



Trends in Cognitive Sciences

Figure 1. Neural Redundancy in Primary Motor Cortex (M1) Suggests a New View of M1 as a Controlled Dynamical System. (A) Illustration of neural redundancy: the same behaviour (natural or BCI driven) could be produced by different trajectories in the state space of neural activity (three shown here). The activity along 'potent' directions is constrained by the desired behaviour and, therefore, is the same for all candidate trajectories (top-right inset). By contrast, activity along 'null' directions has no direct effect on behaviour and, therefore, is free to vary (top-left inset). (B) M1-as-a-controller view. (C) M1-as-a-plant view. (D) Illustration of the fixed-distribution hypothesis. At any time, output-null activity is selected as though drawn from some fixed distribution of neural activity (heat map), conditioned on a momentary desired value of potent activity (white dot). (E) A two-unit neural network (i) is driven by optimal control inputs to generate some desired fluctuations along a given potent direction. (ii) The distribution of network activity (dots) has the same structure irrespective of the potent direction being used (compare orange and green). The black ellipse delineates the region of state space within which the network activity can be steered given a fixed input energy budget.

movement by thinking of M1 (and spinal cord circuits) not only as a body controller, but also as a dynamical system under the control of other neural circuits. This new perspective will suggest principled ways of elucidating the role of motor areas upstream of M1 (e.g., thalamic nuclei, basal ganglia, and cerebellum). Examining neural redundancy at each level of the control hierarchy (e.g., using BCI-inspired techniques) will continue to bring useful insights: null ain't dull under the skull.

Acknowledgment

G.H. is supported by Wellcome Trust Seed Award n. 202111/Z/16/Z.

Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.tics.2018.09.005>.

¹Computational and Biological Learning Lab, Department of Engineering, University of Cambridge, Cambridge, UK

*Correspondence:

g.hennequin@eng.cam.ac.uk (G. Hennequin).
<https://doi.org/10.1016/j.tics.2018.09.005>

References

- Boerlin, M. *et al.* (2013) Predictive coding of dynamical variables in balanced spiking networks. *PLoS Comput. Biol.* 9, e1003258

- Li, N. *et al.* (2016) Robust neuronal dynamics in premotor cortex during motor planning. *Nature* 532, 459
- Kaufman, M.T. *et al.* (2014) Cortical activity in the null space: permitting preparation without movement. *Nat. Neurosci.* 17, 440
- Stavisky, S.D. *et al.* (2017) Motor cortical visuomotor feedback activity is initially isolated from downstream targets in output-null neural state space dimensions. *Neuron* 95, 195–208
- Driscoll, L.N. *et al.* (2017) Dynamic reorganization of neuronal activity patterns in parietal cortex. *Cell* 170, 986–999
- Hennig, J.A. *et al.* (2018) Constraints on neural redundancy. *eLife* 7, e36774
- Todorov, E. (2000) Direct cortical control of muscle activation in voluntary arm movements: a model. *Nat. Neurosci.* 3, 391
- Lillicrap, T.P. and Scott, S.H. (2013) Preference distributions of primary motor cortex neurons reflect control solutions optimized for limb biomechanics. *Neuron* 77, 168–179
- Shenoy, K.V. *et al.* (2013) Cortical control of arm movements: a dynamical systems perspective. *Annu. Rev. Neurosci.* 36, 337–359
- Hennequin, G. *et al.* (2014) Optimal control of transient dynamics in balanced networks supports generation of complex movements. *Neuron* 82, 1394–1406

Spotlight Extraordinary Altruism and Transcending the Self

Molly J. Crockett^{1,*} and
Patricia L. Lockwood²

Longstanding psychological theories posit a link between empathy and altruism. A new study of anonymous kidney donors finds these 'extraordinary altruists' show an increased overlap in neural responses to pain for self and others. These findings, alongside other recent studies of altruism, shed new light on the nature of selflessness.

On 6 June 2014, 21-year-old Michael Campbell was driving his normal delivery route when he witnessed a nearby house burst into flames. Hearing cries for help, Campbell rushed into the burning building and discovered a badly injured man covered in debris in the second-floor bedroom. Campbell dragged the man down the stairs and out of the house just as the second floor of the house collapsed. Both men survived and Campbell received the Carnegie Medal for his heroic actions. Extraordinary acts of selflessness like this are captivating and inspiring, and a deeper scientific understanding of what makes someone risk their life for a stranger has the potential to transform

our society. For obvious reasons, investigating such behavior in the laboratory seems difficult, if not impossible. An important new study makes a significant advance towards uncovering the neural basis of exceptional altruism.

