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The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey

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Neurophysiological studies have shown that some neurons in the cortex in the superior temporal sulcus and the inferior temporal gyrus of macaque monkeys respond to faces. To determine if facial factors such as expression and identity are encoded independently by face-responsive neurons, 45 neurons were tested on a stimulus set depicting 3 monkeys with 3 expressions each. As tested on a two-way ANOVA, 15 neurons showed response differences to different identities independently of expression, and 9 neurons showed responses to different expressions independently of identity. Three neurons showed significant effects of both factors. Six of the neurons with responses related to expression responded primarily to calm faces, while 2 responded primarily to threat faces. Of a further set of 31 neurons tested on pairs of different expressions, 6 showed strong responses to open-mouth fear or threat expressions, while 2 showed stronger responses to calm faces than threat expressions. Neurons responsive to expression were found primarily in the cortex in the superior temporal sulcus, while neurons responsive to identity were found primarily in the inferior temporal gyrus. The difference in anatomical distribution was statistically significant. This supports the possibility that specific impairments of the recognition of the identity of a face and of its expression in man are due to damage to or disconnection of separate neuronal substrates.

INTRODUCTION

For the accurate recognition of individuals, a representation of identity must be formed which is invariant with respect to changes in expression. Likewise, expressions must be interpretable over a range of different individuals. Models of human face recognition postulate separate processes for the encoding of expression and identity[7,13]. In cognitive research, this theoretical dissociation is supported by the fact that reaction time for matching identity is faster for familiar versus unfamiliar faces, while the use of familiar versus unfamiliar faces elicits no difference in reaction time for matching expression[7]. In addition, there is a better retention of the memory for the identity than for the expression of test faces[35], and there is evidence for separate selective attention processes for facial identity and facial emotion[10].

There is also clinical evidence for a dissociation between the processing of face identity and expression. The syndrome of prosopagnosia involves a failure in determining the identity of faces. Prosopagnosics can identify the class of faces[3], parts of faces[9], and even the emotion expressed on a face[32,34]. However, they cannot

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identify an individual from the sight of their face, and must revert to cues such as voice to recognize even their family members. No deficit homologous to prosopagnosia has been produced in monkeys. However, the evidence from monkeys with anterior temporal lesions shows that they are severely impaired on social interactions, both in free-ranging groups and in captivity[15,19]. This may be due to the inability of lesioned monkeys to recognize the identity and rank of other monkeys in the group. Horel[14] found deficits on discrimination and delayed-match-to-sample tasks using face stimuli with cooling of the inferior temporal cortex.

There are fewer cases of agnosia specific for expression. Impairments in the recognition of expression but not identity have been found in patients with cerebral organic brain syndrome[5,16]. This impairment has been related to a disconnection of visual input from affective meaning, rather than a loss of affective understanding. Bowers and Heilman[4] describe a patient with a dissociation between the processing of affective and non-affective faces. Electrical stimulation of the posterior middle temporal gyrus has been shown to disrupt the labelling of facial emotions in humans[12]. This work is of particular interest because it concerns an area homologous with the area where cells responsive to faces are found in monkeys. Lesions of the cortex in the superior temporal sulcus cause deficits on the discrimination of the angle of regard assessed in faces presented at different angles of orientation (A. Cowey and C. Heywood, personal communication, 1987), which may cause difficulties in perceiving social cues.

Neurons responsive to faces could be part of a system for the independent extraction of identity and expression. These neurons are relatively insensitive to most manipulations of facial stimuli such as changes in size, colour, and isomorphic rotation[20], yet they have been demonstrated to respond differentially to different faces in studies by Baylis et al.[1] and Perrett et al.[21]. In the study by Baylis et al., a large range of faces was displayed to the monkey while recordings were made from single face-responsive cells. Of the cells tested, 77% showed differential response to different faces, with a range of selectivities. The different neuronal responses to different stimuli could have been due to differences in the identity or in the expression of the face stimuli. In a test of 66 neurons showing different responses to different faces, 29% responded consistently more to particular individuals independently of expression[21]. Responses dependent on open-mouth threats or yawning but not identity were mentioned for 4 neurons[21], and a more extensive study showed that some face-responsive cells show selectivity for face orientation and direction of gaze[23]. These factors can be important elements in monkey expression, in that for example mouth configuration, fixed gaze and full face orientation are part of the threatening gesture in monkeys.

