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Neuronal Correlates of Face Identification in the Monkey Anterior Temporal Cortical Areas

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Eifuku, Satoshi, Wania C. De Souza, Ryoi Tamura, Hisao Nishijo, and Taketoshi Ono. Neuronal correlates of face identification in the monkey anterior temporal cortical areas. *J Neurophysiol* 91: 358–371, 2004; 10.1152/jn.00198.2003. To investigate the neuronal basis underlying face identification, the activity of face neurons in the anterior superior temporal sulcus (STS) and the anterior inferior temporal gyrus (ITG) of macaque monkeys was analyzed during their performance of a face-identification task. The *face space* was composed by the activities of face neurons during the face-identification task, based on a multidimensional scaling (MDS) method; the *face space* composed by the anterior STS neurons represented facial views, whereas that composed by the anterior ITG neurons represented facial identity. The temporal correlation between the behavioral reaction time of the animal and the latency of face-related neuronal responses was also analyzed. The response latency of some of the face neurons in the anterior ITG exhibited a significant correlation with the behavioral reaction time, whereas this correlation was not significant in the anterior STS. The correlation of the latency of face-related neuronal responses in the anterior ITG with the behavioral reaction time was not found to be attributed to the correlation between the response latency and the magnitude of the neuronal responses. The present results suggest that the anterior ITG is closely related to judgments of facial identity, and that the anterior STS is closely related to analyses of incoming perceptual information; face identification in monkeys might involve interactions between the two areas.

INTRODUCTION

The identification of faces is a distinctive cognitive ability of primates and it plays an important role in social communication (Bruce 1988; Bruce and Young 1998). Face neurons that respond selectively to the sight of faces were first identified in a region of the anterior temporal cortex in monkeys in the 1980s (Bruce et al. 1981; Perrett et al. 1982); such neurons have subsequently been identified in various areas of the monkey brain (Desimone et al. 1984; Harries and Perrett 1992; Hasselmo et al. 1989; Nakamura et al. 1992; Perrett et al. 1985; Scalaidhe et al. 1997; Yamane et al. 1988). In these previous studies, neuronal activity in response to faces was recorded in anesthetized immobilized monkeys or in alert monkeys that performed passive viewing or face-discrimination tasks. Some studies reported the existence of face neurons that might encode facial identity (Hasselmo et al. 1989; Sugase et al. 1999). However, it remains unclear how face neurons are related to the process of face identification; to determine this relationship in an animal model, we would need to have the animals perform face-identification tasks.

Functional imaging (Halgren et al. 1999; Haxby et al. 1999; Hoffman and Haxby 2000; Ishai et al. 1999; Kanwisher et al. 1997) and evoked potential studies (Allison et al. 1999; McCarthy et al. 1997, 1999; Puce et al. 1999) of human brains revealed that multiple regions were involved in face perception. It has been suggested that the core system for face perception in humans includes the inferior occipital gyrus, the lateral fusiform gyrus, and the anterior superior temporal sulcus (STS). The functional heterogeneity of these 3 regions has been indicated by activation findings that differed during different cognitive tasks (Haxby et al. 2000; Hoffman and Haxby 2000). It appears that the lateral fusiform gyrus plays an important role in the recognition of facial identity (George et al. 1999; Sergent et al. 1992), whereas the anterior STS plays important roles in the perception of emotions reflected in the face and in the direction of the gaze (Puce et al. 1998). The inferior occipital gyrus is the main input to both the lateral fusiform gyrus and the anterior STS. It has been debated whether the lateral fusiform gyrus in humans is the functional homolog of the anterior inferior temporal gyrus (ITG) in monkeys, and likewise, it also remains unclear whether the anterior STS in humans is the functional homolog of the anterior STS in monkeys; nonetheless, it is generally agreed that 2 distinct face-perception systems exist in both species. To investigate the neuronal basis underlying face perception, it is necessary to obtain single neuronal recordings from behaving monkeys during the performance of cognitive tasks.

Thus in the present report, to investigate the neuronal basis underlying face identification, we show the behavioral correlates of face-related neurons in the anterior STS and in the anterior ITG of monkeys during the performance of a task that requires the identification of familiar individuals by viewing their faces. Based on the activity of all of the samples of face-related neurons that we recorded during each monkey's performance of this face-identification task, we were able to identify *face spaces* for 2 areas, the anterior STS and the anterior ITG, using a multidimensional scaling (MDS) method. In addition, the temporal correlation between the latency of face-related neuronal responses and the behavioral reaction time required for judgment was analyzed in the 2 areas.

Some of the results of the present study were reported previously in abstract form (Eifuku et al. 1999, 2000).

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METHODS

Subjects

Two adult monkeys (*Macaca fuscata,* female, body weight 5.2–8.5 kg) were used in these experiments. All experimental protocols were approved by the Animal Care and Use Committee of Toyama Medical and Pharmaceutical University; the protocols also conformed to the National Institutes of Health guidelines for the humane care and use of laboratory animals.

Behavioral task

The monkeys were trained to perform a version of the sequential delayed matching-to-sample task, which requires the identification of familiar individuals by face (*I-DMS* task: Fig. 1*A*). In the *I-DMS* task, a sample (480 ms) stimulus was presented after fixation, and then test (match or nonmatch 480 ms) stimuli were presented after a period of interstimulus delay (992 ms). During the *I-DMS* task, the eye position was monitored using a scleral search coil (Judge et al. 1980). The size of the eye control window was ±2.0°. The visual stimuli used in this study were 256 digitized gray-scale images of the faces of people familiar to each monkey; these people were members of the laboratory involved in the daily care of the subjects. The visual stimuli were displayed on a CRT monitor placed 57 cm from the eye while the monkey fixated; the visual stimuli were generated on-line and displayed using a Pentium II–based computer and a Texan graphics (TIGA) card with a resolution of 640 × 480 pixels. The stimulus set consisted of 28 faces (7 facial views × 4 facial identities; see Fig. 1*B*). All visual stimuli were presented within the receptive field (RF) center of each recorded neuron that was mapped in advance of the experiment (see *Recording*): stimuli were usually centered on the fixation point and the size of the stimulus area was 10–15 × 10–15°. Among all the stimuli, luminances of the brightest white and the darkest black (background) were 32.8 and 0.9 cd/m^2, respectively. Although we did not strictly control luminance, the 28 facial stimuli were not associated with differences in the behavioral performance of the individual

