

NEURAL CORRELATES TO SEEN GAZE-DIRECTION AND HEAD ORIENTATION IN THE MACAQUE MONKEY AMYGDALA

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Abstract—Human neuropsychological studies suggest that the amygdala is implicated in social cognition, in which cognition of seen gaze-direction, especially the direct gaze, is essential, and that the perception of gaze direction is modulated by the head orientation of the facial stimuli. However, neural correlates to these issues remain unknown. In the present study, neuronal activity was recorded from the macaque monkey amygdala during performance of a sequential delayed non-matching-to-sample task based on gaze direction. The facial stimuli consisted of two head orientations (frontal; straight to the monkey, profile; 30 degrees rightwards from the front) with different gaze directions (directed toward and averted to the left or right of the monkey). Of the 1091 neurons recorded, 61 responded to more than one facial stimulus. Of these face-responsive neurons, 44 displayed responses selective to the facial stimuli (face neurons). Most amygdalar face neurons discriminated both gaze direction and head orientation, and exhibited a significant interaction between the two types about information. Furthermore, factor analysis on the response magnitudes of the face neurons to the facial stimuli revealed that two factors derived from these facial stimuli were correlated with two head orientations. The overall responses of the face neurons to direct gazes in the profile and frontal faces were significantly larger than that to averted gazes. The results suggest that information of both gaze and head direction is integrated in the amygdala, and that the amygdala is implicated in detection of direct gaze. © 2010 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: amygdala, social cognition, face neurons, gaze direction, head orientation, monkey.

In primates, the gaze direction of other individuals is an important communicative signal in social interaction (Argyle and Cook, 1976; Emery, 2000). This signal can be used to infer the mental state, intention, and attentional direction of other individuals (Baron-Cohen, 1995; Emery, 2000; Hori et al., 2005). Psychological and psychiatric studies have reported that people with autism display def-

icits in cognition of gaze direction (Pelphrey et al., 2005), and inappropriate behaviors in social interaction (Attwood et al., 1988; Kobayashi and Murata, 1998). In neuroanatomical studies, autistic people were also found to display anatomical abnormalities in the amygdala (Bauman and Kemper, 1988; Abell et al., 1999; Schumann and Amaral, 2006). These findings suggest that the amygdala plays an important role in the cognition of gaze direction in social interaction.

Consistent with this suggestion, functional imaging studies have indicated an increase of regional cerebral blood flow in the human amygdala during presentation of animation, in which the gaze of a stimulus model is directed toward the subject (Kawashima et al., 1999), facial photo of fear expression with gaze directed to the subject (Adams et al., 2003), and during a task in which the subjects were required to infer mental states from photographs of the eye region (Baron-Cohen et al., 1999). Human neuropsychological studies reported that patient D.R. with bilateral amygdalar ablation showed profound impairment in discriminating between direct and averted gazes (Young et al., 1995), and that patient S.M. with bilateral amygdalar lesions displayed deficits in directing her gaze (i.e., attention) to the eye region of the facial photos (Adolphs et al., 2005). These results suggest that the amygdala is critical in processing gaze directions, which are important information for social cognition (Allison et al., 2000).

However, neurophysiological evidence relating the primate amygdala to cognition of gaze direction is lacking, although behavioral studies have also reported that monkeys could follow the seen gaze-direction and head orientation of other individuals including humans (see a review by Emery, 2000). Brothers and Ring (1993) found two amygdala neurons that were responsive when the gaze of a conspecific monkey was directed at the subject, but not when the monkey averted its gaze away from the subject. Since the responses of these neurons were not tested further with other control stimuli, it remains unclear whether the monkey amygdala can code the gaze direction of other individuals. The first aim of the present study was to investigate neurophysiologically the role of the primate amygdala in cognition of gaze direction, especially the direct gaze.

Second, previous psychological studies have reported that perception of gaze direction was significantly modulated by head orientation (Hietanen, 1999; Langton, 2000; Langton et al., 2004), even though subjects were not required to discriminate head orientations. This suggests that both kinds of information interact in some areas of the brain. Consistently, imaging studies have reported that the

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Abbreviations: ABI, basolateral nucleus of the amygdala; ABm, basomedial nucleus of the amygdala; AL, lateral nucleus of the amygdala; ANOVA, analysis of variance; AP, anterior posterior; CM, corticomedial group of the amygdala; CRT, cathode ray tube; G-DNMS, delayed non-matching-to-sample task that requires discrimination of gaze direction; STS, superior temporal sulcus.

activity of face-related brain regions is modulated by both gaze direction and head orientation (George et al., 2001; Pageler et al., 2003; Garrett et al., 2004). The second aim of the present study was to examine whether gaze direction-related responses in the amygdala were modulated by head direction although the monkeys were not required to discriminate head orientations. To address these two issues we recorded and analyzed the neural activity of the monkey amygdala during discrimination of gaze direction.

EXPERIMENTAL PROCEDURES

Animals and behavioral-task apparatus

Two adult monkeys (*Macaca fuscata*), weighing 5.8–8.0 kg, were used. Each monkey was individually housed with food available *ad libitum*. The monkeys were deprived of water in their cages and obtained juice as reward during training and recording sessions. Supplemental water and vegetables were given after each day's session. To check the monkey's health, his weight was routinely monitored. The monkeys were treated in strict compliance with the policies of the National Institutes of Health on the Care of Humans and Laboratory Animals, and the Guidelines for the Care and Use of Laboratory Animals at the University of Toyama.