In the experiments presented here, a set of faces varying systematically in both expression and identity was used to test whether there are separate populations of neurons which respond to the identity of a face and to the expression on a face. The experimental design was to present the faces of several individuals with several expressions of each individual, so that the relative contributions of the identity of the face and the expression on a face could be determined using a two-factor analysis of variance.

MATERIALS AND METHODS

The activity of single neurons was recorded with glass-insulated tungsten microelectrodes (after Merrill and Ainsworth, ref. 18, but without the platinum plating) in 3 alert macaque monkeys (1 *Macaca mulatta*, weight 6.5 kg, and 2 *Macaca fascicularis*, weights 3.5 and 4.5 kg) seated in a primate chair using techniques that have been described previously[29]. The action potentials of single cells, amplified using techniques described previously[30], were converted into digital pulses using the trigger circuit of an oscilloscope, and were analysed on-line using a Microvax 2 computer. The computer collected peristimulus rastergrams of neuronal activity for each trial and displayed, printed and stored each trial. For each trial the number of action potentials occurring in a 500-ms period starting 100 ms after the stimulus

onset was printed. This period was chosen because the neurons studied responded to visual stimuli with latencies just greater than 100 ms, and the monkeys consistently fixated the stimuli for this period. Fixation of the stimuli was confirmed using permanently implanted silver/silver chloride electrodes for electro-oculogram (EOG) recording. The EOG recordings provided eye position with an accuracy of 1–2 degrees, and were sampled by the computer every 10 ms and saved with the action potentials for each trial. Data from trials during which the monkey was not already fixating the screen when the stimulus was switched on or during which eye movements of more than 3 degrees occurred in the first 600 ms (while the firing rate was being measured) were rejected.

X-radiographs were used to locate the position of the microelectrode on each recording track relative to permanently implanted reference electrodes and bony landmarks. The position of cells was reconstructed from the X-ray co-ordinates taken together with serial 50-μm histological sections which showed the reference electrodes and micro-lesions made at the end of some of the microelectrode tracks.

Stimulus presentation

Stimuli were stored in digital form on a computer disk, and displayed on a video monitor (Microvitec) using a video framestore (Matrox QRGB 256 or AED 512, refresh rate set to 60 Hz). The resolution of these images was 256 wide by 256 high with 256 grey levels. The monitor provided maximum and minimum luminances of 6.0 and 0.13 footlamberts respectively, and was adjusted internally for linearity to within 3% using a photometer. The computer randomized the order of presentation of these stimuli, switched the stimuli on and off for each trial, and synchronized its data collection so that the stimulus was turned on at the start of the 21st bin of the peristimulus time histogram. This method allowed completely standardized and randomized presentation of quantitatively specified visual stimuli. The monitor on which the images were displayed was placed 1 m from the monkey, and subtended 12 degrees at the retina.

The monkeys performed a visual discrimination task during the testing to ensure that they looked at the stimuli. If a circle — the positive discriminative stimulus (S+) — appeared, the monkeys could lick to obtain a fruit juice reward, and if a square of the same area and luminance — the negative discriminative stimulus (S−) — appeared, the monkey had to withhold licking in order to avoid aversive hypertonic saline. A 0.5-s signal tone (400 Hz) preceded the presentation of the stimulus, and if the monkey was fixating correctly before the stimulus appeared, he had sufficient time to perform the discrimination and obtain multiple licks of the fruit juice tube in the short (1.0-s) period in which the stimulus was on. This procedure was designed to ensure fixation of the stimuli[30]. If any other stimulus appeared (such as a grating, a 3-dimensional object, or a face) and the monkey licked, then he obtained fruit juice (i.e. all stimuli except the square were treated as S+). The order of presentation of the stimuli was randomized. The EOG recordings confirmed that this procedure resulted in consistent fixation of the stimuli.

