

their formal knowledge about probabilities to infer SEUs (remember that participants were university students). Both studies, however, reported several additional key findings when lottery probabilities were not explicitly instructed, which supports a more general, parsimonious, and mechanistic view encompassing all these cases. Rouault *et al.* showed that, consistent with previous proposals by Louie *et al.* [7], reward values independently contributed to choices through a normalization process that made them commensurable to reward probabilities. These authors further noted that if these normalized quantities contributed to choices with equal weights, these choices would be similar to those derived from SEU computations. We can accordingly reason that even in the verbally instructed condition, the choices of participants might derive from an independent, equally weighted contribution of these quantities. Farashahi *et al.* reported a finding that supports this hypothesis: the more volatile (or changing) the decision situation was, the less the probabilities' contribution was outweighed, that is, the more probabilities and values tended to contribute to choices with equal weights [4]. Moreover, the verbally instructed condition actually corresponds to a hypervolatile situation: when verbal instructions made lottery probabilities explicit, participants were *de facto* instructed that each trial differed and was unrelated to the preceding ones. Altogether, these findings lend weight to the idea that whatever the situation, human (and monkey) choices derive from the independent contribution of various subjective quantities including: the probabilities of prospective rewards, their values normalized across choice options and the reinforcement history of the options, with relative weights adjusting to the volatility of the decision context.

This model is parsimonious as the relative weighting of these quantities might replace the need to consider multiple distortions of subjective compared with objective probabilities to make the SEU hypothesis consistent with human data in various contexts [8]. The model may reflect independent brain systems that concurrently influence choices or the valuation of choice options through the addition of multiple value components. As weighted sums may also be viewed as Lagrange functions [9], the model may also reflect that decision-making optimizes some quantities given some constraints (e.g., choose the safest option, unless the associated prospective reward is dramatically smaller). As the weighting depends upon the volatility of the environment [10], the model further bridges the notion of decision-making and adaptive behavior. Thus, the studies of Farashahi *et al.* [4] and Rouault *et al.* [3] both open the way for exciting future research to determine whether and how the model generalizes and adjusts the independent contribution to various uncertain and changing situations, including multiple choice options and outcomes. Future research might notably establish the principles accounting for the efficiency of this adaptive decision model in real-life environments and for its evolution in primates. In other words, the principles that in real-life environments featuring uncertain, changing, and open-ended situations, make this decision model more rational than the Rational Decision Theory.

¹Ecole Normale Supérieure, PSL Research University, Université Pierre et Marie Curie, Institut National de la Santé et de la Recherche Biomédicale, Paris, France

*Correspondence:
etienne.koechlin@upmc.fr
<https://doi.org/10.1016/j.tics.2019.11.001>

© 2019 Elsevier Ltd. All rights reserved.

References

1. Savage, L.J. (1954) *The Foundations of Statistics*, Wiley
2. Kahneman, D. and Tversky, A. (1979) Prospect theory: an analysis of decision under risk. *Econometrica* 47, 263–291
3. Rouault, M. *et al.* (2019) Prefrontal mechanisms combining rewards and beliefs in human decision-making. *Nat. Commun.* 10, 301
4. Farashahi, S. *et al.* (2019) Flexible combination of reward information across primates. *Nat. Hum. Behav.* Published online September 9, 2019. <https://doi.org/10.1038/s41562-019-0714-3>.
5. Kahneman, D. and Tversky, A. (1984) Choices, values, and frames. *Am. Psychologist* 39, 341–350
6. Sutton, R.S. and Barto, A.G. (1998) *Reinforcement Learning*, MIT Press
7. Louie, K. *et al.* (2013) Normalization is a general neural mechanism for context-dependent decision making. *Proc. Natl. Acad. Sci. U. S. A.* 110, 6139–6144
8. Hertwig, R. and Erev, I. (2009) The description-experience gap in risky choice. *Trends Cogn. Sci.* 13, 517–523
9. Hoffmann, L.D. and Bradley, G.L. (2010) *Calculus for Business, Economics, and the Social and Life Sciences*, 10th edn., McGraw-Hill
10. Behrens, T.E.J. *et al.* (2007) Learning the value of information in an uncertain world. *Nat. Neurosci.* 10, 1214–1221

Spotlight

Bridging Motor and Cognitive Control: It's About Time!

Harrison Ritz,¹ Romy Frömer,¹ and Amitai Shenhav^{1,*}

Is how we control our thoughts similar to how we control our movements? Egger *et al.* show that the neural dynamics underlying the control of internal states exhibit similar algorithmic properties as those that control movements. This experiment reveals a promising connection between how we control our brain and our body.

