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FUNCTIONAL DIFFERENCES IN FACE PROCESSING BETWEEN THE AMYGDALA AND VENTROLATERAL PREFRONTAL CORTEX IN MONKEYS

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Abstract—The ability to categorize social information is essential to survive in a primate's social group. In the monkey brain, there are neural systems to categorize social information. Among these, the relationship between the amygdala and the ventrolateral prefrontal cortex (vlPFC) has recently gained focus with regard to emotion regulation. However, the processing of facial information and the functional differences in these two areas remain unclear. Thus, in this study, we examined the response properties of single neurons in the amygdala and vlPFC while presenting video clips of three types of facial emotions (aggressive threat, coo, and scream) in *Macaca mulatta*. Neurons in the amygdala were preferentially activated upon presentation of a scream facial expression, which is strongly negative, whereas the neurons in the vlPFC were activated upon presentation of coo, a facial expression with multiple meanings depending on the social context. Information analyses revealed that the amount of information conveyed by the amygdala neurons about the type of emotion transiently increased immediately after stimulus presentation. In contrast, the information conveyed by the vlPFC neurons showed sustained elevation during stimulus presentation. Therefore, our results suggest that the amygdala processes strong emotion roughly but rapidly, whereas the vlPFC spends a great deal of time processing ambiguous facial information in communication, and make an accurate decision from multiple possibilities based on memory.

Key words: communication, emotion, *Macaca mulatta*, rhesus monkey.

INTRODUCTION

Because the ability to categorize social information is essential to survive in a primate's social group, it is assumed that primates possess neural systems to categorize social information in the brain. Two of several candidates for those systems are located in the amygdala and ventrolateral prefrontal cortex (vlPFC). The primary function of the primate amygdala is emotion processing (LeDoux, 2000; Phelps and LeDoux, 2005), and the amygdala activity is linked with autonomic physiological reactions (Laine et al., 2009). The human amygdala is specifically activated when the subjects see fearful facial expressions (Morris et al., 1996) in addition to body movements of others expressing emotion (Hadjikhani and de Gelder, 2003). Moreover, several researches reported neurons that show different responses to different facial expressions or different directions of gaze of others in the monkey amygdala (Nakamura et al., 1992; Kuraoka and Nakamura, 2006, 2007; Gothard et al., 2007; Hoffman et al., 2007; Tazumi et al., 2010). On the other hand, neurons in the monkey vlPFC have been reported to respond to faces and vocalizations (Ó Scalaidhe et al., 1997; Sugihara et al., 2006; Tsao et al., 2008; Romanski and Diehl, 2011). There are also neurons that show responses to social behaviors of others in the monkey vlPFC (Tsunada and Sawaguchi, 2012).

The interaction between the amygdala and the vlPFC has recently received attention in relation to emotion regulation (Townsend and Altshuler, 2012). Hariri et al. (2000) reported an increase in regional cerebral blood flow in the right vlPFC during a face cognition task, and a decrease in regional cerebral blood flow in the left and right amygdala. These data imply that the vlPFC regulates emotional responses generated by the amygdala in face perception, through conscious evaluation and appraisal (Hariri et al., 2003).

The primate amygdala and vlPFC are closely related with each other as described above. Then, what are the functional differences in categorizing social information between the amygdala and vlPFC? One candidate for the differences is time of processing. The amygdala has been known to process emotion roughly (Vuilleumier et al., 2003) but rapidly (Balderston et al., 2014). In contrast, neurons in the primate vlPFC have been reported to be involved in complex cognitive functions such as memory (Goldman-Rakic, 1995), behavioral planning (Tanji and Hoshi, 2008) and decision-making (Sakagami and Pan, 2007) that require a little time to be accomplished. Thus, we hypothesized that the role of the amygdala is larger than that of the vlPFC at an early stage of

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Abbreviations: PSTH, peristimulus time histogram; SD, standard deviation; vlPFC, ventrolateral prefrontal cortex.

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the processing of social information, whereas the role of the vlPFC becomes larger at a late stage.

In the present study, we directly compared neuronal activity between the amygdala and vlPFC of *Macaca mulatta* during the presentation of face stimuli under the same experimental conditions to elucidate the role of neurons in these two brain regions in face processing. We found rapid phasic peak of information processing about the type of emotion in the amygdala: the information reached a peak of 260 ms after stimulus onset, and maintained more than half of the peak for 170 ms. We also found long-lasting information processing in the vlPFC: the information reached a peak of 630 ms after stimulus onset, and maintained more than half of the peak for 720 ms.

