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NEURONS RESPONSIVE TO FACE-VIEW IN THE PRIMATE VENTROLATERAL PREFRONTAL CORTEX

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Abstract—Studies have indicated that temporal and prefrontal brain regions process face and vocal information. Face-selective and vocalization-responsive neurons have been demonstrated in the ventrolateral prefrontal cortex (VLPFC) and some prefrontal cells preferentially respond to combinations of face and corresponding vocalizations. These studies suggest VLPFC in nonhuman primates may play a role in communication that is similar to the role of inferior frontal regions in human language processing. If VLPFC is involved in communication, information about a speaker's face including identity, face-view, gaze, and emotional expression might be encoded by prefrontal neurons. In the following study, we examined the effect of face-view in ventrolateral prefrontal neurons by testing cells with auditory, visual, and a set of human and monkey faces rotated through 0°, 30°, 60°, 90°, and −30°. Prefrontal neurons responded selectively to either the identity of the face presented (human or monkey) or to the specific view of the face/head, or to both identity and face-view. Neurons which were affected by the identity of the face most often showed an increase in firing in the second part of the stimulus period. Neurons that were selective for face-view typically preferred forward face-view stimuli (0° and 30° rotation). The neurons which were selective for forward face-view were also auditory responsive compared to other neurons which responded to other views or were unselective which were not auditory responsive. Our analysis showed that the human forward face (0°) was decoded better and also contained the most information relative to other face-views. Our findings confirm a role for VLPFC in the processing and integration of face and vocalization information and add to the growing body of evidence that the primate ventrolateral prefrontal cortex plays a prominent role in social communication and is an important model in understanding the cellular mechanisms of communication. © 2011 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: prefrontal cortex, gaze, face cells, vocalizations, multisensory integration, communication.

In social interactions, information from the face is of essential importance. Facial expression and identity are critical pieces of information that guide our communication exchanges. Within a face, the eyes and mouth receive the most attention when we view faces (Haith et al., 1977; Klin et al., 2002; Vinette et al., 2004). This bias toward examining the eyes and mouth is also present in nonhuman primates when looking at pictures or videos of conspecifics (Wilson and Goldman-Rakic, 1994; Nahm et al., 1997; Ghazanfar et al., 2006; Gothard et al., 2009). Of all of the interesting and informative features of a face, it is the eyes and mouth that will provide clues to the emotional state of the viewed person or conspecific and the angle of gaze which will direct our attention within the environment. In nonhuman primates the angle of gaze can indicate submission or dominance in social rank, an important facet of social interactions, and direct gaze is considered a threat in certain social contexts. In contrast, most of our human vocal exchanges are given with direct gaze when we speak to one another, and avoiding direct gaze is informative as well. Thus, areas of the brain involved in communication and language may receive information about the gaze or view of the person with which we are communicating.

The neural circuitry involved in the processing of facial information includes cortical areas within the parietal, temporal, and frontal lobes. In the human brain perception of faces consistently activates an area in the lateral fusiform gyrus known as the fusiform face area (FFA), (Kanwisher et al., 1997). Facial expression, identity, and gaze-direction have been shown to activate specific brain regions within the temporal lobe. Facial expression and gaze direction have been preferentially linked with the superior temporal sulcus (STS) and the amygdala, while the processing of features which occurs during identity processing has been more strongly linked with the inferotemporal cortex and fusiform gyrus (Haxby et al., 2002; Engell and Haxby, 2007; Breiter et al., 1996; Morris et al., 1996; Kawashima et al., 1999). Studies in the nonhuman primate have also revealed selective face-processing areas of the temporal lobe (Tsao et al., 2003, 2006), and single unit responses to faces have been recorded in a variety of brain regions. Work by Perrett and colleagues (1985) have shown that different views of the head and eyes activate different populations of neurons within the STS. Facial expression and identity have been shown to activate neurons in the inferotemporal cortex, the superior temporal sulcus, and in the amygdala (Hasselmo et al., 1989; Young and Yamane, 1992; Eifuku et al., 2004; Kuraoka and Nakamura, 2007; Freiwald and Tsao, 2010), sometimes within the same cells (Gothard et al., 2007) while other studies have shown that amygdala neurons are sensitive to direct gaze (Hoffman et al., 2007).

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Abbreviations: SI, selectivity index; STS, superior temporal sulcus; VLPFC, ventrolateral prefrontal cortex.

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The face processing network, however, extends beyond the temporal lobe and includes areas within the frontal lobe. Several studies have demonstrated activation of human orbitofrontal or prefrontal cortex in the processing of facial expression or gaze-direction (Dolan et al., 1996; Kesler-West et al., 2001; Vuilleumier et al., 2001; Nomura et al., 2004; Ishai et al., 2004, 2005; Sergerie et al., 2005; Engell and Haxby, 2007; LoPresti et al., 2008). Orbital and ventral prefrontal cortex have been shown to be activated during tasks of facial memory (Dolan et al., 1996) or perception of emotional faces (Kesler-West et al., 2001; Iidaka et al., 2001; Ishai et al., 2005; Pourtois et al., 2006). Importantly, face cells, similar to those in the temporal lobe that are selectively responsive to pictures of faces, have been recorded in the nonhuman primate ventrolateral prefrontal cortex (VLPFC) (O'Scalaidhe et al., 1997, 1999) and orbitofrontal cortex (Thorpe et al., 1983; Rolls, 1996). The single unit studies have recently been confirmed with fMRI where activation of VLPFC and orbitofrontal cortex by faces was shown in macaque monkeys (Tsao et al., 2008). Finally, single cells in VLPFC have been found to respond to both vocalizations and the corresponding facial gesture (Sugihara et al., 2006). Thus, VLPFC is a part of the face processing network, although its precise role remains uncertain.