We often describe our mental states through analogy to physical actions. We hold something in mind or push it out of our thoughts. An emerging question in cognitive control is whether this



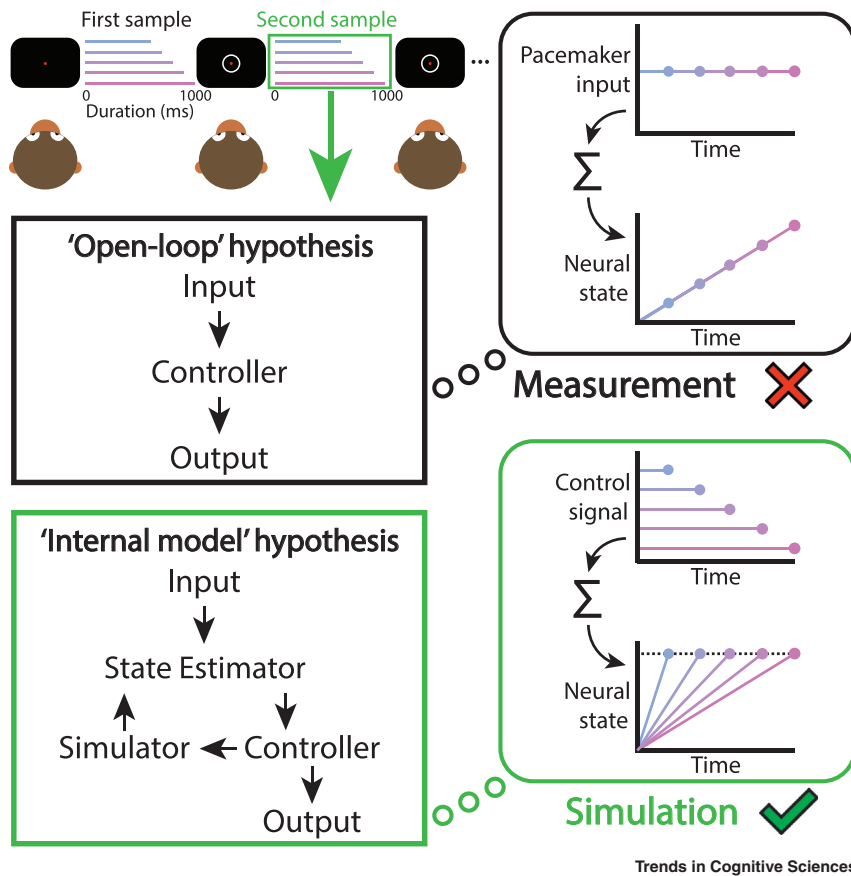


Figure 1. Alternative Hypotheses for Internal State Control.

Monkeys observed two sample time intervals (top) and then tried to reproduce the interval (not shown). There were two competing hypotheses for the form brain dynamics would take during the second sample interval. Under the 'open-loop' hypothesis, neural activity should not distinguish between expected durations, instead reflecting passive measurement of time. Under the 'internal model' hypothesis, neural activity should distinguish between expected durations, producing a simulation that aids in learning and control. The authors observed that neural responses were consistent with the internal model hypothesis, aligning the control of internal states with prominent theories of motor control. Task figure adapted from [3].

relationship runs deeper than metaphor, with similar cognitive architectures underpinning our ability to control our physical actions and our mental states. For instance, recent work has shown that analogous control processes serve to optimize performance and regulate brain dynamics for both motor and cognitive actions [1,2]. A new study by Egger and colleagues [3] provides important new clues that the mechanisms supporting motor and cognitive control are more similar than previously shown.

These researchers tested whether the control of internal states exhibits a signature property of the motor system: the reliance on an internal model to guide adjustments of control [4]. To control one's actions, a person needs to maintain an internal model of their environment (e.g., potential changes in terrain or atmosphere) and of their own motor system (e.g., how successful they are at executing a motor command [5]). This model can be used to generate online predictions about the outcome of an action and to course-correct when there is a mismatch

between that prediction and the actual outcome. This process is thought to be implemented via interactions between: (i) a simulator that makes predictions, (ii) an estimator that learns the current state, and (iii) a controller that implements actions. This new study investigated whether neural activity during the control of cognitive processes reflected this same three-part architecture.

To answer this question, Egger and colleagues recorded neural activity while monkeys performed an interval reproduction task (Figure 1). The monkeys observed two samples of a time interval and then timed a saccade to reproduce this interval. Previous work has shown that population-level neural activity in the dorsomedial frontal cortex (DMFC) during similar tasks systematically scales with the timing of an action [6]. If action timing in this task depends on an internal model, then this temporal scaling should already be present in DMFC activity prior to receiving a cue to respond. If the monkeys were not relying on an internal model, and the activity instead reflected the passive measurement of time ('open-loop' control), then DMFC activity during the second interval should not exhibit such temporal scaling.

The monkeys' behavior and neural activity demonstrated that they combined prior knowledge about the average interval duration with their perception of the current interval duration [7]. This behavior was well-captured by a near-optimal Bayesian algorithm that updated predictions in a way that was biased towards the average interval. By independently varying the duration of the two sample intervals, the authors were further able to show that the monkeys incorporated both samples into their duration estimate.