Face stimuli

The main study (Expt. 1) involved the use of a stimulus set consisting of 3 different monkeys viewed full face with 3 different expressions each as shown in Fig. 1. The monkeys are designated FF, LL and MM. Monkeys FF and LL were rhesus (*Macaca mulatta*) and monkey MM was cynomolgus (*Macaca fascicularis*). Three main expressions were photographed for each monkey. These were a calm expression (c), a slightly open mouth threat expression (t) and a full open-mouth threat expression (T). The open-mouth threat expression is a common aggressive social signal displayed by macaques[24]. (For monkey FF, the expression shown on the right of Fig. 1 included a fear component in that the upper teeth were somewhat exposed, but the expression was not accompanied by a scream, and was associated with threatening behaviour when the photograph was taken.) The photographic negatives were digitized using a Scandig 3 (Joyce-Loebl Ltd, Gateshead, U.K.) scanning digitizer of photographs, and stored in an image file with a resolu-

tion of 256 × 256 × 8 bits, ready for presentation on the framestore. To test further consistency of identity responses, other expressions on these monkeys were also photographed. For use in separate experiments, a further set of 35 novel faces was made up. These consisted of photographs of a large range of individual cynomolgus monkeys in the animal colony. Twenty-one different individuals were photographed, and commonly two photographs of each monkey were digitized, though occasionally one or three were used. The different photographs of each indivi-

