Emotion, Mirror, and Reward:
Reconsidering the Russian Doll Model

Abstracts

A neural extension of the Russian doll model
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The Russian doll model suggested by Prof. de Waal gives a framework to study evolution of social traits in animals. It comprises with three layers of dolls. The core doll has a function of perception-action mechanisms: this enables motor mimicry and emotion contagion. The middle doll contains the core doll, and it enables empathic concern and consolation. The outer doll contains the other two, and it enables perspective taking and targeted helping.

As a first step, to ground the model with neural structures, we explored the process in which the core function of perception-action mechanisms. We have done some experiments that tested whether motor mimicry was supported by dopaminergic reward system. For this, we used the songbird system. We used time differences in behavior driven gene expression reacting both auditory and motor experiences of hearing and singing the song.

We identified auditory-motor mirror neurons in the nucleus HVC, the site of sensory-motor integration. Furthermore, we identified mirror neurons in the area X, a part of the basal ganglia that is known to receive dense dopaminergic inputs from the midbrain VTA/SNc. Results suggest that sensory-motor mirror properties maybe supported by the reward input. Work supported by JSPS #4903 and 17H06380 to KO.

Neural basis of social influences on vocal learning in a songbird
Shin Yanagihara (The University of Tokyo)

As in human speech acquisition, social interactions are critical for vocal learning in songbirds. Juvenile zebra finches hear a song from a live tutor, and faithfully imitate its song. However, passive exposures to a tutor song presented from a speaker in the absence of a live tutor result in a poor imitation. These behavioral studies highlight the importance of social interactions in vocal learning, but underlying neural mechanisms remain unclear. Here, we hypothesized that social
interactions with a tutor enhance the activity of midbrain dopaminergic reward system in juvenile leading to successful memorization of a tutor song. To test this, we recorded multiple single neuron activities from midbrain ventral tegmental area (VTA) and substantia nigra pars compacta (SNc) in juvenile zebra finches, and examined whether the social interactions modulate VTA/SNc activity. We found that a group of VTA/SNc neurons exhibited auditory responses to a tutor song presented through a speaker, and that responses were markedly modulated by social context. These neurons showed greater tutor song responses when a juvenile was in the presence of a tutor compared to alone. Furthermore, similar enhanced auditory responses were found when a juvenile listened to a song from a live tutor. These results suggest that dopaminergic reward system play a role in social enhancement of vocal learning. Work supported by JSPS #4903 and 17H01015 to Kazuo Okanoya, and 17K07066 to SY.

**Mirror self-recognition and partner rescue behavior in fish**
Masanori Kohda (Osaka City University)

We published the paper on the mirror-self recognition (MSR) in fish (Kohda et al. 2019 in PLoS Biology). Here we show the results of additional and other kinds of experiments to reexamine the cleaner fish’s MSR, and all of results support our conclusion. For example, a total of 17 of 18 fish passed the mark tests, much higher passing-rate for mark-test than that of chimpanzee with enough sample sizes. During the mark-test, fish frequently scraped the brown mark resembling fish-parasites, but ignored the blue or green mark not resembling ectoparasites, suggesting visually color perception of the mark is essential, and assist their MSR.

Humans recognize own mirror reflection mainly by gazing on the face. We examined which parts of their mirror reflection this fish using in the MSR, by presenting 4 types of photographs of own and unfamiliar fish, and own face with unfamiliar body and unfamiliar fish face with own body. Facial color pattern of this fish is individual-specific. Our results show they recognize the own mirror reflection depending on their own facial color pattern. They recognize their own photograph, and this implies this fish is likely to have self-concept like as Hominoid species.

**The neural mechanism of cheering: Mirror neuron system and vicarious reward**
Sotaro Shimada (Meiji University)

Cheering a favorite player or team during observing a sports game is one of the most pervasive entertainment. The vicarious reward, which we receive from watching likable others obtaining a positive outcome, is considered to play a critical role in this process. We hypothesized that the
mirror neuron system (MNS) and the reward system work in a coordinated fashion during vicarious reward and conducted several experiments to prove that. The first fNIRS (functional near-infrared spectroscopy) experiment showed that the MNS activated more strongly when the cheered-for player won against the opponent than when he lost. The second fMRI experiment showed that 1) MNS activation was significantly correlated with the participant’s feeling of unity with the cheered-for player, 2) the ventromedial prefrontal cortex (vmPFC), which is the part of the reward system, was activated when the cheered-for player succeeded in the game, but not when the other player did, 3) this vmPFC activation was functionally connected with MNS activation only during the cheered-for player’s success. The third EEG (electroencephalography) experiment basically reproduced the fMRI results. Finally, the fNIRS hyperscanning experiment showed that the observer’s MNS activity was functionally connected with the player’s motor area activity only when the player won, and this connectivity exhibited a significant correlation with the subjective sense of unity between the player and observer. These results suggest that vicarious reward is processed in the MNS-vmPFC network, which is activated specifically by the success of the cheered-for player with whom the individual feels unity and closeness.

Evolution of Emotions and Empathy in the Primates
Frans B.M. de Waal (Emory University, Atlanta, USA and Utrecht University, the Netherlands)

Emotions suffuse much of the language employed by students of animal behavior -- from "social bonding" to "alarm calls" -- yet are still regularly avoided as explicit topic in scientific discourse. Given the increasing interest of human psychology in the emotions, and the neuroscience on animal emotions such as fear and attachment, the taboo that has hampered animal research in this area is outdated. The main point is to separate emotions from feelings, which are the subjective experiences that accompany the emotions. Whereas science has no access to animal feelings, animal emotions are as observable and measurable (face, voice, physiology, neural activity) as human emotions. They are mental and bodily states that potentiate behavior appropriate to mostly social situations. I will discuss early ideas about animal emotions and draw upon research on empathy and the perception of emotions in primates to make the point that the study of animal emotions is a necessary complement to the study of behavior. Emotions are best viewed as the organizers of adaptive responses to environmental stimuli.