Signatures of this biased updating process were also observed in DMFC neural

activity. Replicating previous studies, individual neurons in the DMFC demonstrated ramping activity during the reproduction of an interval, with faster ramping when the monkey reproduced shorter intervals [6]. Critically, neural activity during the second sample interval exhibited the predicted simulation profile: neurons demonstrated interval-dependent ramping during this epoch, prior to the response cue.

Further support for an internal model hypothesis was found across different measures of neural activity, and in their relationship with subsequent behavior. Temporal scaling was evident not only at the level of DMFC single neurons but also in the population-level neural dynamics across this region. Unlike the transient single-unit responses, the rate of change in these population dynamics scaled consistently with interval length throughout the second sample interval. These dynamics reflected the same Bayesian biases observed in monkeys' behavior: an initial bias towards the average interval duration that became less biased with more samples. Critically, these population dynamics also predicted when the monkey would saccade on the upcoming response interval, and did so above and beyond what would be predicted by the lengths of the sampled time intervals alone. Collectively, these findings are consistent with the DMFC implementing an internal model to optimize the learning of task goals and the control of neural population dynamics.

This study provides evidence that DMFC mediates the influence of prior predictions and incoming sensory evidence on planned actions, and lays the groundwork for critical tests of this proposed mechanism using causal manipulations (i.e., stimulation or inactivation). Such causal tests can also help to rule out alternative accounts of neural dynamics during the sample intervals,

for instance, whether they reflect a simulated motor plan (as the authors infer) or an interval expectation (e.g., predicting the onset of the interval cue [8]). Nevertheless, by elaborating on the neuronal dynamics within DMFC during a task that requires online adjustments of learning and control, this study builds on a growing literature that implicates regions along this dorsomedial wall in the control of motor and cognitive commands [9,10].

More generally, this research provides compelling new evidence that motor and cognitive control share a common computational toolbox. Past work has suggested that both forms of control serve similar objectives (achieving a goal state within a dynamic, uncertain, and noisy environment) and that they are also both constrained by some underlying cost, limiting the amount of control that individuals can engage at a given time. As a consequence, decisions about how to allocate one's control are sensitive to whether the reward for goal achievement outweighs these costs [10]. To the extent computational and neural architecture for motor and cognitive control allocation mirror one another, the behavior and neural dynamics observed in the current task should demonstrate sensitivity to performance incentives for both forms of control.

In spite of their abundant bodies of research, the obstacle to bridging our understanding of motor and cognitive control have been similarly abundant, including limitations of tasks, measurement tools, and model organisms. This study demonstrates how a combination of computational modeling and measures of neural dynamics in the monkey can be leveraged towards this goal and, in doing so, provides a valuable path forward in mapping the joints between these two domains of control.

¹Brown University, 190 Thayer Street, Box 1821, Providence, RI 02912, USA

*Correspondence:
amitai_shenhav@brown.edu
<https://doi.org/10.1016/j.tics.2019.11.005>

© 2019 Elsevier Ltd. All rights reserved.

References

1. Manohar, S.G. et al. (2015) Reward pays the cost of noise reduction in motor and cognitive control. *Curr. Biol.* 25, 1707–1716
2. Tang, E. and Bassett, D.S. (2018) Colloquium: control of dynamics in brain networks. *Rev. Mod. Phys.* 90, 031003
3. Egger, S.W. et al. (2019) Internal models of sensorimotor integration regulate cortical dynamics. *Nat. Neurosci.* 22, 1871–1882
4. Miall, R.C. and Wolpert, D.M. (1996) Forward models for physiological motor control. *Neural Netw.* 9, 1265–1279
5. Frömer, R. et al. (2018) I knew that! Confidence in outcome prediction and its impact on feedback processing and learning. *bioRxiv*. Published online October 14, 2018. <https://doi.org/10.1101/442822>
6. Remington, E.D. et al. (2018) Flexible sensorimotor computations through rapid reconfiguration of cortical dynamics. *Neuron* 98, 1005–1019
7. Jazayeri, M. and Shadlen, M.N. (2010) Temporal context calibrates interval timing. *Nat. Neurosci.* 13, 1020–1026
8. Egger, S.W. et al. (2019) A neural circuit model for human sensorimotor timing. *bioRxiv*. Published online July 23, 2019. <https://doi.org/10.1101/712141>
9. Heilbronner, S.R. and Hayden, B.Y. (2016) Dorsal anterior cingulate cortex: a bottom-up view. *Annu. Rev. Neurosci.* 39, 149–170
10. Shenhav, A. et al. (2017) Toward a rational and mechanistic account of mental effort. *Annu. Rev. Neurosci.* 40, 99–124

Forum

Combinatorial Oxytocin Neuropharmacology in Social Cognition

Siqi Fan,^{1,5}
Hannah Weinberg-Wolf,^{1,5}
Matthew Piva,¹
Olga Dal Monte,^{1,2}
and Steve W.C. Chang^{1,3,4,*}

The efficacy and reliability of using intranasal oxytocin (OT) to clinically enhance social functions remains