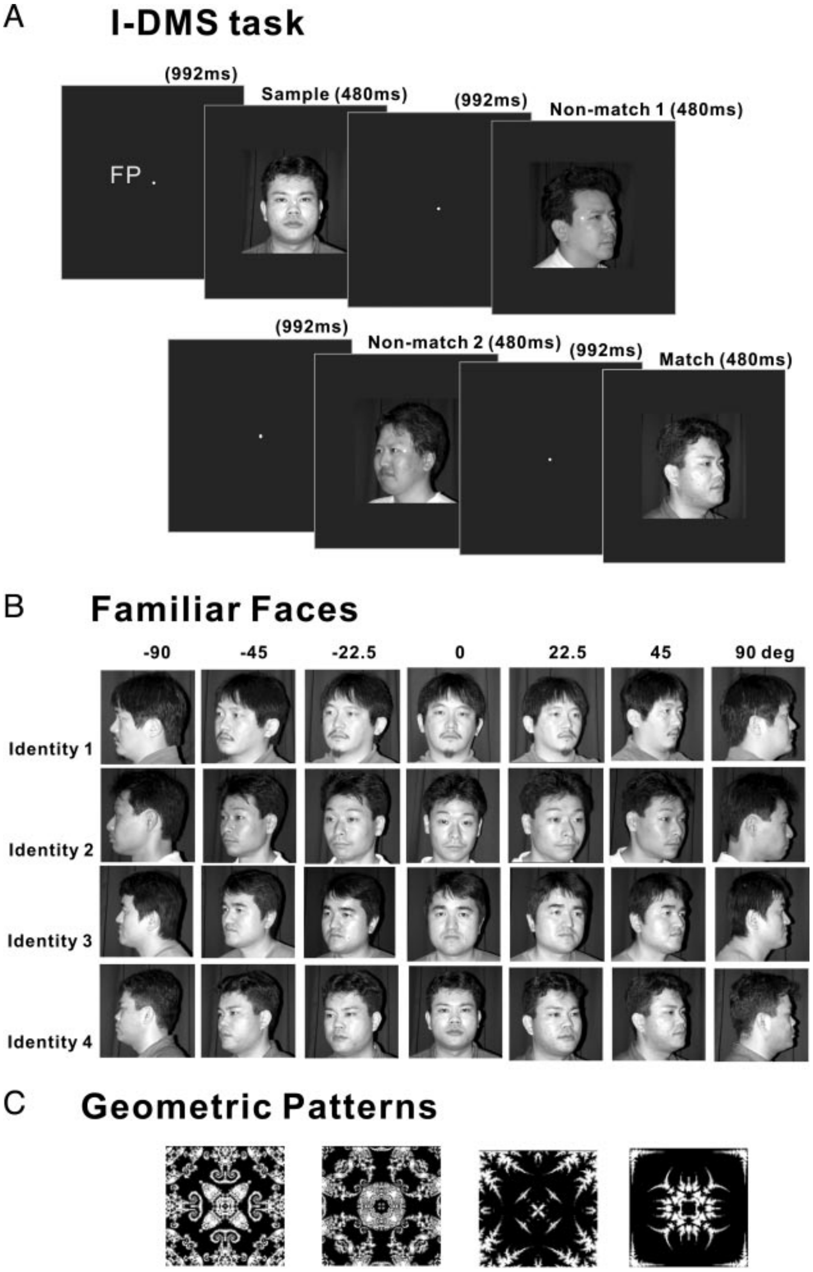

FIG. 1. *A*: delayed matching-to-sample task based on identification (*I-DMS*) task, which was a version of the sequential delayed matching-to-sample task; a sample (480 ms) was presented after each monkey fixated a fixation point (*FP*, 0.2° diameter) that appeared at the center of the display. Then, test (match or nonmatch 480 ms) stimuli were presented after an interstimulus delay (992 ms). Intervening (nonmatch) stimuli were presented 0 to 3 times until a match finally appeared. Sample faces were always in the frontal view (0°), whereas a test face was one of 7 faces viewed from one of 7 different angles (from the *left to right* profile: −90, −45, −22.5, 0, +22.5, +45, and +90°; see also *B*). Both animals were required to identify the same person given in the sample; and if the test stimulus was a match, the monkey was trained to push a lever to obtain juice. Eye position was monitored using a scleral search coil during the *I-DMS* task, and the size of the eye control window was ±2.0°. *B*: facial stimuli. Stimulus set consisted of 28 faces (7 facial views × 4 facial identities). The facial images represented people familiar to each monkey who were members of the laboratory involved in the daily care of the subjects. Visual stimuli were in 256 gray scale, 10–15 × 10–15° in size, and were presented at the center of the display with FP; thus all of the stimuli were within the receptive fields that were mapped before the experiments. *C*: geometric patterns. Neutral geometric patterns were used as control stimuli. Visual stimuli were also in 256 gray scale, 10–15 × 10–15° in size, and were presented at the center of the display with FP.

monkeys. The computer generating the visual stimuli was controlled by the standard laboratory real-time experimental system REX (Hays et al. 1982) running on a dedicated Pentium II–based computer.

In the *I-DMS* task, images of the sample faces were always in the frontal view (0°), whereas the test stimuli were one of 7 images of faces viewed from one of 7 different angles (profiles from *left to right*: −90, −45, −22.5, 0, +22.5, +45, and +90°). Each monkey was required to identify the same person who had been shown in the sample; if the test stimulus was a match, the monkey was trained to push a lever within 800 ms after the onset of a match. Some intervening (nonmatch) stimuli were presented until a match finally appeared (range: 0 to 3 intervening stimuli). All correct trials were rewarded; if the monkey responded correctly, a reward of about 0.2 ml of orange juice was presented for 2.0 s after another 1.0-s delay. If the monkey failed to respond correctly, a 620-Hz buzzer tone was presented and the reward was withheld. A 2.0- to 4.0-s intertrial interval was imposed before the next trial started. Some unfamiliar faces and neutral geometric patterns (Fig. 1*C*) were also used as the control stimuli. The behavioral reaction time was defined as the time lapsed after the onset of the match stimuli until the monkey pushed the response lever, and the reaction on the lever pushing was sampled at 1 kHz for every correct trial.

Preparation

The monkeys were first trained to perform the behavioral task without the use of head fixation or eye position measurement. After the monkeys learned the *I-DMS* task, they were prepared for the cell recordings. Before surgery, the monkeys underwent magnetic resonance imaging (MRI). Appropriate stereotaxic coordinates for the recording chamber were calculated from the MRI scans. Under general anesthesia with sodium pentobarbital [35 mg/kg, intramuscularly (im)], a recording chamber was implanted on the surface of the skull over the anterior STS and the anterior ITG, and a head holder was embedded in a dental acrylic cap that covered the top of the skull and that was compatible with the MRI scans. The cylinders and head holders were plastic and the screws in the skull were made of titanium. In addition, scleral search coils were implanted into the eyes to record the eye movements. During surgery, heart and respiratory function and rectal temperature were monitored on a polygraph (Nihon Kohden, Tokyo, Japan). The rectal temperature was controlled at 37 ± 0.5°C by a blanket heater. Antibiotics were administrated topically and systemically during the recovery period to protect the animals against infection.

Recording

After the monkeys recovered from surgery, we retrained them to perform the *I-DMS* task with head fixation and eye position measurement. After the monkeys learned the *I-DMS* task at a performance level of more than 95% correct, we began recording neuronal activity. For this recording, a grid was placed within recording cylinders to facilitate the insertion of stainless steel guide tubes through the dura to a depth of about 10 mm above the STS (Crist et al. 1988). At the beginning of each recording session, a guide tube stylet was removed and an epoxy-coated tungsten microelectrode (FHC; 1.0–1.5 MΩ at 1 kHz) was inserted. The electrode was advanced using a stepping microdrive (MO95I; Narishige, Tokyo, Japan), whereas neuronal activity was monitored to establish the relative depth of the landmarks, including the layers of gray and white matter, and to determine the characteristics of the neuronal responses.

We first isolated single neuronal activity from the 2 target areas: the anterior STS or the anterior ITG. In advance of the experiment, the size and location of the excitatory RF region were mapped by a mouse-controlled stimulus during a visual-fixation task. For this purpose, 7 types of stimuli were used: a 2° diameter spot, a 10 × 10° random-dot field, and 10 × 10° facial stimuli shown from 5 different angles (−90, −45, 0, +45, and +90°). The RF center was drawn on a tracing made on a monitor that duplicated the stimulus seen by the monkey. We then proceeded to record the neuronal activity during the performance of the *I-DMS* task. Successively studied cells were spaced apart at ≥100-μm intervals.

The behavioral task, stimulus timing, storage of single neuronal activity, and eye position were controlled by REX. Single neuronal activity was digitized using a window discriminator, sampled at 1 kHz, and the data were stored with indicators of the stimulus and associated behavioral events. An on-line raster display showed the occurrence of single neuronal discharges aligned according to stimulus and behavioral events during the experiment. Eye position was monitored by REX for behavioral control during all of the experiments and this information was also was stored.

Data analysis

Because our aim was to examine the behavior of face neurons as it relates to face identification, we primarily analyzed single neuronal activity in response to match test stimuli, that is, during the period 64–496 ms after the onset of the match (the lag time of 64 ms was based on the minimum response latency of neurons); behavioral parameters including behavioral reaction times were simultaneously measured. Control firing was measured during the 208-ms period before the sample stimulus was presented. Unless otherwise noted, the magnitude of responses was computed as the mean neuronal activity during the 64- to 496-ms period in the match period minus the control firing. Off-line data analysis also included spike density (SPD) histograms that were created by replacing the spikes with Gaussian pulses of a width corresponding to a 10-ms SD using the method of MacPherson and Aldridge (1979), as implemented by Richmond et al. (1987).

MULTIDIMENSIONAL SCALING (MDS). In this study, we identified *face space*, which was represented by the population of neurons, using MDS analysis (Kruskal method); neuronal responses to 28 match faces were used to determine the *face space*. It should be noted that the activity of all of the face neurons recorded in the anterior STS and in the anterior ITG that satisfied the criteria (i.e., the significant visual responses to match stimuli and the significantly larger responses to faces than geometric patterns) was used for the analysis; no selection beyond these criteria was made. The neuronal responses were normalized to minimize the inherited influence of differences in the firing rate; for an individual neuron, the averaged neuronal responses to each face was divided by the summation of all of the averaged neuronal responses. For all the combinations of 2 of the 28 faces (378 pairs, 28 × 27/2), the correlation coefficient (Pearson's) between arrays of the normalized neuronal responses of all the face neurons in the population was calculated as the dissimilarity measure; the matrix of dissimilarity measures was defined as the dissimilarity of all combinations of 2 faces. The dimension of the matrix of dissimilarity measures was then reduced using the MDS algorithm, and 28 faces were finally plotted into 2D space.

NEURONAL RESPONSE LATENCY. Neuronal response latency was defined as the time between the onset of the match stimuli and the time point in the SPD function at which the neuronal firing exceeded the mean + 2 SD of the control firing. This method was used to calculate the latency, and multiple trials (i.e., >3 trials) were required, such that only one value for the response latency was determined after multiple trials. We considered the neuronal firing during the *presample* period (i.e., the period just before the *sample* stimulus), and not that during the *prematch* period (i.e., the period just before the match stimulus) as the control firing. Because the period just before the match stimulus (*prematch* period) was an interstimulus delay period, it was inappropriate to serve as the control period for the cognitive task. Also, in our sample of face neurons, the mean firing rate during the *prematch* period (the 208-ms period before the match stimulus) was not significantly different from the mean control firing rate observed during the *presample* period (the 208-ms period before the sample stimulus; paired *t*-test, $P > 0.05$); the face neurons whose mean firing rate during the *prematch* period was significantly different from the mean control firing rate during the *presample* period were excluded from further analysis. This result was partially consistent with that of previous reports on the anterior ITG activities during delay intervals (Miller et al. 1991, 1993, 1996). However, the variance in the firing rates during the *prematch* period was high, and a relatively large variation across trials existed in the *prematch* period. Another reason to have used the *presample* period as the control period was to avoid variation across trials.

To investigate the temporal relationship between the behavioral reaction time and the neuronal response latency, the correlation coefficient (Pearson's) between the mean behavioral reaction time across multiple trials and the neuronal response latency, calculated from those same trials, was also analyzed with a significance level of $P < 0.05$.

