Published in final edited form as:

Behav Brain Sci. 2013 August ; 36(4): 424–425. doi:10.1017/S0140525X12001938.

Brain games: Toward a neuroecology of social behavior

Jean-François Gariépy^{a,b}, Steve W. C. Chang^{a,b}, and Michael L. Platt^{a,b,c,d}

^aDepartment of Neurobiology, Duke University School of Medicine, Durham, NC 27701

^bCenter for Cognitive Neuroscience, Duke University, Durham, NC 27708

^cDepartment of Evolutionary Anthropology, Duke University, Durham, NC 27708

^dDepartment of Psychology and Neuroscience, and Levine Science Research Center, Duke University, Durham, NC 27708

Abstract

In the target article, Schilbach et al. defend a “second-person neuroscience” perspective that focuses on the neural basis of social cognition during live, ongoing interactions between individuals. We argue that a second-person neuroscience would benefit from formal approaches borrowed from economics and behavioral ecology and that it should be extended to social interactions in nonhuman animals.

The “second-person neuroscience” proposed by Schilbach et al. in the target article proffers the intriguing idea that social cognition during real-time interactions with another individual may be fundamentally different from passive observations of another's actions.

Understanding the contribution of neural processes to ongoing interactions with complex beings is a fascinating research direction, with potential implications for the treatment of disorders attended by social deficits, as well as for ethics and public policy.

Several decades of neuroscientific research have sketched out the neural circuits that may translate perceptual information about other individuals into purposeful action. Specifically, regions of the human and nonhuman primate brain including the superior temporal sulcus and fusiform face area contribute to social identification (Tsao et al. 2008). The ventromedial pre-frontal cortex, orbitofrontal cortex, and striatum appear to play a role in translating knowledge of others into motivational signals (Azzi et al. 2012; Burke et al. 2010; Cooper et al. 2010). The anterior cingulate cortex and fronto-insular cortex contribute to empathy and other-regarding cognition (Chang et al. 2013; Decety 2010; Gu et al. 2010). The so-called mentalizing and mirroring networks appear to participate in action and intention understanding (Becchio et al. 2012; Rizzolatti & Sinigaglia 2010). Circuits connecting these areas could translate social perceptual information into appropriate actions via decision-making mechanisms (Baumgartner et al. 2009, 2011; Knoch et al. 2009).

To better understand the neural mechanisms underlying social cognition, we propose that social neuroscience needs to ground its predictions and hypotheses in a formal framework such as that provided by behavioral game theory (Dorris & Glimcher 2004; Gintis 2009; Kosfeld et al. 2005; Lee 2008; Platt & Glimcher 1999; Tomlin et al. 2006). Schilbach et al. criticize game theoretical approaches for not recreating the dynamics of everyday real-life social encounters, but this common opposition has been rebutted before (Gintis 2009). Game theoretical frameworks are general and open, allowing formal delineation of specific hypotheses while not imposing restrictions on the behaviors that are being described. Formal approaches borrowed from economics, game theory, and behavioral ecology have been extremely useful in describing decisions in dynamic foraging or social environments (Chang et al. 2011; Hayden et al. 2011; Lee 2008; Sugrue et al. 2004).

These approaches can be extended to describe the dynamics of interacting individuals, with several advantages. First, they allow us to generate empirically testable and mathematically formalizable predictions about the neural mechanisms that could underlie decisions in complex social environments. Second, they allow for comparative analyses of decision processes in humans and other animals with respect to the demands placed on them in specific physical and social environments (Heilbronner et al. 2008; Kacelnik & Bateson 1996; Stephens et al. 2002).

Schilbach et al. also raise the concern that classical game theory paradigms involve mainly one-shot interactions or turn-taking. Although this structure is often used for simplicity, we contend that continuous interactions in interactive games can also be effectively described using a similar theoretical framework (Braun et al. 2009; Debreu 1952). Such mathematical tools would help translate some of the intuitive aspects of Schilbach et al.'s approach into concrete experimental predictions.