The monkey sat in a monkey chair 30 cm away from the center of a 19-inch computer display for behavioral tasks during the training and recording sessions in a shielded room. The cathode ray tube (CRT) monitor was set so that its center was on the same horizontal plane as the monkey's eyes. The monkey chair was equipped with a responding button, which was positioned so that the monkey could easily manipulate it. An infrared charge-coupled device (CCD) camera for eye-movement monitoring was firmly attached to the chair by a steel rod. During both training and recording sessions, the monkey's eye position was monitored with 33-ms time resolution by an eye-monitor system (Matsuda, 1996). Juice reward was accessible to the monkey through a small spout controlled by an electromagnetic valve. A Psyscope system (Carnegie Mellon University, Pittsburgh, PA, USA) controlled the timing for outputs to the CRT monitor, the electromagnetic valve and sound signal.

Facial stimuli

Fig. 1A, B show the stimulus set used in the present study. Facial stimuli of two persons including one of the experimenters consisted of two head orientations, straight ahead (frontal face) and 30 degrees to the right (profile face). The frontal faces consisted of three gaze directions, directed toward, and averted to the left or right of the monkey; and profile faces had two gaze directions, directed toward and averted to the left of the monkey.

The facial stimuli were 256 digitized color-scale images. The faces with averted gaze directions were artificially created from the faces with directed gaze by replacing direct gazes in the eye region with the averted gazes, so that only difference was a change in gaze direction. In addition, as control stimuli, 256 digitized gray-scale images of two geometric patterns were used. The visual stimuli were displayed on a CRT monitor with a resolution of 640×480 pixels and the size of the stimulus area was 15–20×15–20°.

It is noted that we did not use the facial stimuli with combination of the profiles rotated by 30 degrees to the right and the gaze direction averted to the left. In these facial stimuli, it is hard to recognize the dark iris; only the white sclera could be seen. In monkey faces, the iris can be always recognized since it occupies the major part of the visible eye. Therefore, this kind of the human facial stimuli seems to be unusual to monkeys. Second, the iris can be recognized in all of the frontal faces regardless of gaze

direction. Furthermore, we chose not to include those profiles in which the iris could not be recognized. The lack of the iris induces a qualitative difference among the facial stimuli. According to these two reasons, we avoided those profiles without the iris.

Behavioral paradigms

The monkeys were trained to perform a sequential delayed non-matching-to-sample task that requires discrimination of gaze direction (G-DNMS) (Fig. 1C). The task was initiated by a buzzer tone. Then, a fixation cross appeared on the display for 2 s, followed by a sample stimulus for 2 s (sample phase). The control phase was defined as the period for 1 s before the sample phase. When facial photos were used as sample stimuli, gaze directions of the stimuli were either directed to or averted from the monkey. Then, after an interval of 2.0 s, the same stimulus appeared again for 500 ms from one to four times (comparison phase). The number of the comparison phase was selected randomly from trial to trial. Finally, a new stimulus with different gaze direction was presented (target phase). When the target appeared, the monkey was required to press a button within 2 s to acquire a juice reward (0.2 ml). When the monkey failed to respond correctly during the target phase, or press the button before the target phase, the trials were aborted and a buzzer tone was presented. Inter-trial intervals (ITI) were 15–25 s.

In the G-DNMS, the monkey compared a pair of the two stimuli in each trial (i.e., sample and target stimuli). Stimulus pairs consisted of the same category of the stimuli; only pairs of the facial stimuli and those of the geometric patterns were used, and pairs of the facial stimuli and geometric patterns were not used. In the facial pairs, the averted gazes were always paired with the directed gazes; stimulus pairs of gazes averted to the left and the right were not used. Furthermore, in the target phase of the facial trials, the same facial stimuli as those in the comparison phase except gaze direction were presented (i.e., same model and same head orientation) so that the monkeys were required to detect a difference in gaze direction (directed vs. averted gazes). Thus, a total of 14 stimulus pairs (the control stimuli, two pairs; each model, four pairs in the frontal faces and two pairs in the profile faces) were used. These procedures facilitated monkeys' learning that a shift of gaze direction was an important clue to solve the task.

Training and surgery

The monkey was trained with the G-DNMS task for 3 h/day, 5 days/week. The monkey required about 11 months of training to reach a 97% correct-response rate. After completion of this training period, a head-restraining device (a U-shaped plate made of epoxy resin) was attached to the skull under aseptic conditions and sodium pentobarbital anesthesia (35 mg/kg i.m., see Nishijo et al., 1988a,b). The plate was anchored with dental acrylic to titanium bolts inserted in keyhole slots in the skull. During the surgery, heart and respiratory functions and rectal temperature were monitored on a polygraph system (Nihon Kohden, Tokyo, Japan). The rectal temperature was controlled at 37±0.5 °C by a blanket heater. Antibiotics were administered topically and systemically for 1 week to protect against infection. Two weeks after surgery, the monkey was retrained. The performance criterion was again attained within 10 days. All experimental protocols were approved by the Animal Care and Use Committee of University of Toyama. Every effort was made to minimize the number of animals used and their suffering.

Stereotaxic localization of the amygdala for recording and histology

Before recording from the amygdala in each hemisphere, a marker consisting of a tungsten wire (diam., 500 μm) was in-

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