Recording sites

For all monkeys, MRI was used to place the electrodes into the anterior STS and the anterior ITG (Fig. 2, *A* and *B*). The positions of the anterior STS/ITG and of the recording electrodes were checked by MRI during the experiment, and these MRI pictures were taken with a marker (tungsten, 500 μm in diameter); we verified the calculated recording sites in reference to the coordinate of the marker.

After the final recording session, the locations of the neurons analyzed in this study were reconstructed based on histological investigation (Fig. 2*C*) and MRI images. Several small marking lesions were created in the anterior STS and in the anterior ITG by passing 20–30 μA of anodal current for 40 s through an electrode placed stereotaxically and monitored by MRI. Both animals were then deeply anesthetized with an overdose of sodium pentobarbital (50 mg/kg, im) and perfused transcardially with 0.9% saline followed by 10% buffered formalin. The brains were removed and cut into 50-μm sections through the target areas. Sections were stained with cresyl violet, and the sites of the electrically induced lesions were determined microscopically. The location of each recording site was then calculated by comparing the stereotaxic coordinates of the recording sites with those of the lesions.

The activity of all of the face neurons in the present study was recorded in the range 22 to 14 mm anterior to the interaural line (Fig. 2*C*), where the anterior middle temporal sulcus is located. The activity of most of the neurons of the anterior STS sample in this study was recorded from the lower bank and fundus of the STS in the anteroposterior range. Many neurons of the anterior ITG sample were near the anterior middle temporal sulcus that roughly corresponded to the TEav (Tamura and Tanaka 2001) and AITv (Felleman and Van Essen 1991) areas.

RESULTS

Behavior

In almost all of the recording sessions, the monkeys performed the *I-DMS* task at a performance level of >95% correct. The performance was similar for all of the stimuli in the original set of 28 familiar faces (7 facial views × 4 facial identities).

To investigate the effects of familiarity/unfamiliarity of faces on the performance of identification and to characterize the *I-DMS* task, we tested behavioral transfer of the *I-DMS* task to new facial stimuli in one of the subjects (Fig. 3). Two types of faces were newly introduced; one consisted of faces of 4

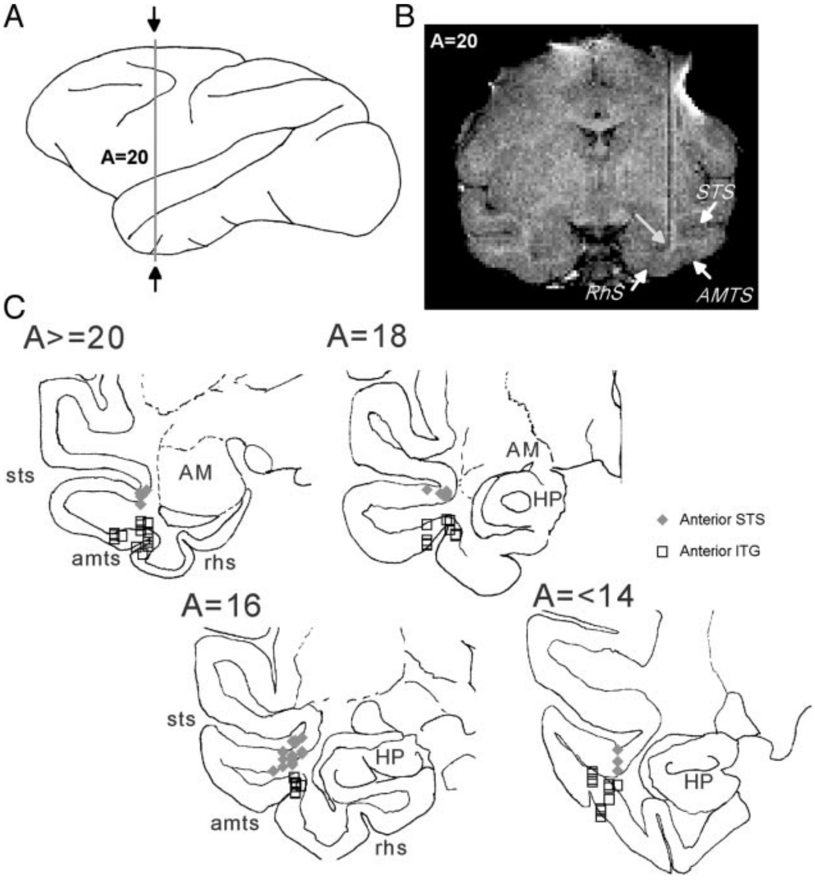

FIG. 2. *A*: lateral view of the macaque brain. Gray bar indicates the anteroposterior level (A = 20) of the coronal MRI section depicted in *B*. In this experiment, we recorded the activity of neurons from 4 hemispheres of 2 monkeys. *B*: MRI (coronal section). To determine the exact location of the target areas, a series of MRI pictures was taken with a marker (tungsten, 500 μm in diameter). Coronal section shown in this figure was at the anteroposterior level of A = 20, where the marker penetrated in the coronal plane (gray arrow). Based on the marker position in the series of MRI pictures, we located target areas for the present experiments: the anterior superior temporal sulcus (STS) and the anterior inferior temporal gyrus (ITG). RhS, rhinal sulcus; AMTS, anterior middle temporal sulcus; STS, superior temporal sulcus. *C*: locations of neurons analyzed in this study. After the experiments were conducted, the locations of neurons were reconstructed based on histological investigation and MRI pictures (see also METHODS). Note that most of the neurons of the anterior STS sample were from the lower bank and fundus of the sulcus, and many neurons of the anterior ITG sample were near the anterior middle temporal sulcus.

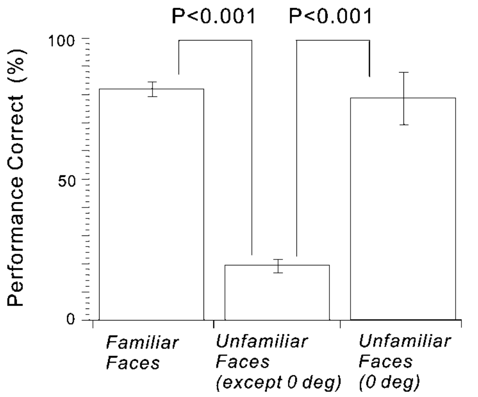

FIG. 3. Behavioral transfer of the *I-DMS* task. After each monkey learned the *I-DMS* task using the original familiar facial stimuli (Fig. 1*B*) with a performance of more than 95% correct, the faces of 4 familiar and 4 unfamiliar persons were newly introduced to test the behavioral transfer. Sample faces were always in the frontal view (0°), whereas the test facial stimuli consisted of one of 7 faces viewed from one of 7 different angles (from the *left to right* profile: -90, -45, -22.5, 0, $+22.5$, $+45$, and $+90°$); 56 test faces were thus used for the behavioral analysis (7 facial views × 4 facial identities × 2 familiar/unfamiliar conditions). For each facial stimulus, the task performance was calculated based on the first 4–7 trials. Average performance on the task involving unfamiliar faces, with the exception of the performance on the frontal view ($n = 24$), was significantly reduced compared with that on the task involving the familiar faces ($n = 28$; *t*-test, $P < 0.001$); the monkey did not show behavioral transfer to these unfamiliar faces. Average performance on the task involving unfamiliar faces in the frontal view ($n = 4$) was not significantly different from that on the task involving any of the familiar faces (*t*-test, $P > 0.05$). Average performance on the task involving unfamiliar faces in the frontal view was significantly different from that on the task involving unfamiliar faces except those in the frontal view (*t*-test, $P < 0.001$).

familiar persons who were members of the laboratory involved in the daily care of the subject, and the other type consisted of the faces of 4 unfamiliar persons the subject had never seen. For each facial stimulus, the task performance was calculated based on 4–7 trials. As the results showed, the *I-DMS* task was easily transferred to the familiar faces. However, the *I-DMS* task was not transferred to the unfamiliar faces, except to those in the frontal (0°) view. Behavioral performance in the case of the new unfamiliar faces in the frontal view was as good as that for new familiar faces. Note that for the unfamiliar faces shown from the frontal view, the monkeys were able to solve the *I-DMS* task by "perceptual" matching; that is, the monkeys needed to see a match only for the physically identical face, given that both the sample and the test appeared in the frontal view. For these trials, the monkeys did not need to perform "identity matching." The results confirmed that in the *I-DMS* task, the monkeys were able to perform identity matching of familiar faces.

In a subsequent experiment, we recorded the neuronal activity observed during the process of identity matching. Because our aim was to examine the neural correlates for face identification, we primarily analyzed single neuronal activity in response to match-test stimuli (i.e., in cases in which the subject monkey judged the identity of the faces).

Anterior STS

INDIVIDUAL DATA. In the anterior STS, we recorded a total of 144 visually responsive neurons that were shown to have significant responses during the match period, either to faces or to geometric patterns (paired *t*-test, $P < 0.05$). Neurons that were revealed as having both significant responses during the match period and significantly larger responses to faces than to geometric patterns (*t*-test, $P < 0.05$) were defined as "face neurons" in this study. By this definition, 48 neurons of the visually responsive neurons (34%) in the anterior STS sample were classified as face neurons. The RF of the face neurons was larger than 25 × 25° and included the fovea.