Second-person neuroscience would also benefit from broadening its inquiry to the interactions of nonhuman animals (Chang et al. 2011; Fujii et al. 2007; Washburn et al. 1990). Social complexity appears to have favored the evolution of higher social cognition in animals that have brains similar to ours, like macaques (Azzi et al. 2012; Barsalou, 2005; Chang et al. 2012; Rudebeck et al. 2006; Tsao et al. 2008) and in animals that have very different brains as well, like scrub jays and rooks (Bird & Emery 2010; Emery & Clayton 2001). We know from research in macaques, sheep, and mice that social cognition in mammals appears to rely on neural circuits that are similar, and perhaps homologous, to those in humans (Azzi et al. 2012; Barsalou, 2005; Jeon et al. 2010; Rudebeck et al. 2006; Sanchez-Andrade & Kendrick 2009; Tsao et al. 2008). One possible explanation is that we inherited those circuits from a common ancestor that possessed some level of social complexity. Alternatively, similar constraints applying to neural circuits could also have caused them to evolve in similar ways to support similar functions. How such functions are accomplished by neural circuits in animals with brains that are very different from our own – such as birds – remains an open question.

We agree with Schilbach et al. that studying the neural processes mediating live interaction between real agents is crucial for the maturation of social neuroscience as a discipline. What we propose is to supplement this approach with formal game theory and value-based

analysis of preferences in humans and nonhuman animals. In our lab, for example, we study pairs of monkeys interacting both in economical and interactive games (Chang et al. 2011; Chang et al. 2013). Estimating preferences allows us to quantify how much monkeys value certain options (e.g., giving juice to another monkey). Game theory will allow us to generate predictions of the equilibriums that could develop over time between two interacting individuals (see Braun et al. 2009). Understanding the neural processes that underlie social cognition in such animals could powerfully inform our understanding of the evolutionary origins of our own social abilities.

References

- Azzi JC, Sirigu A, Duhamel JR. Modulation of value representation by social context in the primate orbitofrontal cortex. *Proceedings of the National Academy of Sciences USA*. 2012; 109:2126–31.
- Barsalou LW. Continuity of the conceptual system across species. *Trends in Cognitive Sciences*. 2005; 9:309–11. [PubMed: 15951226]
- Baumgartner T, Fischbacher U, Feierabend A, Lutz K, Fehr E. The neural circuitry of a broken promise. *Neuron*. 2009; 64:756–70. [PubMed: 20005830]
- Baumgartner T, Knoch D, Hotz P, Eisenegger C, Fehr E. Dorsolateral and ventromedial prefrontal cortex orchestrate normative choice. *Nature Neuroscience*. 2011; 14:1468–74.
- Becchio C, Cavallo A, Begliomini C, Sartori L, Feltrin G, Castiello U. Social grasping: From mirroring to mentalizing. *Neuroimage*. 2012; 61(1):240–48. [PubMed: 22440652]
- Bird CD, Emery NJ. Rooks perceive support relations similar to six-month-old babies. *Proceedings of the Royal Society of London, B: Biological Sciences*. 2010; 277:147–51.
- Braun DA, Ortega PA, Wolpert DM. Nash equilibria in multi-agent motor interactions. *PLoS Computational Biology*. 2009; 5:e1000468. [PubMed: 19680426]
- Burke CJ, Tobler PN, Schultz W, Baddeley M. Striatal BOLD response reflects the impact of herd information on financial decisions. *Frontiers in Human Neuroscience*. 2010; 4:48. [PubMed: 20589242]
- Chang SW, Barter JW, Ebitz RB, Watson KK, Platt ML. Inhaled oxytocin amplifies both vicarious reinforcement and self reinforcement in rhesus macaques (*Macaca mulatta*). *Proceedings of the National Academy of Sciences USA*. 2012; 109:959–64.
- Chang SW, Gariépy JF, Platt ML. Neuronal reference frames for social decisions in primate frontal cortex. *Nature Neuroscience*. 2013; 16:243–50.
- Chang SW, Winecoff AA, Platt ML. Vicarious reinforcement in rhesus macaques (*Macaca mulatta*). *Frontiers in Neuroscience*. 2011; 5:27. [PubMed: 21516263]
- Cooper JC, Krebs TA, Wiebe T, Pirkel T, Knutson B. When giving is good: Ventromedial prefrontal cortex activation for others' intentions. *Neuron*. 2010; 67:511–21. [PubMed: 20696386]
- Debreu G. A social equilibrium existence theorem. *Proceedings of the National Academy of Sciences USA*. 1952; 38:886–93.
- Decety J. The neurodevelopment of empathy in humans. *Developmental Neuroscience*. 2010; 32:257–67. [PubMed: 20805682]
- Dorris MC, Glimcher PW. Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron*. 2004; 44:365–78. [PubMed: 15473973]
- Emery NJ, Clayton NS. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature*. 2001; 414:443–46. [PubMed: 11719804]
- Fujii N, Hihara S, Iriki A. Dynamic social adaptation of motion-related neurons in primate parietal cortex. *PLoS One*. 2007; 2:e397. [PubMed: 17460764]
- Gintis, H. *The bounds of reason: Game theory and the unification of the behavioral sciences*. Princeton University Press; 2009.
- Gu X, Liu X, Guise KG, Naidich TP, Hof PR, Fan J. Functional dissociation of the frontoinsula and anterior cingulate cortices in empathy for pain. *Journal of Neuroscience*. 2010; 30:3739–44. [PubMed: 20220007]

