

For Love or Money: A Common Neural Currency for Social and Monetary Reward

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Two papers in the current issue of Neuron (Izuma et al. and Zink et al.) report that activity in specific regions of the brain, especially the striatum, reflects a common signal of reward in both the economic (e.g., money) and social (e.g., praise and status) domains.

Reputation, reputation, reputation! O, I have lost my reputation! I have lost the immortal part of myself.

-Cassio in Shakespeare's Othello

Folk wisdom suggests that there are rewards in life more valuable than money. Chief among them are love (or social acceptance) and reputation (or social status). To say that love is worth more than money, though, is to imply some third scale, a common "currency" in which physical and social rewards can be measured and thus compared. Neuroeconomists are currently taking this idea literally.

One salient kind of social reward is social acceptance, a positive evaluation of the self by others. Izuma et al. (2008) (this issue of Neuron) directly compared participants' neural responses to receiving money versus praise using functional MRI. Each participant was scanned on 2 days. On the first day, they played a simple gambling game and received monetary rewards. The neural response during high versus low payoffs identified brain regions that respond to positive monetary reward. As expected from previous studies (Knutson et al., 2001; O'Doherty et al., 2001), these regions included parts of the striatum (putamen and caudate nucleus) and orbitofrontal cortex, as well as the insula.

In the scanner on the second day, the participants received social feedback: supposedly observers' assessments of their personality. The feedback included relatively high (positive traits, like "sincere") and relatively low reward (neutral traits, like "patient"). The neural response during high versus low social reward iden-

tified brain regions that respond to positive social reward. Again, this contrast revealed regions in the striatum and insula. (The authors also included a control condition in which the participant saw the social evaluation of a fictitious other participant. Brain regions representing social reward responded selectively during positive evaluations of the self, but not of the other participant.)

Izuma et al.'s key finding is thus the existence of substantial overlap between the neural representation of monetary and social reward. In particular, the left putamen and caudate nucleus showed greater activity in response to both higher monetary payoffs and more positive evaluations of the self.

Zink et al. (2008) (this issue of Neuron) arrive at the same general conclusion. These authors manipulate a different dimension of social reward: relative social status. In their experiment, participants played a simple reaction time game in the presence of two other players. Monetary payoff was determined only by the participant's own performance, but the relative "status" of the three players was marked throughout the experiment. This design created the potential for socially rewarding outcomes, independent of monetary payoffs: loss of relative status (being outperformed by an inferior player) or gain of relative status (outperforming a superior player). Regions in the striatum were recruited during trials involving potential loss or gain of status.

One puzzle is that Zink et al. observed anatomically distinct activation in the striatum for negative and positive social rewards. Another recent paper has reported a related, but not identical, division for

monetary rewards (Seymour et al., 2007). Closer study of these functional divisions with the striatum is warranted.

In addition to parts of the striatum, both papers also report recruitment of a cortical brain region specifically for social feedback: the medial prefrontal cortex (MPFC). In particular, Izuma et al. found that the MPFC response was higher when participants received any evaluations of their own personality relative to receiving personality evaluations of an unfamiliar person or monetary rewards. These results are neatly complementary to a robust result in social cognitive neuroscience: activation in the MPFC when participants themselves evaluate their own personality relative to when they evaluate the personality of an unfamiliar person (Macrae et al., 2004; Northoff et al., 2006; Saxe et al., 2006).

On the whole, the central message remains: social rewards, including positive social feedback and relative social status, are represented in the same brain regions as monetary rewards. These results are thus consistent with previous fMRI evidence (Fliessbach et al., 2007) and with predictions, based on computational models (e.g., Montague and Berns, 2002), of a literal common currency for reward in the brain. Of course, fMRI results cannot establish that the very same neurons, within these brain regions, are being recruited across these different tasks. For a relatively narrower range of possible goods (apple versus grape juice), singlecell recordings have recently revealed neurons in macaque orbitofrontal cortex that encode the value of chosen outcomes independently of the currency (Padoa-Schioppa and Assad, 2006). Whether common currency encoding extends even



to social rewards at the single-neuron level remains to be seen.