The selectivity of neuronal responses to faces was further analyzed by 2-way ANOVA (factors: facial view and facial identity; significance level: $P < 0.05$). Forty-two of the responsive neurons showed the effects of facial view, a typical example of which is shown in Fig. 4. The face neurons were shown to have a significant facial view effect (2-way ANOVA factors: facial view and facial identity; significance level: $P < 0.05$), and activities of this face neurons were tuned to the frontal view [Fig. 4, *A* and *B*, post hoc test (Newman–Keuls), $P < 0.05$). Eleven (26%), 20 (48%), and 11 (26%) of the face neurons with a significant facial view effect were optimally tuned to profiles (±90°), to the oblique (±45 and ±22.5°), and to the frontal (0°) views, respectively. For the neuron in Fig. 4, the effects of facial identity were not significant ($P > 0.05$), but the interaction between facial view and facial identity was significant ($P < 0.05$). Nine and 15 of the face neurons showed significant effects of facial identity and significant interactions of facial views and facial identity, respectively. Behavioral reaction times for pushing the lever are shown in Fig. 4*C*; reaction times were proportional to the angle between the sample and match stimuli, which reproduced the results of human behavioral studies using a similar identification task (Valentine and Bruce 1988; also see the DISCUSSION). The response latency of this face neuron is depicted in Fig. 4*D*. Latencies did not significantly differ with different facial views (χ^2 test, $P > 0.05$), and there was no correlation between the behavioral reaction time and the neuronal response latency ($r = 0.47$, $P > 0.05$).

POPULATION DATA. Figure 5*A* shows the *face space* that was calculated using the MDS of the facial stimuli based on the responses to the match faces of 48 face neurons in the anterior STS. In the design of the *I-DMS* task used in the present study, the sample was always in the frontal view, and only the test stimuli were rotated. The MDS *face space* thus consisted of only the match stimuli in this particular design. In the graph, 28 facial stimuli (7 facial views × 4 facial identities) were plotted: the same facial view was presented using the same colors and the same facial identity was presented using the same letters (A to D). For the MDS, we used a correlation coefficient (Pearson's) between arrays of neuronal responses as the dissimilarity measure, and 85.1% of the variance in the data was accounted for by the plot. In this figure, symbols of the same colors are grouped separately. Distances (Euclidean) between the same-facial views or same-facial identities, and the across-facial views or across-facial identities are compared in Fig. 5, *Ba* and *Bb*, respectively. Distances (means ± SE) between the same-facial views (0.48 ± 0.04; Fig. 5*Ba*) were significantly smaller than those of the across-facial views (1.42 ± 0.03; *t*-test, $P < 0.05$). Distances (means ± SE) between the same-facial identities (1.42 ± 0.06; Fig. 5*Bb*) were not significantly different from those of the across-facial identities (1.29 ± 0.03;

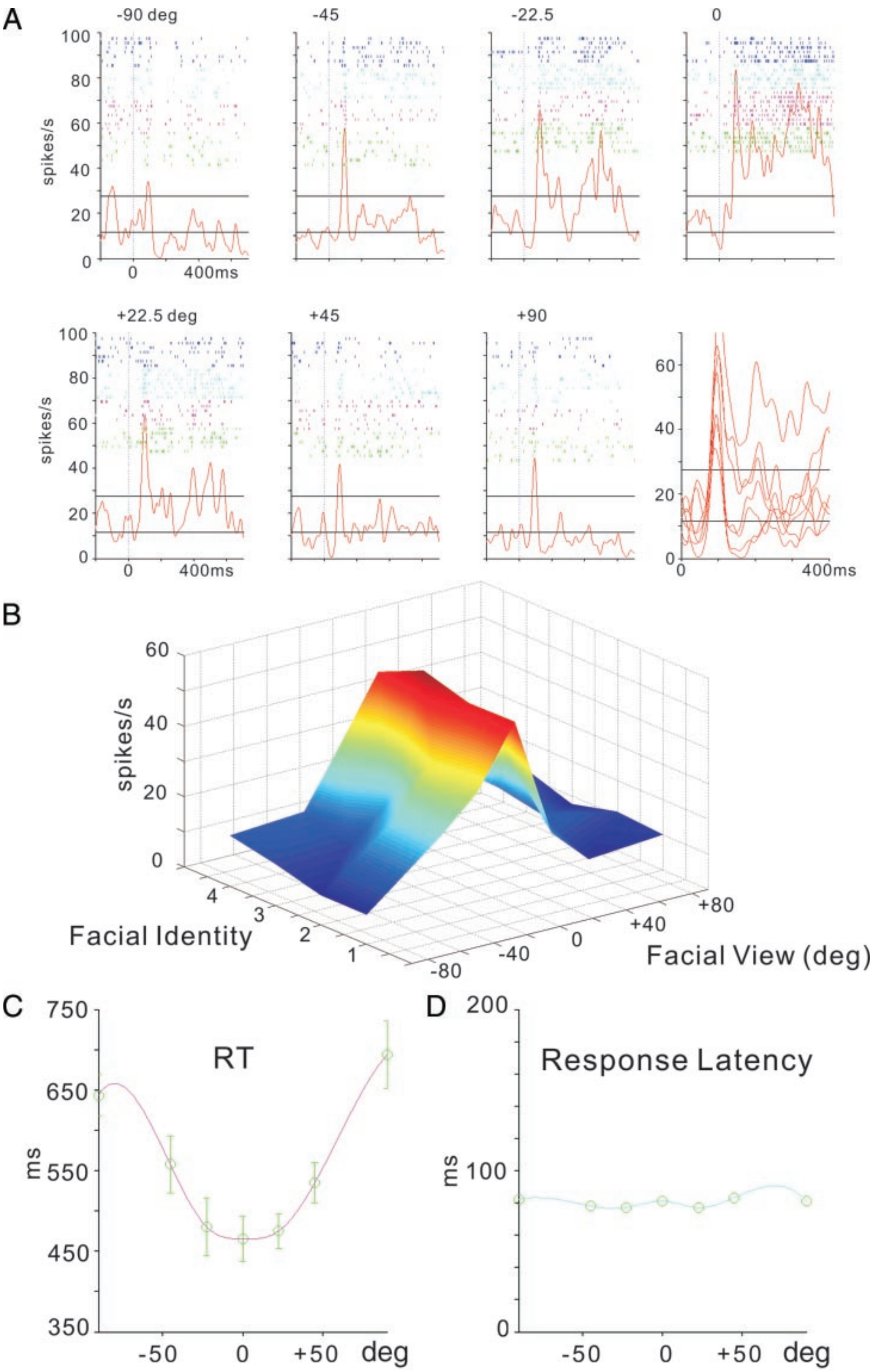

FIG. 4. Example of an anterior STS neuron. *A*: neuronal responses to a match face during the face-identification task. Responses to 7 different facial views (from *left to right*, −90 to +90°) were displayed in rasters, and spike density functions (SPD; SD = 10 ms) were aligned to the onset of a match (time = 0). Difference in raster colors indicates 4 different identities. Solid lines on the graphs indicate the mean firing rates during the control period (208-ms period before presentation of the sample faces) ± 2SD. Last panel shows superimposed responses to display the time course. *B*: neuronal responses to the match face of 7 facial views × 4 facial identities, as summarized in the 3D plot showing tuning to facial views. *C*: behavioral reaction time to the match faces presented in 7 different facial views (means ± SE). Behavioral reaction time was defined as the time between the onset of the match and the time point at which the monkey pushed the lever. Tuning curve was fitted by cubic spline functions. *D*: neuronal response latency in response to the match faces in 7 different facial views. Neuronal response latency was defined as the time between the onset of the match and the time point at which the SPD curve exceeded the mean + 2SD of the control firing; the neuronal response latency for each facial view includes all 4 facial identities. Tuning curve was fitted by cubic spline functions. Latencies were not significantly different with different facial views (χ^2 test, $P > 0.05$). Face neuron showed a significant effect of facial view (2-way ANOVA, factors: facial view and facial identity; significance level: $P < 0.05$) and activities of the face neuron were tuned to the frontal view [post hoc test (Newman–Keuls), $P < 0.05$]. Effects of facial identity were not significant ($P > 0.05$), but the interaction between facial view and facial identity was significant ($P < 0.05$). Pearson's correlation coefficient (r) between the behavioral reaction time and the neuronal response latency was 0.47 (n.s.).

t-test, $P > 0.05$). It was thus concluded that the *face space* in the anterior STS represents facial views rather than facial identity.