Brethel-Haurwitz and colleagues [1] recruited a sample of 'extraordinary altruists', adults who have donated a kidney to an anonymous stranger. Such individuals are rare, and their stories fit the textbook definition of behavioral altruism: they undertook significant personal costs to benefit a total stranger. Longstanding theories of altruism posit that empathy is closely linked, suggesting that extraordinary altruists might show extraordinary empathy. The research team tested this hypothesis by comparing altruists with matched controls on neural responses to the anticipation and delivery of pain for self and others. Prior work has linked neural responses to others' pain with more mundane acts of altruism, like donating \$20 to charity [2].

Relative to controls, altruists showed a higher degree of overlap in neural responses to pain for self and others in the left anterior insula (AI). Altruists also exhibited greater functional coupling than controls between left AI and mid-insula during both vicarious pain and its anticipation. Intriguingly, despite these neural differences, altruists did not differ from controls in self-reported empathy. They did, however, report a significantly higher sense of connectedness with strangers, as measured by inclusion of others in the self, and this sense of connectedness explained many of the neural differences between altruists and controls. Together, these findings point to important differences in self-other processing between extraordinary altruists and the typical population at both phenomenological and neural levels. The results also support a link between empathy and altruism, a topic that has been subject to ongoing controversy,

both in the measurement of empathy and in effectively creating opportunities for altruism in a controlled laboratory setting.

Research on the neural correlates of empathy and social cognition more broadly has highlighted both common and distinct substrates for processing the experiences of self and others. Some of this work attributes prosocial behavior to overlapping neural responses to self and others' outcomes [1,3]. Other recent work, however, has identified networks that may be specific for social processing [4]. For example, studies of vicarious reward have revealed brain areas that specifically respond to others' and not one's own rewards, and responses in other-specific areas covary with empathy and prosocial behavior [5,6]. It would be fascinating to test whether self-other overlap in vicarious experience is a general feature of extraordinary altruism, or whether it is context specific. A further question concerns whether the self-other overlap observed in extraordinary altruists reflects activation of the same neurons, or whether distinct but co-mingling neuronal populations encode outcomes for self versus other. Future studies could address this question with multivariate pattern analysis techniques, such as those used in a recent study to demonstrate that first-hand and empathic pain recruit shared activity patterns in left AI, while right AI carries unique information about the target of pain [7]. This lateralized pattern of responses becomes all the more intriguing in light of new evidence that extraordinary altruists are distinguished from controls in the response patterns of left, but not right, AI [1].

By definition, 'extraordinary' altruists are markedly different from typical individuals. It remains unknown whether their behavior, and the neural mechanisms that guide it, differ from the rest of us as a matter of degree or a matter of kind. Recent neuroimaging studies of the neural processes that unfold as ordinary people are making

altruistic decisions have identified other neural systems whose engagement predicts altruistic choice. For example, when people distribute money between themselves and others, distinct regions in temporoparietal junction and ventromedial prefrontal cortex encode money for others and predict generous choices [8]. Likewise, when deciding whether to sacrifice money to spare others from pain, value-sensitive regions including the striatum and lateral prefrontal cortex differentially encode decisions for self and others and predict altruistic behavior [9]. More 'ordinary' acts of altruism may therefore engage rather different mechanisms entirely than extraordinary decisions, which seem to rely on a high degree of phenomenological and neural overlap between self and other. If ordinary and extraordinary altruism differ in kind rather than degree, this raises questions about the level of selflessness that is attainable for most people.

Nevertheless, contemplative traditions advocate that exceptional altruism is achievable through sustained meditative practices that focus on dissolving the boundaries of the self. Such practices have recently been shown to modulate the very same neural processes that distinguished extraordinary altruists from ordinary folk [10]. Intriguingly, psychedelic substances, particularly those that activate the serotonin system, are also reported to produce profound feelings of connectedness with others and increased overlap in neural correlates of self- and other-processing, although whether this involves similar or different mechanisms to those characterizing meditative practices remains to be seen [10]. These converging lines of evidence connect modern neuroscience with ancient wisdom that transcending the self may ultimately be the key to unlocking the human potential for altruism. What it means to be truly 'selfless' is perhaps even more literal than previously thought.

¹Department of Psychology, Yale University, New Haven, CT 06511, USA

²Department of Experimental Psychology, University of Oxford, Oxford, OX2 6HG, UK

*Correspondence:

molly.crockett@yale.edu (M.J. Crockett).