One immediate implication of these results is for patients with dysfunction of these brain regions. The striatum is among the targets of some neurological disorders, such as Parkinson's disease (PD). Overtreatment of PD with dopamine agonists is known to induce abnormal economic decision-making, including compulsive gambling (Voon et al., 2006). If the same brain structures are responsible for the reward-value of love and reputation, pharmacological manipulation of the striatum may also have social consequences.

The broader questions raised by the current results concern the relationship between two basic domains of human cognition: the social and the economic. Beyond the common currency, what distinguishes the processing of social versus

monetary reward? How and when does sensitivity to these different domains of reward emerge, during child development or in evolution? And finally, what neural processes are engaged when an individual must trade off one kind of reward against the other? Taken together, the tools of behavioral economics, psychology, and neuroscience could provide an answer to how we decide, in the end, whether to choose love or money.

REFERENCES

Fliessbach, K., Weber, B., Trautner, P., Dohmen, T., Sunde, U., Elger, C.E., and Falk, A. (2007). Science 318, 1305-1308.

Izuma, K., Saito, D.N., and Sadato, N. (2008). Neuron 58, this issue, 284-294.

Knutson, B., Adams, C.M., Fong, G.W., and Hommer, D. (2001). J. Neurosci. 21, RC159.

Macrae, C.N., Moran, J.M., Heatherton, T.F., Banfield, J.F., and Kelley, W.M. (2004). Cereb. Cortex 14, 647-654.

Montague, P.R., and Berns, G.S. (2002). Neuron 36, 265-284.

Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., and Panksepp, J. (2006). Neuroimage 31, 440-457.

O'Doherty, J., Kringelbach, M.L., Rolls, E.T., Hornak, J., and Andrews, C. (2001). Nat. Neurosci. 4.95-102.

Padoa-Schioppa, C., and Assad, J.A. (2006). Nature 441, 223-226.

Saxe, R., Moran, J., Scholz, J., and Gabrieli, J. (2006). Soc. Cogn. Affect. Neurosci. 1, 229-234.

Seymour, B., Daw, N., Dayan, P., Singer, T., and Dolan, R. (2007). J. Neurosci. 27, 4826-4831.

Voon, V., Hassan, K., Zurowski, M., Duff-Canning, S., de Souza, M., Fox, S., Lang, A.E., and Miyasaki, J. (2006). Neurology 66, 1750-1752.

Zink, C.F., Tong, Y., Chen, Q., Bassett, D.S., Stein, J.L., and Meyer-Lindenberg, A. (2008). Neuron 58, this issue, 273-283.

Schizophrenia: Genome, Interrupted

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Structural chromosomal variation is increasingly recognized as an important contributor to human diseases, particularly those of neurodevelopment, such as autism. A current paper makes a significant advance to schizophrenia genetics by establishing an association with rare copy number variants (CNV), which are over-represented in neurodevelopmental genes.

Geneticists have become increasingly aware of a large amount of previously unidentified and unanticipated structural variation within the human genome. These variations, duplications and deletions of relatively small genomic segments that range from 1 kb to several million bases, are referred to as copy number variants (CNVs). CNVs, like other genetic variants, come in many forms: they may be inherited or de novo, rare or common. Similar to single base pair changes, rare de novo CNVs are often interpreted in the

same way as Mendelian mutations that may play a causal role in disease and have been associated with several neurodevelopmental disorders, including intellectual disability and autism (de Vries et al., 2005; Jacquemont et al., 2006; Stankiewicz and Beaudet, 2007; Sebat et al., 2007; Szatmari et al., 2007). Some CNVs arise in chromosomal regions of segmental duplications that allow for inexact crossovers when the gametes are being formed (Mehan et al., 2004; Sharp et al., 2006). Sporadic cases of single-gene

neurological disorders such as Charcot-Marie-Tooth neuropathy and Smith-Magenis syndrome derive from de novo CNVs generated by this mechanism (Lupski, 2007). However, most of the rare de novo CNVs arise in the absence of such repeat regions, consistent with what appears to be random DNA breakage.

The role of CNVs in common complex disorders is an area of intense investigation. Using the molecular technology of microarray-based methods designed for both single-nucleotide polymorphism