[Communicative & Integrative Biology 2:4, 365-367; July/August 2009]; ©2009 Landes Bioscience

Mini-Review

Searching for an integrated self-representation

Istvan Molnar-Szakacs[1-3,*] and Shahar Arzy[3-5]

[1]Tennenbaum Center for the Biology of Creativity; Semel Institute for Neuroscience and Human Behavior; and [2]Department of Psychiatry and Biobehavioral Sciences; David Geffen School of Medicine; University of California, Los Angeles; Los Angeles, CA USA; [3]Laboratory of Cognitive Neuroscience; Brain Mind Institute; Ecole Polytechnique Fédérale de Lausanne (EPFL); Lausanne, Switzerland; [4]Department of Neurology; University Hospital; Geneva, Switzerland; [5]Department of Neurology; Hadassah Hebrew University Hospital; Jerusalem, Israel

Key words: autobiographical memory, physical self, mental self, theory of mind, resting state, mirror neurons, temporo-parietal junction

Recent inquiries into the nature of self-representation have put forward a new and interesting conceptualization of the self, as a "center of gravity" of one's private and social behavior. We review recent neuroimaging work that has suggested interactions among brain regions comprising the default state network, including medial and temporo-parietal cortical regions and the mirror neuron system including lateral fronto-parietal regions as two interacting neural systems that work in concert to produce a cohesive self-representation through simulation. Simulation processes—broadly construed here as using existing representations as templates for understanding novel information—are instantiated by these brain systems across a wide range of domains including time, space, physical and social, giving rise to the multi-faceted Self that we all are. Accumulating evidence also suggests, that these simulation processes are used in a multitude of cognitions that constitute the self, including autobiographical memory and prospection, perspective taking, understanding other's actions and mental states and embodied self-representation.

Introduction

The existence of a "default mode" for brain function—an organized baseline mode that is suspended during specific goal-directed behaviors—has become established.[1-4] It has recently been proposed that the core set of brain regions including cortical midline structures comprising the "default mode network" may also underlie certain high level human behaviors such as autobiographical memory, prospection, spatial navigation and imagination of another person's perspective (theory of mind,ToM) processes.[5] A meta-analysis of neuroimaging studies found support for this proposal, showing a high degree of correspondence within the lateral prefrontal cotex, medial-temporal lobe, precuneus, posterior cingulate, retrosplenial cortex, the temporo-parietal junction and the occipital lobe across these domains.[6]

Another substantial cerebral network is the fronto-parietal mirror neuron system (MNS), which is active when an agent performs an action, but also when it observes that same action being performed by another agent. The MNS together with the "default network", have been hypothesized to represent abstract and concrete aspects of the self, respectively, and interact to give rise to a unified representation of the self as a social being.[7] It had been suggested in earlier work that areas of the default network may be involved in self-referential mental activity,[8] and that this activity may represent the "projection of oneself into another time, place or perspective."[5] Thus, these lines of research on time, space, physical representations and social cognition appear to converge on a common set of brain regions, centered on the default mode network, as well as a set of cognitive processes that are anchored by the Self as point of reference.

Here, we would like to advance the proposal that the Self emerges as an integration of representations across the domains of time, space, physical embodiment and social cognition. Furthermore, the self-representation across all of these domains—time, space, physical and social—is accomplished through simulation. Simulation is a term that has been used in cognitive psychology to describe a variety of processes including Ingvar's "anticipatory programming" of behavior,[9] estimates of likelihood of a behavior,[10] the imitative representation of an event,[11] "reenactments of sensory-motor states"[12] and understanding the mental states of others.[13] For our current purpose, we define simulation as the rather broad process of using existing representations as templates for processing novel information from one's own perspective. Essentially, this means humans use information that is already known, as a template for re-presenting and understanding new information, in order to plan our short- and long-term behaviors. In the following sections, we will briefly describe how this simulation process may subserve each of the domains constituting the Self—time, space, physical and social—and the brain regions supporting these re-presentations.

Autobiographical Memory and Self-Projection

A growing interest in understanding human consciousness has led to a flurry of research on all aspects of simulation, including the

*Correspondence to: Istvan Molnar-Szakacs; Tennenbaum Center for the Biology of Creativity; Semel Institute for Neuroscience and Human Behavior; University of California, Los Angeles; 760 Westwood Plaza, Room C8-846; Los Angeles, CA 90095 USA; Email: imolnar@ucla.edu

