SOCIAL NEUROSCIENCE

Social subjective value in the primate midbrain

How we value our own rewards depends on what others have. A new study shows that neurons in the medial prefrontal cortex selectively monitor the value of rewards received by oneself or by another individual, whereas midbrain dopaminergic neurons integrate these values to generate social subjective reward values.

Olga Dal Monte, Siqi Fan and Steve W. C. Chang

You've just been awarded a grant that offers you significant funding for 3 years. Then you find out that your colleague has received far greater funding for 5 years. It is only natural that your own grant now seems much less satisfying. We constantly update our own reward-valuation system through social comparison, a feature shared among primates[1]. How does the brain calculate reward values based on what others have? A new study in this issue of *Nature Neuroscience* demonstrates that neurons in the primate prefrontal cortex monitor the value of rewards received either by oneself or by another individual, whereas midbrain dopaminergic neurons integrate this information to generate 'subjective' value.

The primate prefrontal cortex has been implicated in representing individual-specific (or agent-specific) social information. Neurons in the lateral prefrontal cortex encode actions performed by oneself or by the partner during human–monkey interactions[2]. Furthermore, a large number of neurons located in the dorsomedial prefrontal cortex encode correct and erroneous actions of a partner monkey during a task in which the partner's actions and outcomes must be monitored to maximize one's own reward[3,4]. In another task where monkeys chose to donate or withhold rewards from a conspecific, neurons in the rostral anterior cingulate gyrus of the medial prefrontal cortex (mPFC) represented reward outcome information in an agent-specific manner, including neurons that encoded reward allocations to the other monkey exclusively[5]. The importance of the midline frontal areas in social decision-making was further corroborated by a study showing the causal contribution of anterior cingulate cortex neurons in promoting cooperative decisions during a prisoner's dilemma game in monkeys[6]. Although these studies indicated that the mPFC processes agent-specific information, it remained to be determined whether and how mPFC neurons discriminate changing reward values assigned to self and others.

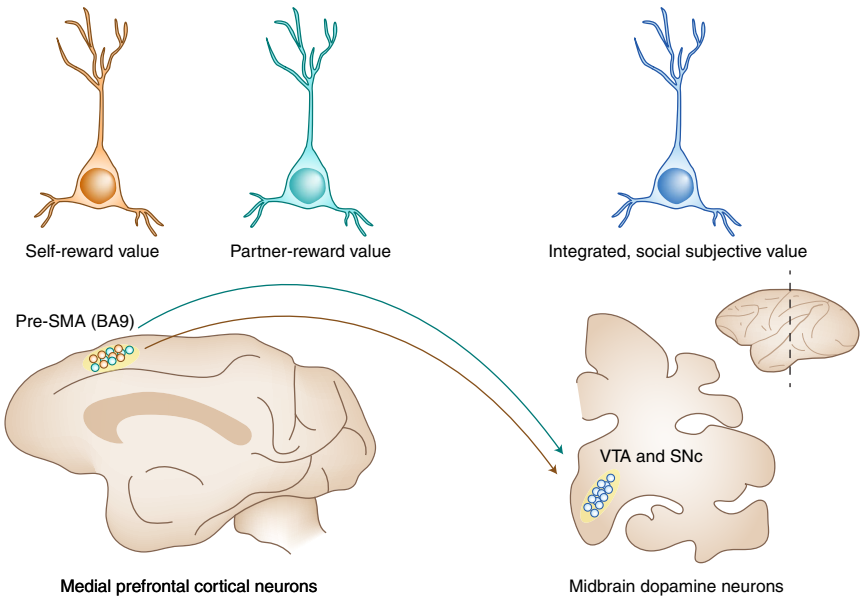

Fig. 1 | Neural response types encoding reward values for the self and others. Self-type mPFC neurons (orange) positively scale their activity to the reward probability of self-reward (relative to partner's reward) but not to the partner-reward probability, whereas partner-type mPFC neurons (green) scale their activity to the partner-reward probability but not to the self-reward probability. By contrast, midbrain dopaminergic neurons (blue) scale their activity according to the subjective value of both self-reward and partner-reward, suggesting that these dopamine neurons represent integrated social subjective value. The arrows indicate a possible scenario in which mPFC neurons directly or indirectly convey agent-specific reward value signals to midbrain dopamine neurons, where these signals are integrated into a social subjective value. Pre-SMA, presupplementary motor area; BA9, Brodmann area 9; SNc, substantia nigra pars compacta; VTA, ventral tegmental area.