In the present study, we asked whether prefrontal neurons would be differentially responsive to different views of rotated faces. Since previous studies have shown that some VLPFC neurons respond to both faces and vocalizations, we predicted that neurons might also respond differentially to face stimuli that vary in face-view/head orientation, where face features vary in their visibility. Moreover, we hypothesized that VLPFC neurons which are responsive to auditory stimuli including vocalizations (Romanski et al., 2005) are likely to be involved in communication and therefore may be responsive to forward face stimuli since this face-view is most commonly utilized during communication. Our results support our hypothesis and indicate that VLPFC neurons respond to face-view. Neurons that were selective for a particular face-view were most often responsive to forward face-view/head orientations, and all of these neurons were responsive to complex auditory stimuli.

EXPERIMENTAL PROCEDURES

Surgery and electrophysiological recording

We recorded auditory and visual responsive cells in the prefrontal cortex of three naïve rhesus monkeys (*Macaca mulatta*) that had not yet been tested with combined face and vocalization stimuli. All methods were in accordance with NIH Guidelines for the Care and Use of Laboratory Animals, and the Yale Animal Care and Use Committee Guidelines or the University of Rochester committee on Animal Care and Use. The recording methods have been previously described (Romanski et al., 2005; Sugihara et al., 2006) and are briefly described here. A stainless steel recording cylinder was chronically implanted overlying the inferior convexity of the prefrontal cortex including areas 12 and 45 as defined anatomically (Preuss and Goldman-Rakic, 1991) and physiologically (O'Scalaidhe and Goldman-Rakic, 1993). Animals were trained in a fixation task for juice reward. Each trial consisted of a 500 ms prestimulus fixation period, a 1000 ms stimulus (auditory or visual) period, and a 500 ms poststimulus period. Animals initiated the trial by fixating the central fixation point. A juice reward was delivered at the termination of the poststimulus fixation period and the fixation requirement was released. There was a 2–3 s inter-trial interval. Breaking fixation at any time during the trial caused the trial to abort, and the data for that trial was discounted. Stimuli were presented in blocks of 10 and randomly presented eight to 12 times resulting in 80–120 total trials per stimulus set. The timing of the behavioral contingencies, presentation of all stimuli, delivery of reward, and monitoring of eye position were controlled by a PC system running CORTEX (NIH derived software, Bethesda, MD, USA) or other custom software.

Stimuli and presentation

Because of the heterogeneity of ventral prefrontal cortex neurons, which include auditory, visual, somatosensory, saccade, and reach neurons, our standard testing procedure involved the presentation of auditory and visual stimuli that covered a wide range of potential visual and auditory features in order to find responsive cells. In this study, we did not test overall auditory or visual selectivity, except within the face-view stimulus list. The auditory stimuli which were presented were used to determine general auditory responsivity but not selectivity and so were drawn from a large library of sounds used previously (Romanski and Goldman-Rakic, 2002). The vocalizations, which were unfamiliar to the recorded subjects, included exemplars from a larger colony housed separately from the recorded subjects and included coos, screams, grunts, pant threats, chirps, and barks which are common macaque vocalizations. In addition we used exemplars from a library of macaque vocalizations provided by Marc Hauser in his recordings on the island of Cayo Santiago, which we have used previously in our recordings (Romanski et al., 2005). The nonvocalization auditory stimuli included FM sweeps, noise bursts, clicks, environmental sounds, tones, and chords. Auditory stimuli were presented in 10-item lists ($n=12$ lists). One stimulus was presented per trial. Each 10-item-list contained two monkey vocalizations, two human vocalizations, two band passed noise stimuli, two FM sweeps, and two environmental sounds (door slamming, keys jangling, car honking, whistle, etc). Because of the heterogeneity in our auditory lists, we were not able to test categorical responses to auditory stimuli. This would require a much larger list with more exemplars per category, which has been performed in other studies (Romanski et al., 2005).

Auditory stimuli were presented via a PC connected to a Yamaha MSP5 monitor speaker (Buena Park, CA, USA; overall frequency response 50 Hz–40 kHz) located just below the video monitor and placed 30 inches directly in front of the monkey. The auditory stimuli varied from 65 to 75 dB SPL measured at the level of the monkey's ear with a B & K sound level meter (Naerum, Denmark).

Visual stimuli were also presented in 10-item lists. There were $n=40$ lists which each contained —one to three monkey faces, one to three human faces, two familiar objects, two clipart objects, one solid color square, and one pattern or fractal square. Visual stimuli were presented on a computer monitor (30 inches in front of the monkey) so that they spanned ~7 degrees. These studies were performed on a CRT monitor with a refresh rate of 72 Hz. Neurons which demonstrated a response to any of the auditory or visual stimuli from the presented list or showed any task related activity were tested further with additional stimulus lists including the face-view/head rotation list shown in Fig. 1. The human face in this list is taken from the Tarrlab Object Data Bank (Brown University, Providence, RI, USA). The monkey face is a digitized photo of an unfamiliar 4-year-old male rhesus monkey. The frames for each face-view/head orientation were separate digital pictures taken when the monkey looked to a cued location as the picture was taken.