Submitted: 02/21/09; Accepted: 02/24/09

Previously published online as a *Communicative & Integrative Biology* E-publication:
http://www.landesbioscience.com/journals/cib/article/8290

human ability for mental time travel (MTT), which allows one to recall the past and pre-experience or predict the future (reviewed in refs. 14 and 15). This productive feature of memory is described in the constructive episodic simulation hypothesis recently outlined,[16,17] and supported by several neuroimaging studies, finding an overlap in the core neural network that underlies both remembering the past and imagining the future.[18-20] Accordingly, patients with amnesia were shown to be markedly impaired relative to matched control subjects not only in retrieving past events, but also at imagining new experiences.[21] More specifically, Klein and colleagues found that a particular aspect of this deficit in thinking about the future, is an impairment in predicting events about one's *personal* future, rather than public or world events.[22] Furthermore, it was also found that patients with memory deficits who confabulate about their personal past also confabulate about their personal future.[23,24] These findings appear to hint at the privileged nature of information related to the self, and the central role of the self in using memory to mentally construct or simulate a personal future. Schacter and Addis also noted that "imagining personal future events may involve processes above and beyond the general processes involved in constructing non-personal events and generating images."[16] In a recent study of MTT, which involved self-projection to both past and future, we also found an effect of self, whereby participants responded significantly faster to personal (self-relevant) events than to world (non-self-relevant) events.[20] The results of our study also suggested that self-location in time recruits a distributed neural network—including anterior temporal, occipitotemporal and temporo-parietal regions—that are part of the default network, and overlap with the regions recruited during other self-relevant tasks, such as visuo-spatial perspective taking[25] and spatial self-location.[26-28]

Spatial Self-Location and Perspective Taking

Mesulam referred to self-projection as transposing "the effective reference point (of perception) from self to other, from here to there, and from now to then."[29] Studies of spatial self-location and perspective taking parallel studies of MTT, by asking participants to imagine themselves in another spatial, rather than temporal location.[25,26,30-33] These studies tend to show activations within a core neural network similar to self-projection in time, with a particular focus at the temporo-parietal junction. We have also found activation of the temporo-parietal junction in experiments in which participants imagined themselves from their own bodily self-location and from a different imagined location[26-28] similarly to imagining oneself at different points in time.[20] The correspondence between neural processes of self-location in time and self-location in space extends beyond the cortical regions involved, and electrophysiological correlates show remarkably similar timing of brain activations.[20,26,27] Such spatio-temporal coherence at the neural level also supports the notion that simulation of the Self in a different place and a different time, share a common mechanism.

Physical and Psychological Self-Representation

The Self has been broadly divided into two main aspects—the mental and the physical self.[34] As the face is the most identifiable marker of the physical aspect of the Self, it has been the subject of extensive study at the behavioral and neural level.[35-39] Recent functional magnetic resonance imaging (fMRI) studies of self-face recognition have consistently found right fronto-parietal areas associated with identification of the self-face.[36,38,40] These areas, predominantly activated in the right hemisphere including the posterior inferior frontal gyrus and the inferior parietal cortex appear to broadly overlap the human MNS.[41] Mirror neurons are active when an agent performs an action, and when it observes that same action being performed, in essence, creating an agent-independent connection between actor and observer.[42] Based on the property of mirror neurons to internally simulate actions performed by others, it has been proposed that the MNS may provide the link between the physical representation of the Self as related to the physical representation of others.[7,38,39] In fact, the MNS and the default network show opposing patterns of activation during the process of self-other distinction, such that mirror regions show increased activity to "self" relative to "other," while default network regions deactivate less to "other" relative to "self."[38] Paradigms asking participants to evaluate the self-relevance of personality traits have been commonly used to study the mental aspects of the self.[43-45] Components of the default state network, particularly the medial prefrontal cortex and the posterior cingulate cortex have been implicated in representing aspects of the mental self.[7,46,47] These medial fronto-parietal regions of the default network, may subserve the representation and integration of self-relevant traits within the context of autobiographical memory as well as future goals.

Mentalizing and Theory of Mind by the Social Self

Is it possible to study the mental self in isolation from its social context?[46] The answer to this question may be a matter of "degrees", and by varying the degree of similarity between the self and the other person, we may come closer to a clear answer.[48] A review of neuroimaging studies in which participants were asked to simulate another person's perspective revealed a special role for frontal midline regions only subtly different from those found in studies of self-relevant trait judgments.[49] These data provide support at the neural level, for the notion that the Self is grounded in its social relationships. As a result, the brain has evolved mechanisms for understanding others and their mental states (thoughts, emotions and beliefs) as motivating factors behind their actions.[50] ToM, or mentalizing, often involves a change in "reference point" as suggested by Mesulam, in other words, taking the perspective of another person. According to simulation accounts of ToM, these perspective shifts are accomplished through self-projection,[50,51] in a manner similar to what happens during MTT, or spatial perspective shifts. In mentalizing about others' goals and behaviors, one can simulate other's mental states as if they were his/her own, and use the Self to predict possible actions and reactions. ToM has been found to share a neural signature with autobiographical memory and self-projection, including activations in the medial and lateral prefrontal cortex, medial temporal lobe and parietal regions, including the temporo-parietal junction, the occipital lobe and the lateral prefrontal cortex.[6] Thus, this network of brain regions, subserves in part the processes necessary to connect the self to its social world, through simulating the mental states of others.