In addition to prefrontal cortex, subcortical structures play a central role in signaling reward value. In nonsocial contexts, a subset of midbrain dopaminergic neurons is involved in calculating value-related predictions, including reward value[7,8]. In social contexts, dopamine-release patterns from the rat nucleus accumbens, which receives major projections from midbrain dopaminergic neurons, are modulated by reward delivery to a conspecific[9]. However, whether the firing rates of midbrain dopaminergic neurons themselves encode reward value in social contexts had remained unclear.

One exciting hypothesis is that the dopaminergic cells in the midbrain derive social subjective value by integrating agent-specific information from the mPFC neurons. Testing this prediction would require monitoring the activity of both the midbrain dopaminergic neurons and mPFC neurons simultaneously with behavioral measures to track subjective value. A study by Noritake and colleagues has accomplished this challenging goal, using a novel social Pavlovian conditioning experiment[10]. In this task, one monkey sat opposite another monkey across a monitor showing stimuli that predicted the value of an upcoming reward to the monkey itself or to the other monkey. The two monkeys never received the reward simultaneously.

Importantly, the reward probability for one monkey varied while the reward probability for the other monkey was kept constant. This key manipulation enabled the authors to examine how the same objective reward value is modulated to yield various subjective reward values based on different social contexts. With this setup, the authors first obtained robust evidence of social subjective value, based on anticipatory licking behavior—that is, the subjective value of a self-reward decreased as the reward probability for the partner monkey increased, even though the objective value of the self-reward remained identical in both amount and probability. Notably, these value modulations disappeared in a nonsocial context where the conspecific was replaced with an empty bottle, indicating that the changes in self-reward value were driven by the reward received by the other monkey.

Building on these elegant behavioral findings, the authors recorded both spiking activity and local field potential activity simultaneously from mPFC neurons (presupplementary motor area and Brodmann area 9, which is located rostrally to the presupplementary motor area) and dopaminergic neurons in the midbrain's substantia nigra pars compacta and ventral tegmental area. Firing rates of midbrain dopamine neurons correlated with the subjective reward value as indicated by anticipatory licking behavior, with the activity scaling positively with the probability for self-reward (relative to other-reward probability) and scaling negatively with the increasing reward probability for the partner monkey (relative to self-reward probability). By contrast, the mPFC neurons encoded reward probability in an agent-specific fashion, with activity of 'self-type' and 'partner-type' mPFC neurons positively scaling with the probability of the self-reward and partner-reward, respectively. Notably, in a nonsocial setting without a partner monkey, neuronal modulations associated with different reward probabilities were markedly reduced in both the mPFC and midbrain. The authors further reported that following the reward-predicting cue, the agent-specific value signal in the mPFC emerged earlier than the subjective value signal in midbrain dopaminergic neurons, consistent with a cortex-to-midbrain information flow. This finding supports the hypothesis that the agent-specific value information from self-type and partner-type mPFC neurons may be integrated and transformed into subjective value signals by midbrain dopamine system (Fig. 1).

The study by Noritake and colleagues is an important first step toward understanding how the mPFC conveys agent-specific information to the midbrain dopamine system to generate social subjective value. It is possible that, more generally, agent-referenced information flows from cortical areas to various subcortical areas, where this information is integrated to guide social behaviors, including social decision-making (Fig. 1). Support for this idea comes from a finding that neurons in the basolateral amygdala, a subcortical area, encode reward values in an agent-independent manner[11]. Furthermore, interactions between different neuromodulators—for instance, the oxytocin system interacting with the dopamine[12], serotonin[13], and opioid[14] systems—seem to play a role in social cognition. Experiments that directly test how different cortical and subcortical regions or distinct neuromodulator systems work together to regulate social cognition will be particularly informative in elucidating the neurobiological mechanisms underlying this behavior.

It is likely that multiple types of specialized processing at the single-neuron level (for example, agent-specific mPFC cells) are consolidated and integrated in order to derive a fuller picture of social context to guide behaviors. The new findings by Noritake and colleagues reveal insights into the role of the prefrontal–subcortical dopaminergic pathway in this process and provide a neural, mechanistic foundation for understanding the remarkable and sophisticated social cognition seen in humans[15]. It also offers a new footing for examining whether errors in calculating social subjective value are associated with social dysfunction. Given the recently expanded interest in circuit-level understanding of social behavior across rodents, nonhuman primates, and humans, the future of social neuroscience looks brighter than ever. ❐

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Competing interests

The authors declare no competing interests.