EXPERIMENTAL PROCEDURES

Subjects

We used three rhesus monkeys (*M. mulatta*, 5–7 kg) for neuron recordings in the amygdala and two rhesus monkeys (5–7 kg) for neuron recordings in the vlPFC. Water was withheld before each daily session and juice was given as a reward in the experimental room. Supplemental water and vegetables were given after the session when needed, and monkey chow was available *ad libitum*. All experiments were carried out in accordance with the 'Guide for the Care and Use of Laboratory Animals' of the National Institutes of Health (1996), the 'Guide for Care and Use of Laboratory Primates' published by the Primate Research Institute, Kyoto University (2002, 2010). The research was conducted under experimental license No. 2010-012 approved and issued by Kyoto University, and the 'Guide for Care and Use of Laboratory Primates' published by the National Institute of Neuroscience, National Center of Neurology and Psychiatry (2005) under experimental license No. 002; approved and issued by the NCNP. The research adhered to the legal requirements of Japan.

Behavioral tasks and stimuli

All experiments were performed in a dark, soundproof room where a monkey sat in a primate chair and faced a 21-inch multiscan monitor (GDM-F520; SONY, Tokyo, Japan, or FlexScan T961; EIZO NANANO, Ishikawa, Japan) placed 30–40 cm from its eyes. When the monkey pressed a lever, a yellow fixation spot appeared at the center of the monitor. After keeping the lever pressed and fixating on the spot for 1000 ms, a test stimulus was presented for 1000 ms behind the fixation spot; thereafter, the yellow fixation spot was replaced with a red spot after 300–1500 ms. If the monkey released the lever within 800 ms of spot replacement, it was rewarded. Eye position was continuously monitored using a charge-coupled device camera system. If the monkey's gaze deviated more than 1.5° from the fixation spot or if it released the lever during a trial, the trial was terminated without providing any reward. The test stimuli were 13 full color video clips (approximate size was 20×15 in degree of visual angle), each lasting 1000 ms, presented on a gray background. All stimuli were from monkey, human, or artifact categories, with nine monkey species-specific facial expressions, two human faces, and two artifacts. The monkey face stimuli consisted of three types of emotion recorded from three model monkeys, who were unfamiliar to the subject monkeys. The three types of facial expressions were aggressive threats, screams, and coos. An *aggressive threat* is often expressed by a dominant individual demonstrating an inclination to attack. A *scream* is often expressed by a subordinate who is attacked or threatened by a dominant individual. A *coo* has multiple meanings, and it is often expressed in response to food or separation from the mother or social group (Hinde and Rowell, 1962; Van Hooff, 1962). The type of video clips was not associated with reward. We separately presented the visual elements and auditory elements of the video clips. However, we only analyzed the data for the visual elements because few neurons recorded from the vlPFC responded to the auditory elements.

Recording procedure

The action potentials of single neurons were recorded extracellularly from the amygdala in four hemispheres of three monkeys and the vlPFC in three hemispheres of two monkeys using a polyurethane-coated tungsten microelectrode (1.5–3.0 MΩ, 0.3 mm in diameter). The tungsten microelectrode was inserted through a guide tube (1.1 mm in diameter) that was fixed to a grid into the brain without distortion. A stainless steel guide tube was inserted through the dura to a depth of ~5 mm above the amygdala or to just below the dura over the vlPFC, as estimated from magnetic resonance images taken in advance of the placement. The electrode was advanced using a hydraulic Microdrive (Narishige, Tokyo, Japan) while neuronal activity was monitored. The action potentials were discriminated and converted into pulses using a window discriminator (Model DIS-1; BAK Electronics, Germantown, MD, USA) or a multi-spike detector (Alpha Omega Engineering, Nazareth, Israel). The timing of action potentials and task events was stored on a personal computer with a time resolution of 0.5 ms in four monkeys or 1.0 ms in one monkey. When the activity of a single neuron was isolated, a recording session was started. We presented the visual stimuli pseudo-randomly until each had appeared 10 times. We tested all stimuli 10 times during a recording session even if a single neuron did not appear to show responses to any stimuli. After the test, we advanced the electrode further until the activity of the next single neuron was isolated.

Data analysis

The stored data were processed off-line using custom-made MATLAB programs and the statistical analyses were conducted using IBM SPSS Statistics software. A neuron was regarded as responsive to the stimulus if the number of spikes during a 1000-ms period, from 100