Conclusion

We have attempted to outline a common thread linking aspects of the self across the domains of time, space, physical embodiment and the social world as may be accomplished through a simulation mechanism. In our interpretation of the process of simulation, the self uses available knowledge as a template for processing, representing and understanding new information. Whether simulation involves self-projection in time for the purposes of planning the future, or projection of a perceived image onto the self-image during self-other differentiation; at their core, mental time travel, perspective taking, self-representation and mentalizing are all cogitations that in the broadest sense appear to involve a simulation mechanism. These high-level functions rely on a distributed network of brain structures, including the medial prefrontal cortex, medial temporal lobe, parietal regions and the temporo-parietal junction forming the core of the default mode network, and the posterior inferior frontal gyrus and inferior parietal lobule forming the core of the human mirror neuron system.

Acknowledgements

The authors would like to thank Olaf Blanke for mentorship and Lucina Q. Uddin for scholarly advice.

References

1. Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL. A default mode of brain function. Proc Natl Acad Sci USA 2001; 98:676-82.
2. Gusnard DA, Raichle ME. Searching for a baseline: functional imaging and the resting human brain. Nat Rev Neurosci 2001; 2:685-94.
3. Raichle ME, Mintun MA. Brain work and brain imaging. Annu Rev Neurosci 2006; 29:449-76.
4. Fox MD, Raichle ME. Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. Nat Rev Neurosci 2007; 8:700-11.
5. Buckner RL, Carroll DC. Self-projection and the brain. Trends Cogn Sci 2007; 11:49-57.
6. Spreng RN, Mar RA, Kim AS. The common neural basis of autobiographical memory, prospection, navigation, theory of mind and the default mode: a quantitative meta-analysis. J Cogn Neurosci 2008; Epub ahead of print (doi: 10.1162/jocn.2008.21029).
7. Uddin LQ, Iacoboni M, Lange C, Keenan JP. The self and social cognition: the role of cortical midline structures and mirror neurons. Trends Cogn Sci 2007; 11:153-7.
8. Gusnard DA, Akbudak E, Shulman GL, Raichle ME. Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. Proc Natl Acad Sci USA 2001; 98:4259-64.
9. Ingvar DH. "Hyperfrontal" distribution of the cerebral grey matter flow in resting wakefulness; on the functional anatomy of the conscious state. Acta Neurol Scand 1979; 60:12-25.
10. Kahneman D, Tversky A. On the psychology of prediction. Psychol Rev 1973; 80:237-51.
11. Taylor S, Schneider S. Coping and the simulation of events. Soc Cogn 1989; 7:174-94.
12. Hesslow G. Conscious thought as simulation of behaviour and perception. Trends Cogn Sci 2002; 6:242-7.
13. Gallese V, Goldman A. Mirror neurons and the simulation theory of mind-reading. Trends Cogn Sci 1998; 2:493-501.
14. Schacter DL, Addis DR, Buckner RL. Episodic simulation of future events: concepts, data and applications. Ann NY Acad Sci 2008; 1124:39-60.
15. Schacter DL, Addis DR, Buckner RL. Remembering the past to imagine the future: the prospective brain. Nat Rev Neurosci 2007; 8:657-61.
16. Schacter DL, Addis DR. The cognitive neuroscience of constructive memory: remembering the past and imagining the future. Philos Trans R Soc Lond B Biol Sci 2007; 362:773-86.
17. Bar M. The proactive brain: using analogies and associations to generate predictions. Trends Cogn Sci 2007; 11:280-9.
18. Addis DR, Wong AT, Schacter DL. Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. Neuropsychologia 2007; 45:1363-77.
19. Szpunar KK, Watson JM, McDermott KB. Neural substrates of envisioning the future. Proc Natl Acad Sci USA 2007; 104:642-7.
20. Arzy S, Molnar-Szakacs I, Blanke O. Self in time: imagined self-location influences neural activity related to mental time travel. J Neurosci 2008; 28:6502-7.
21. Hassabis D, Kumaran D, Vann SD, Maguire EA. Patients with hippocampal amnesia cannot imagine new experiences. Proc Natl Acad Sci USA 2007; 104:1726-31.
22. Klein S, Loftus J, Kihlstrom J. Memory and temporal experience. The effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. Soc Cogn 2002; 20:353-79.