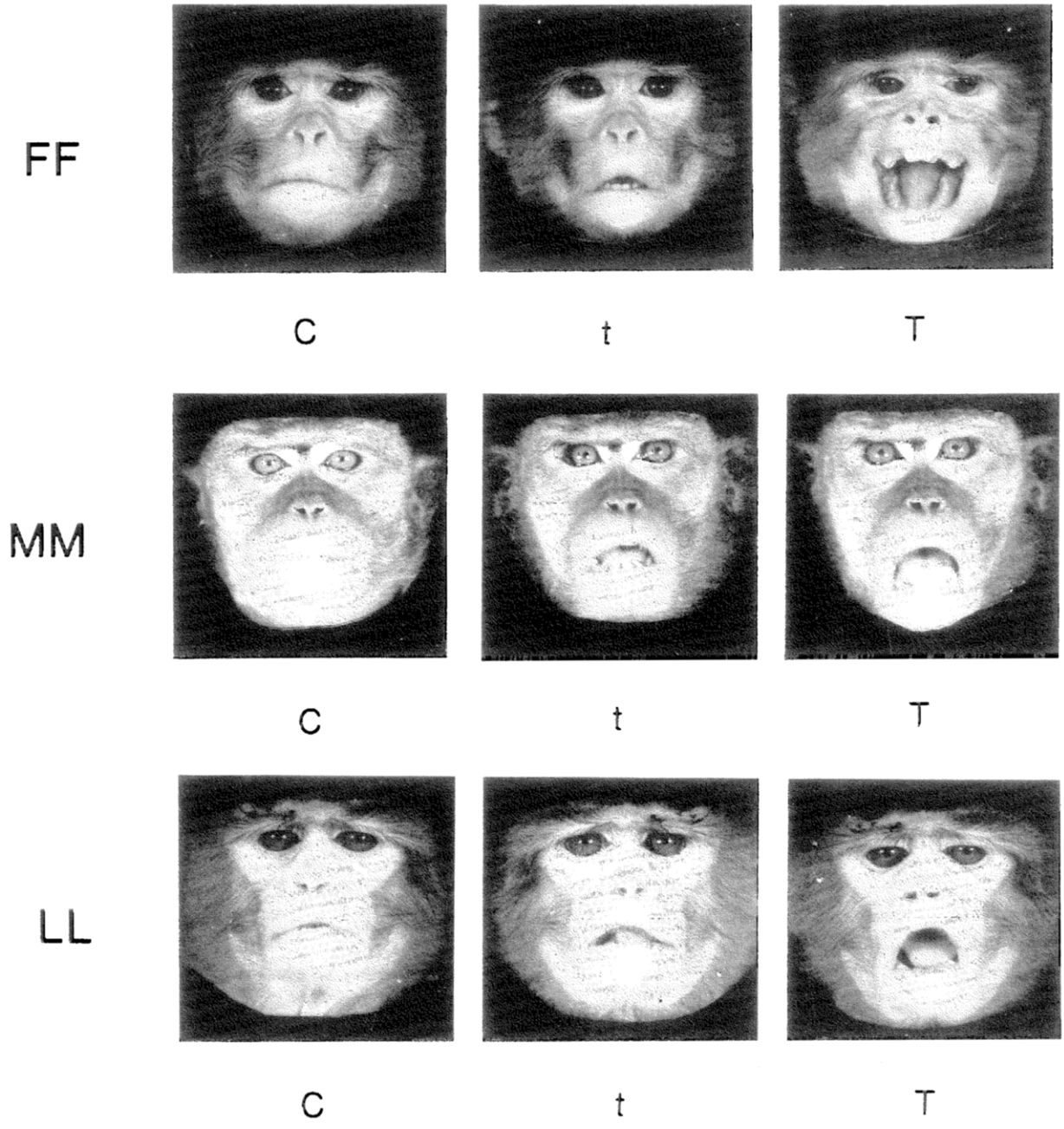


Fig. 1. The set of stimuli which included 3 expressions from each of 3 monkeys, FF, MM and LL. The expressions represented are as follows: C = closed-mouth, calm; t = mouth partly open, slight threat; T = full open-mouthed, threat face.

dual were chosen for differences in expression. These expression pairs were used to test expression sensitivity in one of the experimental monkeys in a pilot experiment and to gather data for multi-dimensional analysis of expression responses.

Non-face stimuli

The responses of the cells were tested to a wide range of non-face stimuli, including sine wave gratings, boundary curvature descriptors, complex 2-dimensional images, and 3-dimensional junk objects, as described previously[1].

Procedure

As tracks were made into the cortex in the superior temporal sulcus, the responses of each neuron were measured to a standard digitized set of stimuli of different faces and of non-face stimuli[1]. If a neuron responded to one or more of the faces, but to none of the non-face stimuli in the set, then a wide range of digitized and real 3-dimensional non-face stimuli were shown, to determine wether the response of the neuron was selective for faces. The criteria were that the response to the optimal face stimulus should be more than twice as large as to the optimal non-face stimulus, and that this difference should be significant. (In fact, the majority of the neurons in the cortex in the superior temporal sulcus classified as showing responses selective for faces responded much more specifically than this. For half these neurons, their response to the most effective face was more than 5 times as large as to the most effective non-face stimulus, and for 25% of these neurons, the ratio was greater than 10 : 1. These ratios show that while responding preferentially to faces, these neurons do not have absolute specificity for faces. The proportion of neurons which met these criteria in this study was 11.2%. Further information on and discussion of the extent to which these neurons have selective responses is given by Rolls[26,28] and by Baylis et al.[1]. The non-face stimuli from which the optimal was chosen included sine wave gratings, boundary curvature descriptors, complex 2-dimensional stimuli, and complex 3-dimensional junk objects, as described above.) If the neuron satisfied the criteria, then experiments were conducted as described below.

Treatment of results

For each cell measures of responses were calculated from the total number of action potentials occurring on each trial in the period 100–600 ms following stimulus onset. This period was chosen because the cells studied typically responded to visual stimuli with latencies just greater than 100 ms. Recordings of fixation usually confirmed that the monkeys fixated during this period of firing rate measurement, but trials with poor fixation were rejected from the analysis. The neuronal response shown in the figures is the firing rate to a given stimulus minus the mean spontaneous firing rate, to show how much the neuron altered its firing rate to a stimulus.