For 45 of 48 face neurons, we also analyzed the temporal correlations between the behavioral reaction time and the neuronal response latency using Pearson's correlation coefficients; 3 neurons were excluded from the analysis because the mean firing rate during the *prematch* period was significantly different from the mean control firing rate during the *presample* period (paired *t*-test, $P > 0.05$). The results are shown in Fig. 6*A*, and no significant correlation between the behavioral reaction times and the neuronal response latency was found in any of the neurons (0 of 45 neurons; $P < 0.05$). Figure 6*B* shows the scatter plot between the minimum and maximum values in the facial view tuning curve for the neuronal response latencies of all of the face neurons recorded in the anterior STS. The minimum response latency was 90.9 ± 3.1 ms (means ± SE) and the maximum response latency was 119.9 ± 4.5 ms. Most of the symbols that represented each of the face neurons fell roughly along orthogonal lines in the plot; there

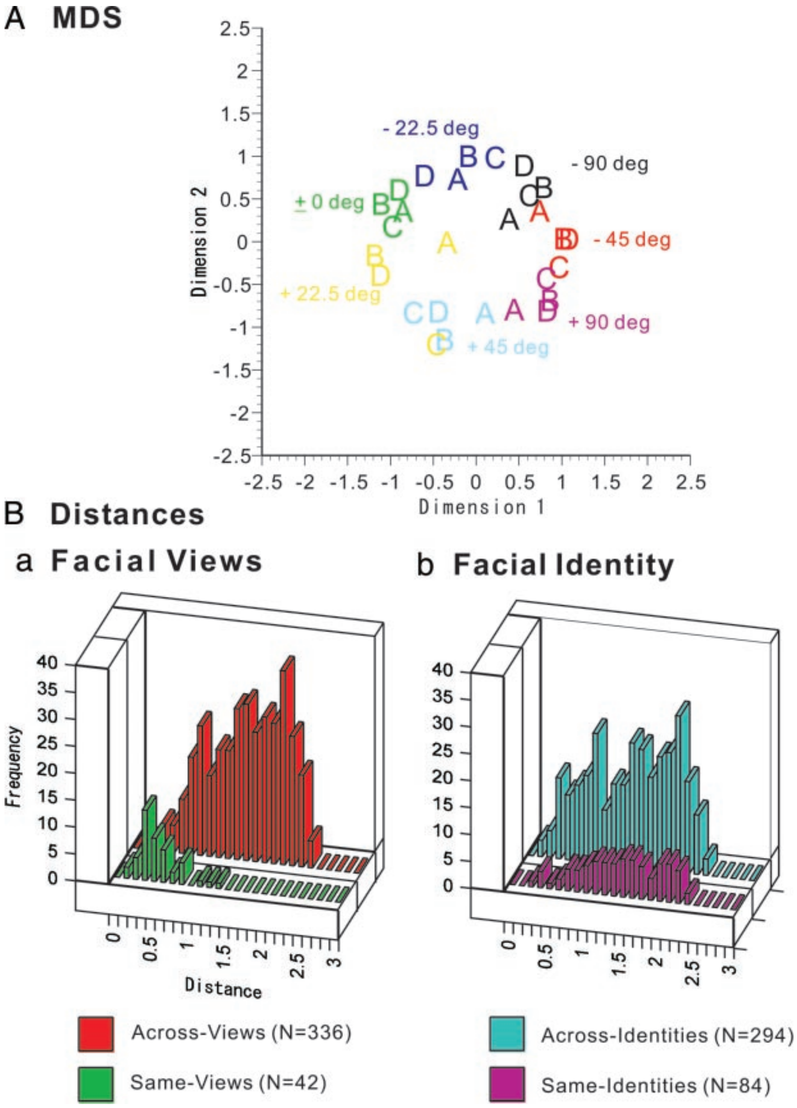

FIG. 5. *A*: face space represented in the anterior STS. *Face space* was calculated using MDS (Kruskal method) based on the neuronal responses to the match faces. For the dissimilarity measure, we used a correlation coefficient (Pearson's) between arrays of normalized neuronal responses. Twenty-eight facial stimuli (7 facial views × 4 facial identities, shown in Fig. 1*B*) used in the experiment were plotted 2-dimensionally: 85.1% of the variance was accounted for by the plot. In the plot, the same facial view was presented using the same colors (−90 to +90°) and the same facial identity was presented using the same letters (A to D). *Ba*: *frequency histogram* of distances (Euclidean) in the *face space* between the same-facial views and the across-facial views. Distances between the same-facial views were significantly smaller than those of the across-facial views (*t*-test, $P < 0.05$). *Bb*: *frequency histogram* of distances (Euclidean) in the *face space* between the same-facial identities and the across-facial identities. Distances between the same-facial identities were not significantly different from those of the across-facial identities (*t*-test, $P > 0.05$). Results demonstrated that the *face space* in the anterior STS represents facial views rather than facial identity.

were only relatively small differences between the minimum and maximum values.

Anterior ITG

INDIVIDUAL DATA. In the anterior ITG, we recorded a total of 204 visually responsive neurons that showed significant responses during the match period, either to faces or to geometric patterns (paired *t*-test, $P < 0.05$). Fifty-nine neurons among them (29%) showed both significant responses during the match period and significantly larger responses to faces than to geometric patterns (*t*-test, $P < 0.05$), and these neurons were therefore classified as face neurons. The RF of the face neurons in the anterior ITG was larger than 25 × 25° and included the fovea.

Again, the selectivity of neuronal responses to faces was further analyzed by 2-way ANOVA (factors: facial view and facial identity; significance level: $P < 0.05$). A typical example is shown in Fig. 7. The face neuron in Fig. 7 had a significant effect of facial identity (Fig. 7*B*, $P < 0.05$). Neither the effect of facial views nor the interaction between facial views and facial identity was significant ($P > 0.05$) for this face neuron. Fifty-two of the recorded face neurons showed significant effects of facial identity although the tuning was, by visual inspection, usually broad. Ten and 21 of the face neurons showed significant effects of facial views and significant interactions between facial views and facial identity, respectively. The reaction time measured during the recording of the neuron in Fig. 7, *A* and *B* is depicted in Fig. 7*C*, and was similar to that shown in Fig. 4*C*. The response latency of this face neuron, measured from the SPD function and shown in Fig. 7*D*, was significantly different with different facial views (χ^2 test, $P < 0.05$). Correlation analysis revealed that there was a significant correlation between the behavioral reaction time and the neuronal response latency (Pearson's correlation coefficients, $r = 0.91$, $P < 0.05$). Another example of a face neuron in the anterior ITG revealed a significant correlation between the behavioral reaction time and the neuronal response latency (Fig. 8, *A* and *B*; $r = 0.85$, $P < 0.05$). These findings indicate the possibility that these neurons might be essentially related to the determination of facial identity (see DISCUSSION).

POPULATION DATA. Figure 9*A* shows the *face space* represented in the anterior ITG derived from the MDS. This analysis was based on responses to the match faces of 59 face neurons in the anterior ITG. Twenty-eight facial stimuli (7 facial

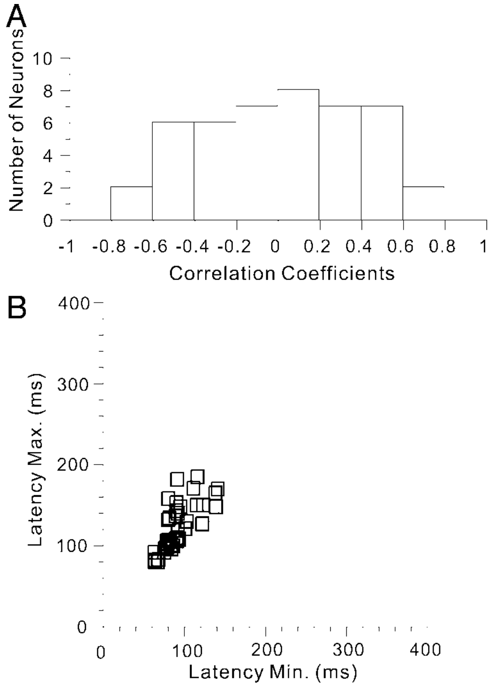

FIG. 6. *A*: *frequency histogram* of the correlation coefficients (Pearson's) between behavioral reaction time and response latency of the anterior STS neurons ($n = 45$). No significant correlation was obtained for this sample ($P >$ 0.05). *B*: *scatter plot* between the minimum and maximum values in the tuning curve for neuronal response latencies of each neuron in the anterior STS ($n =$ 45).

views × 4 facial identities) are plotted in the figure: the same facial views are presented using the same colors and the same facial identities are presented using the same letters (A to D). It was found that 81.9% of the variance in data could be explained by the plot. The figure shows that symbols using the same letters were grouped separately. Distances (Euclidean) between the same-facial views or same-facial identities and those of the across-facial views or across-facial identities are compared in Fig. 9, *Ba* and *Bb*, respectively. Distances (means ± SE) between the same-facial views (1.30 ± 0.03) were not significantly different from those of the across-facial views (1.44 ± 0.08; *t*-test, $P > 0.05$; Fig. 9*Ba*). Distances (means ± SE) between the same-facial identities (0.81 ± 0.06) were significantly smaller than those of the across-facial identities (1.47 ± 0.03; *t*-test, $P < 0.05$; Fig. 9*Bb*). This finding indicates that the *face space* in the anterior ITG represents facial identities rather than facial views.

For 51 of 59 face neurons, we also analyzed the temporal correlations between the behavioral reaction time and the neuronal response latency using Pearson's correlation coefficients; 8 neurons were excluded from the analysis because the mean firing rate during the *prematch* period was significantly different from the mean control firing rate during the *presample* period (paired *t*-test, $P > 0.05$). In our analysis, it was found that 8 (15.6%) of 51 neurons showed a significant correlation (dark bars, Fig. 10*A*; Pearson's correlation coefficients, $P <$ 0.05). The results indicate that latencies of the neuronal responses of the anterior ITG paralleled the behavioral reaction time, suggesting that the anterior ITG is closely related to the processing of the determination of facial identity (see DISCUSSION). Figure 10*B* shows the scatter plot between the minimum and maximum values of the tuning curve for neuronal response latencies of all the face neurons recorded in the anterior ITG. The minimum response latency (means ± SE) was 117.1 ± 8.0 ms and the maximum response latency was 198.4 ± 10.3 ms. The dark symbols indicate neurons with a significant correlation; these symbols correspond to the dark bars shown in Fig. 10*A*. This finding indicates that the neurons associated with a significant correlation between behavioral reaction time and neuronal response latency had relatively slower latencies (means ± SE) (minimum response latency was 196.6 ± 20.8 ms and the maximum response latency was 294.1 ± 12.5 ms). This finding suggests that the small number of neurons with relatively slower latencies in the anterior ITG might be responsible for the correlation with the behavioral reaction times (see DISCUSSION).