<https://doi.org/10.1016/j.tics.2018.09.003>

References

1. Brethel-Haurwitz, K.M. *et al.* (2018) Extraordinary altruists exhibit enhanced self–other overlap in neural responses to distress. *Psychol. Sci.* Published online 21 August 2018. <http://dx.doi.org/10.1177/0956797618779590>
2. Ashar, Y.K. *et al.* (2017) Empathic care and distress: predictive brain markers and dissociable brain systems. *Neuron* 94, 1263–1273.e4
3. Sul, S. *et al.* (2015) Spatial gradient in value representation along the medial prefrontal cortex reflects individual differences in prosociality. *Proc. Natl. Acad. Sci. U. S. A.* 112, 7851–7856
4. Wittmann, M.K. *et al.* (2018) Neural mechanisms of social cognition in primates. *Annu. Rev. Neurosci.* 41, 99–118
5. Lockwood, P.L. *et al.* (2016) Neurocomputational mechanisms of prosocial learning and links to empathy. *Proc. Natl. Acad. Sci. U. S. A.* 113, 9763–9768
6. Morelli, S.A. *et al.* (2018) Neural sensitivity to personal and vicarious reward differentially relates to prosociality and well-being. *Soc. Cogn. Affect. Neurosci.* 13, 831–839
7. Corradi-Dell'Acqua, C. *et al.* (2016) Cross-modal representations of first-hand and vicarious pain, disgust and fairness in insular and cingulate cortex. *Nat. Commun.* 7, 10904
8. Hutcherson, C.A. *et al.* (2015) A neurocomputational model of altruistic choice and its implications. *Neuron* 87, 451–462
9. Crockett, M.J. *et al.* (2017) Moral transgressions corrupt neural representations of value. *Nat. Neurosci.* 20, 879–885
10. Millière, R. *et al.* (2018) Psychedelics, meditation, and self-consciousness. *Front. Psychol.* 9, Published online 4 September 2018. <http://dx.doi.org/10.3389/fpsyg.2018.01475>

Forum

Modelling the Human Cortex in Three Dimensions

Esther Kuehn^{1,2,3,*} and Martin I. Sereno⁴

In cognitive neuroscience, brain-behaviour relationships are usually mapped onto a 2D cortical sheet. Cortical layers are a critical but often ignored third dimension of human cortical function.

Improved resolution has put us on the threshold of beginning to image human cognition in three dimensions.

From 2D to 3D Cognition

Cognitive neuroscience investigates the fascinating question of how neuronal computations give rise to mental processes such as sensory perception, learning, and memory. The cortex, which plays an important role in all of these processes, is often pictured as a 2D, folded sheet. However, this 2D model disregards the third (depth) dimension of the cortex, both anatomically and with respect to function (Figure 1). By contrast, modelling the human cortex as a 3D sheet takes into consideration the structured decomposition of laminar function long known from invasive experiments in rodents. Thus, this approach extends brain-behaviour mapping by one dimension. Recent developments in human neuroimaging technology (e.g., ultra-high field imaging at 7 Tesla) are finally making it possible to non-invasively investigate cortical depth-dependent computations in the living human brain. Here, we introduce ‘3D cognition’ and discuss how this concept may help to unpack the ‘hidden variables’ of human cognition.

Columnar Overlap Does Not Mean Computational Equivalence

Brain parcellation atlases attempt to distinguish cortical areas using microarchitectonic features, such as the arrangement of cells or myelin. In early sensory areas, there is excellent correspondence between the boundaries of repeated neighbour-preserving maps of receptor sheets and architectonically-defined brain areas. There is no doubt that position tangential to the cortex is relevant for mental processes. However, cortical layers have strikingly different

influences and functions, as revealed by experiments conducted with rodents and monkeys. Middle granular layers function as input layers for thalamic and earlier cortical area afferents; feedforward supragranular layers contribute to sensory signal elaboration, sensory memory, and have associative functions; deep infragranular layers are often involved in intra-columnar processing, important for perceptual sharpening and feedback; layer 5, containing neurons with huge dendrites, functions as an output layer and sends projections to subcortical areas; and finally, fibre-filled layer 1 receives both feedforward and feedback inputs (e.g., [1,2]).

The glutaminergic pathways in the cortex and thalamus were recently subdivided into two principal classes: ‘drivers’ and ‘modulators’ [2]. Whereas driver inputs carry sensory information, modulators modify or gate it (e.g., by control of firing mode, switching, or gain control). In the cortex, modulators often involve deeper cortical layers, particularly those in the deep layer 6. Critically, both driver and modulator inputs are topographically precise, and their tangential positions coincide, albeit at different depths, in a single cortical column.

Tangential overlap within a column does therefore not imply computational equivalence. Within the same columnar unit, different and perhaps even orthogonal functions may be computed. Though different hierarchical processing levels are typically assigned to different tangential cortical areas, different layers within one tangential area may perform computations at different levels, too. Advances in ultra-high field imaging now allow, for the first time, cortical depth-dependent non-invasive imaging in the living human brain. Continual optimisation of software and hardware components of ultra-high field MR scanners by MR physicists have