



To summarize, the analytical approach described by Maei et al. (2009) provides a more effective and accurate new measure in terms of its superb sensitivity and statistical validity in water maze studies. Furthermore, the H measure will contribute greatly to the advancement of behavioral assays that, in conjunction with molecular genetic approaches, are designed to elucidate the molecular mechanisms underlying learning and memory.

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Decisions of voluntary action: what vs when

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A commentary on

Dissociating what and when of intentional actions

by Veronika Krieghoff, Marcel Brass, Wolfgang Prinz and Florian Waszak

Voluntary action is a fundamental characteristic of human behavior and identifies our ability to realize intentionally driven tasks. Functional imaging work has indicated that intentional performance activates neural circuitry confined to the fronto-medial cortex (Cunnington et al., 2002; Lau et al., 2004; Nachev et al., 2005). This network activity integrates, besides the conscious experience of intending (Haggard and Clark, 2003; Lau et al., 2004), a series of processes in relation to the intentional act (Brass and Haggard, 2007). Accordingly, intentional behavior can be viewed as a form of decision making that consists of various components with different types of information processing (Brass and Haggard, 2008; Haggard, 2008). This distinctive viewpoint is important as voluntary action has often been regarded as a unitary concept without little con-

sideration for the component functions. In this respect, it has been suggested that voluntary action has at least two decisional processes: what action to perform (selection component) and when to perform it (timing component), (Mueller et al., 2007). Thus, the “what” decision specifies which action to perform from a range of alternative options, whereas the “when” decision denotes the moment in time at which to execute the action.

In their recent contribution to *Frontiers in Neuroscience*, Krieghoff et al. (2009) presented an fMRI study that provides new insights into voluntary behavior. In particular, the authors proposed a well-designed protocol in which they simultaneously and independently manipulated the selection and timing component within one experimental paradigm. Moreover, the participants were instructed to perform one of two possible actions at one of two possible moments in time. Furthermore, the action and moment in time were freely chosen or externally triggered by means of a cue. In other words, the “what” (selection) and “when” (timing) decision of the impending action were based on an internal judgment or imposed by an external stimulus. This distinction between internally and exter-

nally generated responses is relevant as both types of activities are known to have (partly) dissociable neural circuitry in respect to the component process of selection, as well as timing (Deiber et al., 1999; Cunnington et al., 2002, 2006; Lau et al., 2006).

As the main objective of Krieghoff et al. (2009) was to investigate the decisional processes of voluntary behavior, the data analysis focused primarily on the cue-related activity that specified the decision making process rather than on the target-related activity that represented the implementation of that decision. In view of that premise, the whole-brain analysis of the cue-related signal showed that two fronto-medial wall areas associated with distinct component functions of voluntary action: whereas the selection component linked strongly with the rostral cingulate zone (RCZ), the timing component tied closely with the superior medial frontal gyrus (SFG), which is localized close to pre-SMA (Rushworth, 2008). These results indicate that separate brain regions are involved in distinct decisional processes, and accordingly highlight a functional dissociation of intentional action. However, an additional



signal strength analysis revealed that both processes interact with one another. In particular, neural activity within the paramedial frontal cortex was increased for internal as compared to external timing, but only when action selection was specified externally. Combined, these observations challenge the idea of a unitary control system and underscore the existence of distinct, albeit interdependent, decisional processes that together shape voluntary action (Brass and Haggard, 2008). Of note is that this dependency is in accordance with the argument that aspects from the component processes have to be considered in order for an action and its consequences to be evaluated.

By introducing an innovative experimental paradigm, the work of Kriehoff et al. (2009) has provided a significant step into the understanding of intentional control by specifying dissociable brain regions that deal with component functions. Further research into the dynamics of voluntary action is necessary in order to detail the functional architecture of intentional behavior and its neural correlates.

Future studies may elaborate on the inter-regional influences and coordination of the brain areas that make up the network activity, and the means by which context-related factors modify intentional processing within the circuitry.

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Forget before you remember: dynamic mechanism of memory decay and retrieval

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A commentary on

Neurophysiological bases of exponential sensory decay and top-down memory retrieval: a model

by Ariel Zylberberg, Stanislas Dehaene, Gabriel B. Mindlin and Mariano Sigman

Sensory systems are confronted with a continuous stream of inputs, but only a small fraction of these sensory stimuli reaches our awareness, is consciously perceived and can be remembered. Perception is never driven solely by the bottom-up stimulation, but crucially depends on the

top-down modulations. Top-down signals convey behavioral context, such as attention, expectation and perceptual task, and are reflected in the context-specific response modulation in single neurons (Miller and Cohen, 2001; Corbetta and Shulman, 2002). Top-down interactions can be of many different kinds: augmenting or multiplying responses, sharpening tuning curves, controlling contextual influences, or acting as a modulator of plasticity (Desimone and Duncan, 1995; Maunsell and Treue, 2006). Although a lot of empirical knowledge has been accumulated on how top-down interactions modulate neural responses, only a few theoretical attempts have been made so

far to explain the underlying biophysical mechanisms and to bridge the gap between the behavioral and single-cell data (Buia and Tiesinga, 2006; Deco and Rolls, 2006; Ardid et al., 2007).

The recent study by Zylberberg et al. (2009) published in *Frontiers in Computational Neuroscience* aims to uncover these biophysical mechanisms in a particular setting of top-down memory retrieval. The authors try to answer several general and long-standing questions: How do the bottom-up and top-down signals interact to produce a perception? What are the neural mechanisms of effortless (iconic) vs voluntary (working) memory?