To rule out the possibility that the significant correlation between behavioral reaction times and neuronal response latencies was apparent and ascribed to the correlation between response latencies and response magnitudes of the neuronal responses, we performed a correlation analysis that was similar to that shown in Fig. 10*A*, but instead, we considered the correlation between neuronal response latencies and neuronal response magnitudes. In the analysis, the response magnitude to each face of the face neurons was the neuronal activity in response to a match (64–496 ms after the match) *minus* the control firing (0- to 208-ms period before the sample). The results are summarized in the frequency histogram in Fig. 11. It was found that only a small number of face neurons (2 of 51, 3.9%; $P < 0.05$) shown in Fig. 11 were associated with a significant correlation, compared with those shown in Fig. 10*A*. The results confirmed that a significant temporal correlation between behavioral reaction times and neuronal response latencies existed in some face neurons of the anterior ITG sample.

DISCUSSION

BEHAVIOR. *Behavioral transfer.* We tested the behavioral transfer of the performance on the *I-DMS* task using 2 types of facial stimuli that were newly introduced; one type consisted of the faces of 4 familiar persons and the other type consisted of the faces of 4 unfamiliar persons. The reason for the introduction of new stimuli was to control the monkeys' visual experience with the stimuli, given that both the unfamiliar and the familiar facial stimuli were "novel" in terms of being visual stimuli displayed on a CRT monitor, whereas the original familiar facial stimuli were not novel in that same sense.

The results (Fig. 3) showed easy transfer of the performance on the *I-DMS* task to a task involving familiar faces. However, the only aspect of the behavioral task that was transferred to unfamiliar faces was the viewing of faces from a frontal (0°) perspective. With respect to the monkeys' behavioral performance on the frontal-view trial, they performed as well when stimulated by images of unfamiliar faces as they did in the trials involving familiar faces. It is of note that in the frontal-view trials, both the sample and the test faces were presented from the same perspective (i.e., the frontal view). In these trials, the monkeys did not have to identify matching faces, but had to perform only perceptual matching of the subjects to produce correct answers. Thus differences in cognitive strategies account for the disagreement between the results obtained

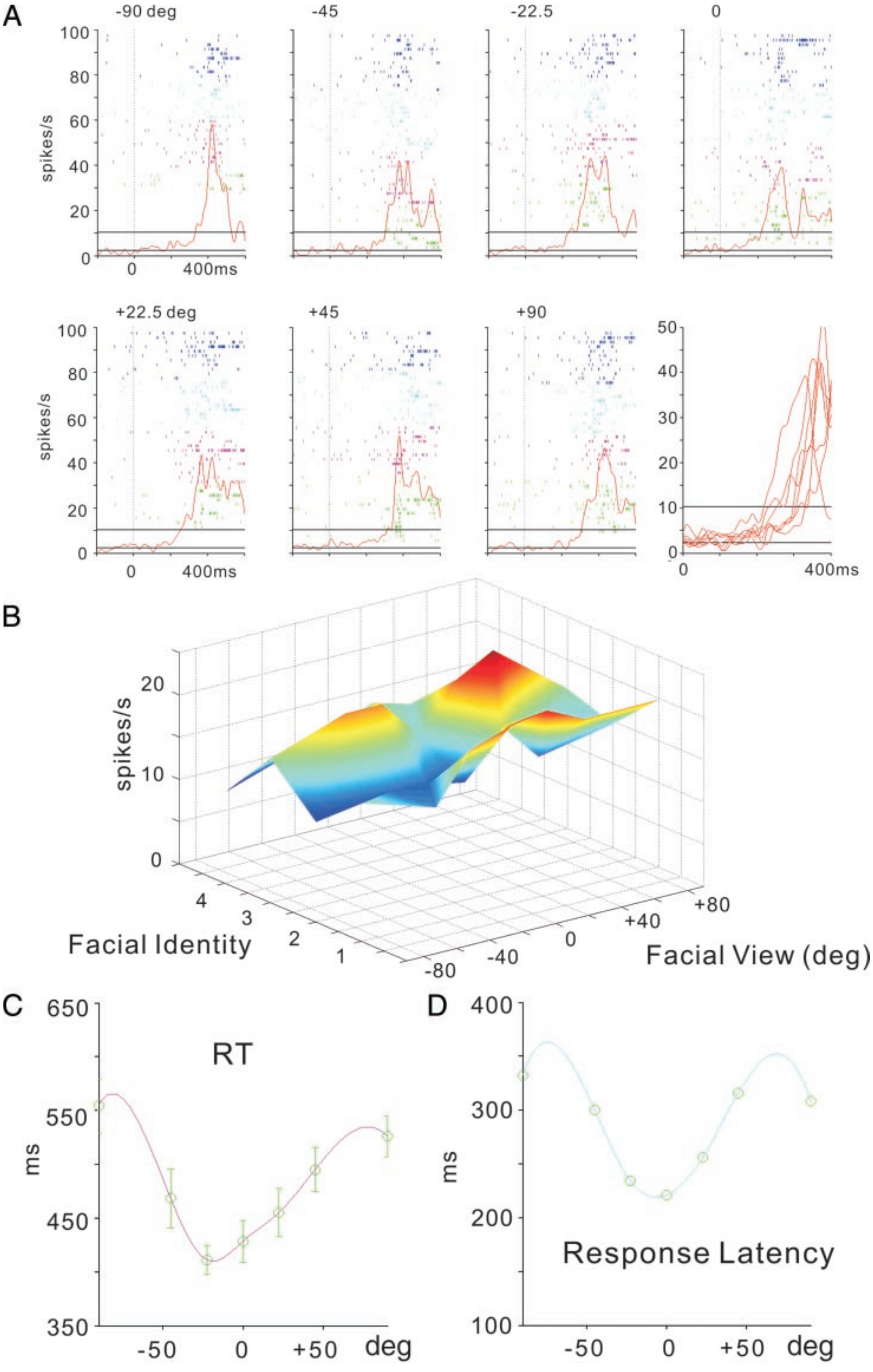

FIG. 7. Example of an anterior ITG neuron. *A–D*: configuration of this figure is the same as that shown in Fig. 4. This face neuron had a significant facial identity effect (2-way ANOVA, factors: facial view and facial identity; significance level: $P < 0.05$); neither the effect of facial views nor the interaction between facial views and facial identity was significant ($P > 0.05$) for this face neuron. Response latency was significantly different with different facial views (χ^2 test, $P < 0.05$). Correlation coefficient (r) between behavioral reaction time and neuronal response latency was significant for this neuron ($r = 0.91$, $P < 0.05$). Reaction time curve and the neuronal response latency curve were fitted by cubic spline functions.

from considering the familiar faces, the frontal view, unfamiliar faces, and the unfamiliar faces except for those in the frontal view. The results confirmed that the monkeys were able to perform identity matching of familiar faces during the *I-DMS* task.

The results also indicated that the identification of familiar faces by macaque monkeys was based on a type of processing that differed from that used for unfamiliar faces. Moreover, the present results using these monkeys were consistent with the results of previous human psychological studies (Bruce 1988; Bruce and Young 1998). When processing the identification of familiar faces, it is likely that incoming or "bottom-up" perceptual information about the face at which the subject is looking is compared with mnemonic information about that person, whereby the latter information is thought to be stored in long-term memory. Previous studies have suggested the involvement of active memory mechanisms in the sequential delayed matching-to-sample task (Miller and Desimone 1992; Miller et al. 1991, 1993, 1996). Thus in the *I-DMS* task, the sample face may have triggered "top-down" signals. Later, at

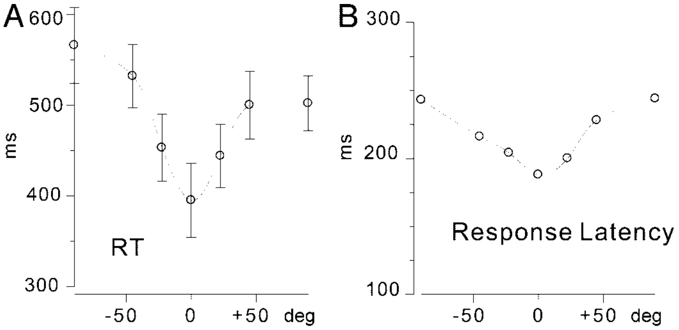

FIG. 8. Another example of an anterior ITG neuron. *A*: behavioral reaction time in the different 7 facial views (means ± SE). *B*: neuronal response latency in response to the match faces in 7 different facial views. Correlation coefficient (r) between the behavioral reaction time and the neuronal response latency was significant ($r = 0.85$, $P < 0.05$).

the presentation of each test face, bottom-up signals associated with the test face might be actively compared with mnemonic information produced by the top-down signals.

Behavioral reaction time. Figures 4*C*, 7*C*, and 8*A* show the behavioral reaction time lapses until the monkeys pushed the lever when performing the *I-DMS* task. The results indicated that the reaction times were proportional to the angle between the sample and the match stimuli, such that the reaction time curve assumed a V-shape. The present results reproduced the results of human behavioral studies using a similar identification task involving faces (Valentine and Bruce 1988). Also, in a similar identification task involving more complex 3D objects, it was already shown in the 1970s that reaction times are proportional to the angle between the sample and the match stimuli (Shepard and Meltzer 1971). The basic finding in this context is that the time required for the matching of 2 views of an object (which differs according to a rotation in depth or orientation in the picture plane) is linearly related to the 3D angular difference between views. These results by Shepard and Meltzer have been very important for subsequent theoretical discussions of "mental rotation."

