural patterns in ventral visual cortex and the hippocampus. First, a pattern representing the specific target memory gradually evolves. Second, the neural pattern unique to the individual competing memory is progressively suppressed below the activation state of other, non-competing memories. The magnitude of this competitor suppression was related to the degree to which participants engaged lateral prefrontal regions implicated in resolving retrieval competition, and, critically, predicted later forgetting of suppressed memories. These findings provide strong evidence for a targeted cortical pattern suppression mechanism acting during selective retrieval, and causing adaptive forgetting in human memory. Together, we demonstrate that multivariate pattern tracking can be used to observe adaptive changes of behaviourally invisible memory traces during selective retrieval.

### **A species-general, retrieval-specific mechanism of adaptive forgetting in the mammalian brain**

*Pedro Bekinschtein*

Neurobiological research on memory often presumes that forgetting is a negative outcome arising from passive mechanisms such as decay and interference. In the last two decades, however, a growing literature with human participants has revealed adaptive forgetting mechanisms that actively impair interfering memories via inhibitory control. Here we report an animal model of adaptive forgetting that establishes that its central theoretical properties are conserved across species. Using spontaneous object recognition, we found that when rats selectively retrieved a memory of an object encountered in a particular context, it dramatically impaired competing memories of other objects encountered in that context. Critically, in agreement with the inhibitory control hypothesis, this retrieval-induced forgetting was competition-dependent, cue-independent, long-lasting, and reliant on control mechanisms mediated by the medial prefrontal cortex. As competing memories were inhibited over repetitions, medial prefrontal cortex engagement declined, reflecting a key adaptive benefit of forgetting. These findings demonstrate a species-general adaptive forgetting process and establish an animal model that permits the study of its circuit-level, cellular and molecular mechanisms.

*Matt Shapiro (for Howard Eichenbaum)*

## **Symposium 4: Valuation, appraisal, attention and choice: Perspectives on the role of orbitofrontal cortex in the control of behavior**

Conventional views of prefrontal (PFC) control processes often cast orbitofrontal and ventromedial PFC as the villain, while dorsolateral PFC plays the hero in the struggle between emotion and reason. This symposium brings OFC/VMPPFC out of the shadows, proposing it to be of central importance in filtering value-relevant information, in turn biasing behavior towards motivationally-important goals. This region is thus key in putting the “goal” in goal-directed behavior. We will highlight recent findings from a range of methods, in humans and non-human primates, on the roles of OFC/VMPPFC in the inter-related processes of valuation, attention and choice. We look for common ground in understanding value within economic, psychological, physiological and ecological frameworks. We report on work that shows a critical role for OFC/VMPPFC in biasing attention towards value-predictive information in humans, and on recordings from macaque OFC that argue that attention in turn can drive value signals carried by single cells. We highlight distinctions in this region’s contributions to wanting and liking, and provide evidence that subjective value computations in OFC/VMPPFC align better with ecological than psychological theory. We argue that OFC/VMPPFC has a role in prioritizing specific value information in the face of multiple potential sources of such information, depending on current goals and contexts. We show that ideas about the roles of this region in relation to constructing value representations of complex objects in the world may also apply to how we appraise the current value of our own complex selves. Just as OFC/VMPPFC seems to be important in identifying “the good” in our environment, to orient controlled behavior towards advantageous goals, it also contributes to recognizing the good in ourselves. Together, this work makes a case for an integrative understanding of the linkages between motivational value, attention and decisions in moving towards a complete description of executive control.

### **Lesley Fellows (chair)**

*Professor, Dept. of Neurology & Neurosurgery, McGill University*

### **Philippe Tobler**

*Professor, Department of Economics, University of Zurich*

### **Jennifer Beer**

*Professor, Department of Psychology, University of Texas at Austin*

### **Vince McGinty**

*Assistant Professor, Center for Molecular and Behavioral Neuroscience, Rutgers University*

### **Large-scale properties of orbitofrontal value processes**

*Philippe Tobler*

The adaptive control of actions requires computing the subjective value of stimuli and choice alternatives and appropriate interactions among value processing regions such that the value signal that is relevant for the current context controls actions. I will present two ongoing studies on how subjective value processes in orbitofrontal cortex interact with other components of corticostriatal loops during wanting and liking judgments and on how orbitofrontal cortex computes subjective value. The findings suggest that in contrast to the ventral striatum, distinct orbitofrontal regions process wanting and liking and these regions tend to differentially interact with the ventral striatum according to which judgment is currently relevant. Moreover, theories of subjective value computation from behavioral ecology (mean-variance-skewness) explained value processing in the orbitofrontal cortex during risky decisions better than theories from psychology (prospect theory).

## **Value is in the eye of the beholder: Visual attention and value signals in the primate orbitofrontal cortex**

*Vincent B. McGinty*

The frontal lobes play a key role in computing the subjective value of sensory stimuli. While these value signals can be used to direct attention towards important objects, recent human imaging and computational work has suggested a reciprocal mechanism, in which frontal lobe value signals are themselves attentionally-driven, reflecting attended items over unattended ones. Recently, we demonstrated an attentionally-driven value signal in monkey orbitofrontal cortex (OFC), expressed in single neurons at the rapid time scale of saccadic eye movements – i.e. the endogenously-generated shifts in visual attention during natural free viewing. In this talk, I will discuss an ongoing project that addresses the function of this saccade-driven OFC value signal in economic choice. Our preliminary findings suggest that visual attention influences both choice behavior and OFC value signals, and that residual variability in these value signals can predict choices on a trial-by-trial basis.

## **Seeing the value in the world: Orbitofrontal cortex contributions to motivated attention**

*Lesley K. Fellows*

While orbitofrontal cortex plays a necessary role in value-based decisions, at least under some conditions, the mechanisms by which this region influences choice behavior remain unclear. We present findings in support of a role for orbitofrontal cortex in biasing attention to reward-predicting cues. Humans with focal damage to this region (and not to other frontal lobe regions) show loss of reward-modulated attentional priming in a rewarded visual search task. When making pair-wise choices between complex real-world stimuli, such as faces or artworks, they seem to systematically neglect or under-weight some (but not all) value-relevant information. These results argue that orbitofrontal cortex may guide decision-making by biasing attention, in turn entraining choice behavior. They also highlight the need to better specify the content of value representations underpinning decisions between the multi-attribute options that are typical of most of our everyday choices.

## **Seeing the value of one's self: The Role of VMPFC in motivated appraisal**

*Jennifer S. Beer*

People expend a great deal of cognitive control to maintain positive self-views. In a series of studies that incorporated computational modeling, we find that the VMPFC supports the motivated evidence accumulation that underlies positive self-view maintenance. Study 1 identified a VMPFC region associated with self-protective appraisals in response to threatening social feedback (Hughes & Beer, 2013). Study 2 combined fMRI with Signal Detection Theory and found that VMPFC mediates self-protective appraisals through the adjustment of decision thresholds (Hughes & Beer, 2012). Decision thresholds may reflect a priori expectations that are imposed regardless of available evidence, preferential evidence processing, or both. Therefore, Study 3 combined fMRI and Drift Diffusion Modeling to more precisely characterize VMPFC's role in self-protection. VMPFC activation was associated with preferential processing of self-flattering information when interpreting ambiguous social feedback (rather than a priori expectations of flattery without regard for contextual cues: Flagan, Mumford, & Beer, 2017).