23. Dalla Barba G, Nedjam Z, Dubois B. Confabulation, executive functions and source memory in Alzheimer's disease. Cogn Neuropsychol 1999; 16:385-98.
24. Dalla Barba G. Recognition memory and recollective experience in Alzheimer's disease. Memory 1997; 5:657-72.
25. Vogeley K, Fink GR. Neural correlates of the first-person-perspective. Trends Cogn Sci 2003; 7:38-42.
26. Blanke O, Mohr C, Michel CM, Pascual-Leone A, Brugger P, Seeck M, et al. Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. J Neurosci 2005; 25:550-7.
27. Arzy S, Thut G, Mohr C, Michel CM, Blanke O. Neural basis of embodiment: distinct contributions of temporoparietal junction and extrastriate body area. J Neurosci 2006; 26:8074-81.
28. Arzy S, Mohr C, Michel CM, Blanke O. Duration and not strength of activation in temporo-parietal cortex positively correlates with schizotypy. NeuroImage 2007; 35:326-33.
29. Mesulam M. The human frontal lobes: Transcending the default mode through contingent encoding. In: Stuss D, Knight R, (eds). Principles of Frontal Lobe Function. Oxford: Oxford University Press 2002; 8-30.
30. Ruby P, Decety J. Effect of subjective perspective taking during simulation of action: a PET investigation of agency. Nat Neurosci 2001; 4:546-50.
31. Parsons LM. Imagined spatial transformation of one's body. J Exp Psychol Gen 1987; 116:172-91.
32. Zacks J, Rypma B, Gabrieli JD, Tversky B, Glover GH. Imagined transformations of bodies: an fMRI investigation. Neuropsychologia 1999; 37:1029-40.
33. Ratcliff G. Spatial thought, mental rotation and the right cerebral hemisphere. Neuropsychologia 1979; 17:49-54.
34. Gillihan SJ, Farah MJ. Is self special? A critical review of evidence from experimental psychology and cognitive neuroscience. Psychol Bull 2005; 131:76-97.
35. Keenan JP, Nelson A, O'Connor M, Pascual-Leone A. Self-recognition and the right hemisphere. Nature 2001; 409:305.
36. Platek SM, Loughead JW, Gur RC, Busch S, Ruparel K, Phend N, et al. Neural substrates for functionally discriminating self-face from personally familiar faces. Hum Brain Mapp 2006; 27:91-8.
37. Sugiura M, Kawashima R, Nakamura K, Okada K, Kato T, Nakamura A, et al. Passive and active recognition of one's own face. NeuroImage 2000; 11:36-48.
38. Uddin LQ, Kaplan JT, Molnar-Szakacs I, Zaidel E, Iacoboni M. Self-face recognition activates a frontoparietal "mirror" network in the right hemisphere: an event-related fMRI study. NeuroImage 2005; 25:926-35.
39. Uddin LQ, Molnar-Szakacs I, Zaidel E, Iacoboni M. rTMS to the right inferior parietal lobule disrupts self-other discrimination. Soc Cogn Affect Neurosci 2006; 1:65-71.
40. Sugiura M, Watanabe J, Maeda Y, Matsue Y, Fukuda H, Kawashima R. Cortical mechanisms of visual self-recognition. Neuroimage 2005; 24:143-9.
41. Rizzolatti G, Craighero L. The mirror-neuron system. Annu Rev Neurosci 2004; 27:169-92.
42. Gallese V. The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. Psychopathology 2003; 36:171-80.
43. Molnar-Szakacs I, Uddin LQ, Iacoboni M. Right-hemisphere motor facilitation by self-descriptive personality-trait words. Eur J Neurosci 2005; 21:2000-6.
44. Kelley WM, Macrae CN, Wyland CL, Caglar S, Inati S, Heatherton TF. Finding the self? An event-related fMRI study. J Cogn Neurosci 2002; 14:785-94.
45. Macrae CN, Moran JM, Heatherton TF, Banfield JF, Kelley WM. Medial prefrontal activity predicts memory for self. Cereb Cortex 2004; 14:647-54.
46. Amodio DM, Frith CD. Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci 2006; 7:268-77.
47. Northoff G, Bermpohl F. Cortical midline structures and the self. Trends Cogn Sci 2004; 8:102-7.
48. Mitchell JP, Banaji MR, Macrae CN. The link between social cognition and self-referential thought in the medial prefrontal cortex. J Cogn Neurosci 2005; 17:1306-15.
49. Gallagher HL, Frith CD. Functional imaging of 'theory of mind'. Trends Cogn Sci 2003; 7:77-83.
50. Carruthers P, Smith P. Theories of theories of mind. 1996; Cambridge University Press.
51. Blakemore SJ, Decety J. From the perception of action to the understanding of intention. Nat Rev Neurosci 2001; 2:561-7.