However, as previously noted (Perrett et al. 1998), such findings do not necessarily indicate that mental rotation or transformation is required for the processing of object/face identification. Several investigators have shown that "view-specific representations" are used for cognitive processes in various situations (Bulthoff and Edelman 1992; Edelman and Bulthoff 1992; Logothetis et al. 1995; Tarr 1995). Because

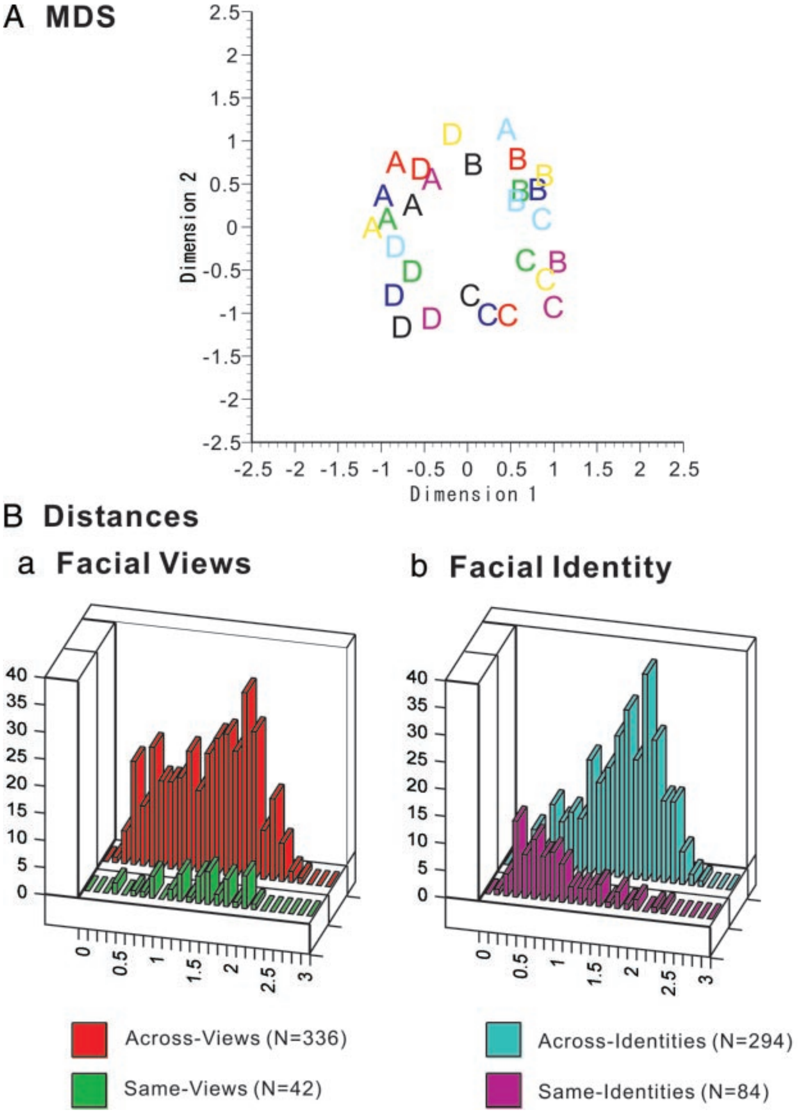

FIG. 9. *A*: face space represented in the anterior ITG. Twenty-eight facial stimuli (7 facial views × 4 facial identities) were again plotted 2-dimensionally: 81.9% of the variance was accounted for by the plot. Same-facial view was presented using the same colors (−90 to +90°) and the same-facial identity was presented using the same letters (A to D), as shown in Fig. 5*A*. *Ba*: *frequency histogram* of distances (Euclidean) in the *face space* between the same-facial views and the across-facial views. Distances between the same-facial views were not significantly different from those of the across-facial views (*t*-test, $P > 0.05$). *Bb*: *frequency histogram* of distances (Euclidean) in the *face space* between the same-facial identities and the across-facial identities. Distances between the same-face identities were significantly smaller than those of the across-face identities (*t*-test, $P < 0.05$). Results show that the *face space* in the anterior ITG represents facial identity rather than facial views.

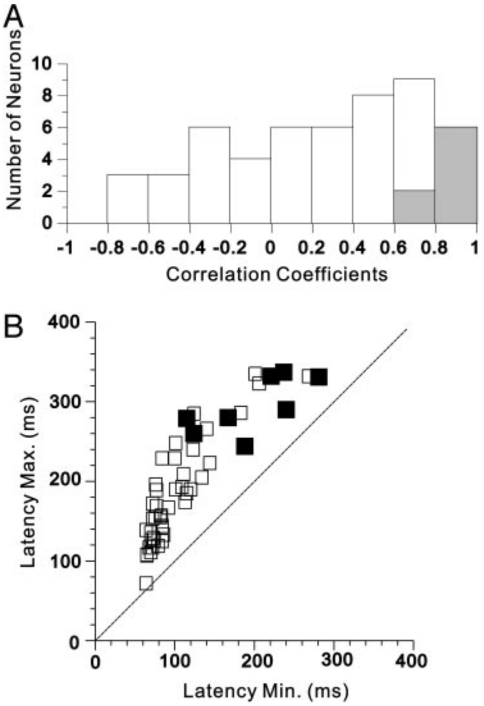

FIG. 10. *A*: *frequency histogram* of the correlation coefficients (Pearson's) between behavioral reaction time and response latency of the anterior ITG neurons ($n = 51$). Dark bars indicate a significant correlation ($P < 0.05$). *B*: *scatter plot* between the minimum and maximum values in the tuning curve for neuronal response latencies of each neuron in the anterior ITG ($n = 51$). Dark symbols indicate neurons with a significant correlation in *A*.

there is some behavioral evidence to support both view-specific representations and mental rotation-like operations, it seems likely that a viable explanation for model object/face recognition (identification) might encompass elements of both (Tarr and Bulthoff 1998). It is possible that certain cognitive processes, including face identification, rely essentially on mental rotation-like operations or on the use of view-specific representations, and that these events might depend on the requirements of the particular task at hand (Perrett et al. 1998); such a conclusion may also hold true for the *I-DMS* task.

We performed single neuronal recordings of face neurons from the anterior STS and the anterior ITG of macaques during the performance of an *I-DMS* task that was behaviorally characterized as described above. This is the first report of the neural recording of the *I-DMS* task in monkeys.

Anterior STS

In the anterior STS sample, 34% of the visually responsive neurons were classified as face neurons. This percentage was larger than the percentages obtained in previous studies of face neurons, which produced results of about 10% of the neurons tested (Hasselmo et al. 1989; Perrett et al. 1982). However, our sample might be somewhat biased, given that we analyzed neurons that showed only significant visual responses to match faces.

With respect to the *face space* composed by the MDS analysis shown in Fig. 5, *A*, *Ba*, and *Bb*, the facial views were represented by the population of face neurons in the anterior STS. It should be noted that the *face space* reflected the data obtained from all of the face neurons recorded in that area of interest. It was decided on anatomical locations whether the face neuron belonged to the anterior STS or to the anterior ITG; however, no other selection was made in this regard. The result showing that the anterior STS represented facial views was consistent with the results of previous studies using passive viewing tasks (Perrett et al. 1982, 1995). Our results revealed the behavior of the population of face neurons in the anterior STS; facial stimuli depicting systematic changes in facial views (7 facial views × 4 facial identities) were analyzed in the *face space*. In addition, our recordings were made while each monkey performed a relevant cognitive task, and the behavioral parameters were simultaneously measured.

In the anterior STS, the response latency of face neurons in response to facial views was relatively constant (i.e., about 90–120 ms), as shown in Figs. 4*D* and 6*B*. This finding was in agreement with that of previous reports (Oram and Perrett 1994; Perrett et al. 1982, 1998). Moreover, the face neurons in the anterior STS showed no significant correlation with the behavioral reaction time, as shown in Fig. 6*A*. The relatively constant, short-latency period observed among neuronal responses to facial views suggested that the area was more closely involved in the processing of incoming (or bottom-up) visual information, rather than the processing of feedback (or top-down) information (Oram and Perrett 1992). In addition, it does not appear to be the case that lateral interactions were as greatly involved as was incoming (or bottom-up) visual information, given that the responses rapidly increased and were fixed in time to the onset of the presentation of the stimulus, irrespective of facial views. As the correlation between the neuronal response latency and the behavioral reaction time suggested, there was no indication of a direct link between the behavior of face neurons in the anterior STS and the determination of facial identity. Based on these results, it was thus concluded that the anterior STS processes face parameters by bottom-up perceptual information.

The anterior STS was found to represent different facial views; this finding supports the existence of "view-specific representations," as previously noted in related studies (Oram and Perrett 1994; Perrett et al. 1998). "View-specific representations" that are coded in the anterior STS might be important in a behavioral context in which the processing of bottom-up perceptual information is thought to be predominantly required.