- Hayden BY, Pearson JM, Platt ML. Neuronal basis of sequential foraging decisions in a patchy environment. *Nature Neuroscience*. 2011; 14:933–39.
- Heilbrunner SR, Rosati AG, Stevens JR, Hare B, Hauser MD. A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters*. 2008; 4:246–49. [PubMed: 18364305]
- Jeon D, Kim S, Chetana M, Jo D, Ruley HE, Lin SY, Rabah D, Kinet JP, Shin HS. Observational fear learning involves affective pain system and Cav1.2 Ca²⁺ channels in ACC. *Nature Neuroscience*. 2010; 13:482–88.
- Kacelnik A, Bateson M. Risky theories: The effects of variance on foraging decisions. *American Zoology*. 1996; 36:402–34.
- Knoch D, Schneider F, Schunk D, Hohmann M, Fehr E. Disrupting the prefrontal cortex diminishes the human ability to build a good reputation. *Proceedings of the National Academy of Sciences USA*. 2009; 106:20895–99.
- Kosfeld M, Heinrichs M, Zak PJ, Fischbacher U, Fehr E. Oxytocin increases trust in humans. *Nature*. 2005; 435:673–76. [PubMed: 15931222]
- Lee D. Game theory and neural basis of social decision making. *Nature Neuroscience*. 2008; 11:404–409.
- Platt ML, Glimcher PW. Neural correlates of decision variables in parietal cortex. *Nature*. 1999; 400:233–38. [PubMed: 10421364]
- Rizzolatti G, Sinigaglia C. The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*. 2010; 11(4):264–74. Available at: <http://dx.doi.org/10.1038/nrn2805>.
- Rudebeck PH, Buckley MJ, Walton ME, Rushworth MF. A role for the macaque anterior cingulate gyrus in social valuation. *Science*. 2006; 313:1310–12. [PubMed: 16946075]
- Sanchez-Andrade G, Kendrick KM. The main olfactory system and social learning in mammals. *Behavioural Brain Research*. 2009; 200:323–35. [PubMed: 19150375]
- Stephens DW, McLinn CM, Stevens JR. Discounting and reciprocity in an Iterated Prisoner's Dilemma. *Science*. 2002; 298:2216–18. [PubMed: 12481142]
- Sugrue LP, Corrado GS, Newsome WT. Matching behavior and the representation of value in the parietal cortex. *Science*. 2004; 304:1782–87. [PubMed: 15205529]
- Tomlin D, Kayali MA, King-Casas B, Anen C, Camerer CF, Quartz SR, Montague PR. Agent-specific responses in the cingulate cortex during economic exchanges. *Science*. 2006; 312(5776):1047–50. Available at: <http://dx.doi.org/10.1126/science.1125596>. [PubMed: 16709783]
- Tsao DY, Moeller S, Freiwald WA. Comparing face patch systems in macaques and humans. *Proceedings of the National Academy of Sciences USA*. 2008; 105:19514–19.
- Washburn DA, Hopkins WD, Rumbaugh DM. Effects of competition on video-task performance in monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*. 1990; 104:115–21. [PubMed: 2364656]