Anterior ITG

In the anterior ITG sample, 29% of the visually responsive neurons were classified as face neurons. Again, this percentage was larger than the percentages observed in previous studies of

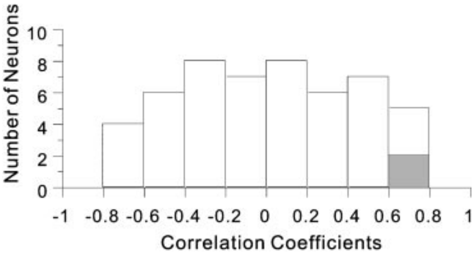

FIG. 11. *Frequency histogram* of the correlation coefficients (Pearson's) between neuronal response latency and response magnitude of the anterior ITG neurons ($n = 51$). Dark bars indicate a significant correlation ($P < 0.05$).

face neurons (Hasselmo et al. 1989; Perrett et al. 1982), an effect that is likely to have been attributable to the sampling bias, as mentioned above. We reproduced suppression effects against the previously reported match stimuli (Miller et al. 1991, 1993, 1996; Riches et al. 1991) in about one-third of the face neurons ($n = 22$, paired *t*-test, $P < 0.05$). However, the other neurons showed either an enhancement of the response ($n = 19$) or no significant change ($n = 18$). The present results were consistent with those of a previous report (Tamura and Tanaka 2001). It should also be noted that changes in neuronal responses to the presentation of additional faces were also reported in studies involving behavioral tasks other than face or identity matching (Baylis and Rolls 1987; Rolls et al. 1989; Sohal and Hasselmo 2000).

With respect to the *face space* composed by the MDS analysis depicted in Fig. 9, *A*, *Ba*, and *Bb*, the population of face neurons in the anterior ITG was found to represent facial identity. The conclusion that the anterior ITG represented facial identity was consistent with those of previous MDS studies using face-discrimination tasks (Hasselmo et al. 1989; Young and Yamane 1992); however, the present recordings were carried out while the monkeys performed the *I-DMS* task, and the behavioral parameters were simultaneously measured.

The behavioral measurement demonstrated that 8 (15.4%) neurons in the anterior ITG exhibited a significant correlation between response latency and behavioral reaction time (Figs. 7*D* and 8*B*, dark bars in Fig. 10*A*). These results suggest the possibility that the anterior ITG is closely related to the determination of facial identity. As pointed out above, concerning the identification of familiar faces, 2 types of information appear to be necessary, that is, not only immediate incoming perceptual information, but also top-down information based on the long-term memory of faces. The correlation observed in the anterior ITG might therefore be important in a behavioral context in which the processing of top-down information is thought to be predominantly required.

As the results demonstrated (Fig. 10*B*), the response latencies of those face neurons associated with a significant correlation between behavioral reaction time and neuronal response latency were larger than those without this correlation. Tamura and Tanaka (2001) previously reported the existence of a population of anterior ITG neurons with response latencies of >250 ms. The findings presented here might be comparable with those of studies showing "built-up" responses in the anterior ITG; such studies have considered neural correlates for associative pairing (Naya et al. 2001; Sakai and Miyashita 1991). The behavior of this small number of neurons with relatively slower latencies indicated that the neurons in the anterior ITG might have specialized functions because these neurons exhibited a temporal correlation between the behavioral reaction times and the neuronal response latencies.

Most of the face neurons in the anterior ITG in our sample were located in the ventral portion of the anterior ITG, corresponding to the TEav area defined in a previous report (Saleem et al. 2000). It has been suggested that the anterior part of the STS lower bank has a strong reciprocal connection with the TEav area (Saleem et al. 2000; Seltzer and Pandya 1994). The TEav area is known to be related to the organization of visual long-term memory, which is under the influence of the perirhinal cortex (Higuchi and Miyashita 1996) and is also most probably under the influence of the hippocampus as well (Aggleton and Brown 1999). Retrieval from the TEav area's visual long-term memory storage is under the top-down control of both the perirhinal cortex (Naya et al. 2001) and the prefrontal cortex (Tomita et al. 1999). The TEav area has also been demonstrated to have a strong mutual connection with the limbic emotional system (Amaral and Price 1984; Barnes and Pandya 1992; Suzuki et al. 2000). Thus the anterior ITG may be responsible for the determination of facial identity by the influence of the top-down control of these structures; therefore the behavioral correlates of some face neurons are probably in the anterior ITG.

However, this conceptualization might be an oversimplification. For the majority of face neurons (51 of 59) in the anterior ITG, we did not observe sustained or "built-up" activity during the interstimulus-delay periods in the *I-DMS* task. For the remaining 8 face neurons, 6 elicited a significantly large amount of activity during the delays before match test stimulus [i.e., the *prematch* period (paired *t*-test, $P < 0.05$)], whereas 2 elicited a significantly small amount of activity during these delays (paired *t*-test, $P < 0.05$). None of these neurons elicited systematic changes in neuronal activity in relation to either facial identity or facial views (2-way ANOVA factors: facial view and facial identity, $P > 0.05$). The results were partially consistent with those of previous studies using sequential delayed matching-to-sample tasks (Miller et al. 1991, 1993, 1996). Our results demonstrated that face neurons with a behavioral correlation usually fired after the onset of a match-test stimulus. These findings might be attributable to the use of retrospective, not prospective, strategies for solving the *I-DMS* task (Mazur 1998). However, at this point, we have no direct evidence regarding whether the subjects used a retrospective strategy or a prospective strategy for solving the *I-DMS* task.

RESPONSE LATENCY VERSUS RESPONSE MAGNITUDE. We demonstrated a significant correlation between behavioral reaction times and neuronal response latencies in some of the anterior ITG neurons, as shown in Fig. 10*A*. It has been reported that response latency was correlated with response strength (Tamura and Tanaka 2001). It was therefore thought that if there is indeed a correlation between neuronal response latencies and neuronal response magnitudes, then the correlation between behavioral reaction times and neuronal response latencies (as described above) might be explained by the correlation between response latencies and response magnitudes. However, this hypothesis was not clearly supported by our sample. The frequency histogram in Fig. 11 showed that only 2 neurons were associated with a significant correlation between response latency and response magnitude. The results did confirm the existence of a correlation between behavioral reaction times and neuronal response latencies in some of the face neurons in the anterior ITG. Our results are therefore not consistent with the findings reported by Tamura and Tanaka (2001). Discrepancies between the results regarding the correlation between response latency and response magnitude might be partially explained by the fact that, in our study, only 7 facial views were used for comparison in the correlation analysis. Another possible explanation would be that we analyzed only the match responses in the *I-DMS* task. As noted above, we found both suppression and enhancement effects in terms of the match stimuli in about one-third of the face neurons.

Neuronal mechanisms for face identification in monkeys

Human studies have suggested the existence of 2 distinct systems responsible for face recognition. The first system includes the lateral fusiform gyrus, which plays a crucial role in the recognition of facial identity (George et al. 1999; Sergent et al. 1992), whereas the second system includes the anterior STS, which plays a crucial role in the perception of facial emotions and gaze direction (Puce et al. 1998). The schema we proposed in the present study using monkeys was consistent with that of previous studies demonstrative of the functional heterogeneity of these 2 cortical systems in humans. In the process of face identification, the face neurons in 2 different cortical areas (i.e., the anterior STS and the anterior ITG) were revealed to behave differently. The present results suggest that the anterior ITG is closely related to judgments of facial identity, and that the anterior STS is closely related to analyses of incoming perceptual information.

There are 2 possible neuronal mechanisms involved in the performance of the *I-DMS* task; one possibility is that the 2 cortical areas—the anterior STS and the anterior ITG—interact to solve the *I-DMS* task, and the other possibility is that the 2 cortical areas are independent (or parallel) and that the anterior ITG is primarily responsible for performing this task. Heywood and Cowey (1992) showed that lesions localized in the anterior STS did not significantly affect the performance on face-identification tasks, suggesting that the anterior STS contributed little to the performance on face-identification tasks. However, it should be noted that face identification is usually composed of 2 cognitive strategies: perceptual matching (in other words, looking at faces as pictorial patterns) and identity matching (in other words, looking at faces as representative of an individual identity), discussed earlier in BEHAVIORAL TRANSFER. Without behavioral manipulation considered in the *I-DMS* task in the present study, it would be difficult to dissociate these 2 cognitive strategies. Lesion studies of either of the 2 areas using the *I-DMS* task would be required to clarify the interactions of the 2 cortical areas in monkeys; however, no such lesion studies have been performed using this *I-DMS* task.

It is important in this context to emphasize the advantages of a mechanism by which some functional modules would be specialized for face processing. Such advantages have been clearly demonstrated in humans as “face-inversion effects” (Farah et al. 1995; Haxby et al. 1999). Our behavioral results also indicate that monkeys can avail themselves of 2 different cognitive strategies: perceptual matching and identity matching of familiar faces. Thus the present results also suggested that the identification of faces occurred by a pathway different from that dedicated for pattern recognition. Neurons in the anterior ITG are generally sensitive to complex patterns, including those that represent faces (Tanaka 1996); thus it is unlikely that the anterior ITG functions as a face-specific module in monkeys. On the other hand, it has been reported that the majority of neurons in the anterior STS are exclusively sensitive to the sight of body parts, including faces and hands (Perrett and Oram 1993). Whether the anterior STS functions as a face-specific module for monkeys remains unknown; however, the present study showed that face neurons in the anterior STS represented face parameters such as facial views, and a previous study showed that face neurons in the anterior STS processed configurations of facial parts (Young and Yamane 1992). Thus in monkeys, the anterior STS may be involved in the recognition of facial identity. Furthermore, in this framework, this area is thought to facilitate the behavioral performance of face-identification tasks in concert with some involvement of the anterior ITG.

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DISCLOSURES

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