The spike counts measured during presentation of each expression stimulus were tested on a two-way ANOVA, with expression (C, t, T) as one dimension, and identity (FF, LL, MM) as the other dimension. For comparison of expression pairs, a one-way ANOVA was followed by post-hoc Tukey tests of individual response differences. Multi-dimensional scaling was performed by computing a correlation matrix of the responses to each stimulus, followed by the computation of a stimulus space using a software package (E. Roskam, MDSX project, MRSCAL).

RESULTS

Pilot experiment

The cells in monkey II were tested with expression pairs drawn from the large set of video images of monkeys as well as human imitations of monkey expressions presented through a shutter. Eight cells showed strong and consistent responses dependent on expression across these stimuli. Six of these cells responded better to threat than to calm expressions, while two cells responded better to calm than to threat expressions. Examples of the responses of a cell (II0826) which responded to threat expressions are shown in Figs. 2 and 3. This cell responded better to open-mouth threat and fear expressions

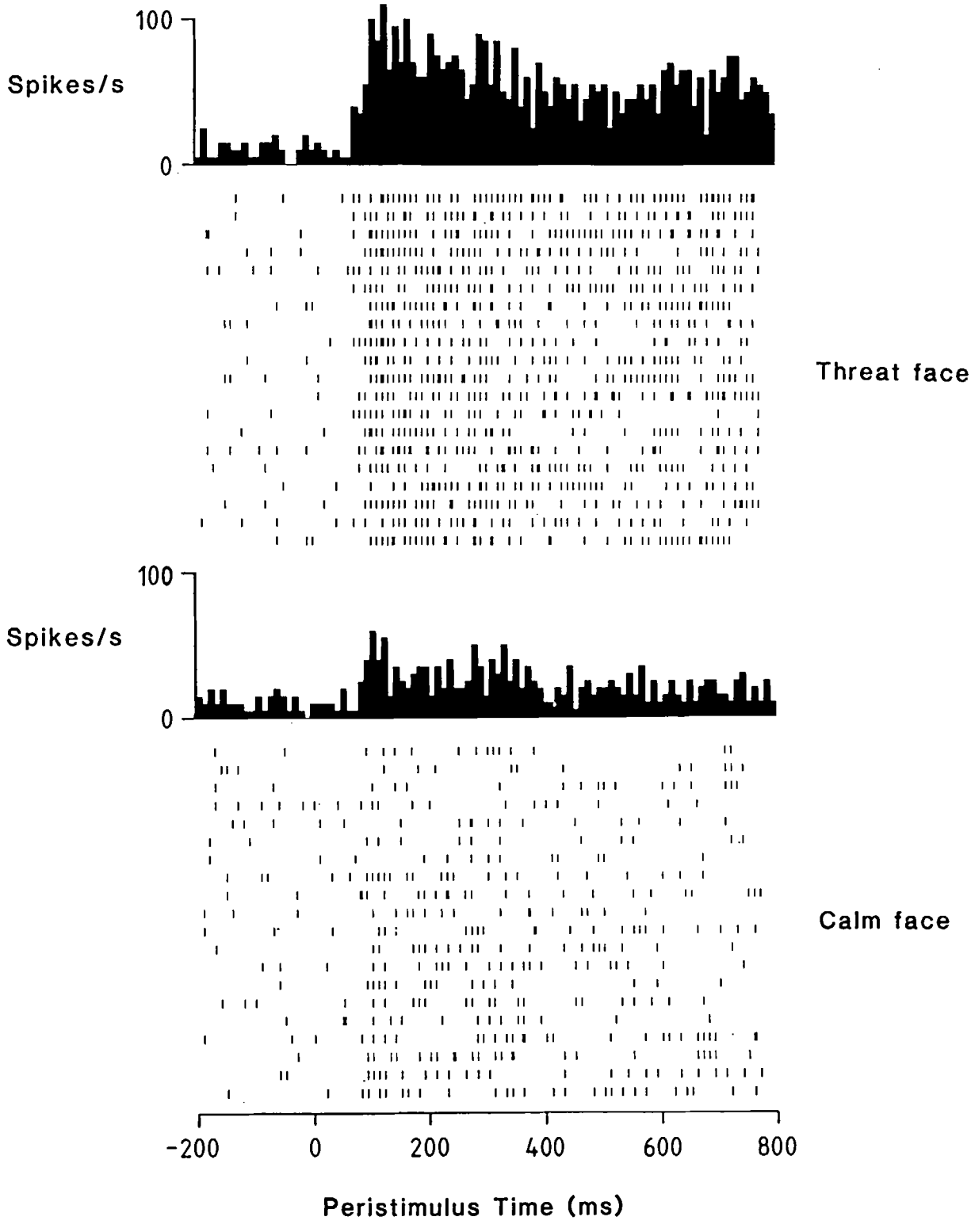


Fig. 2. Examples of the responses of one expression-selective neuron (II0826) to expression stimuli. At the top, the responses to 5 presentations of each of 4 different open-mouth threat or fear expressions are shown. At the bottom, the responses to 4 different calm expression faces are shown. The onset of the visual stimuli was at time 0. The bin width was 10 ms. The stimuli were presented on a video-monitor.

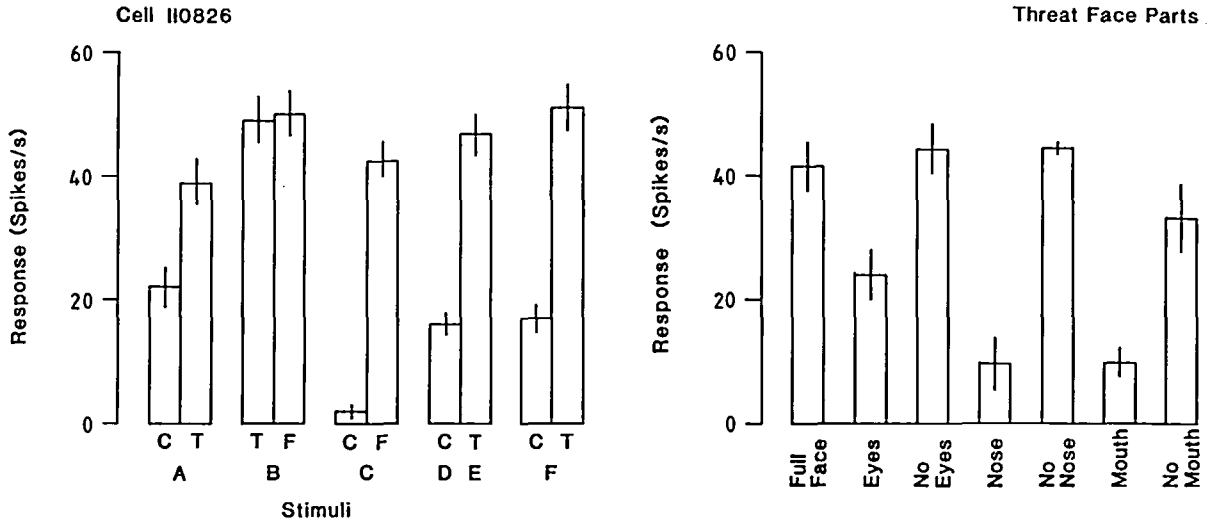


Fig. 3. Left: the mean responses of neuron II0826 (the same as in Fig. 2) to faces A–F expressed in histogram form. F = fear expression (teeth showing). Other abbreviations as in Fig. 1. Right: the responses of the same neuron to the monkey E threat face with various parts either shown separately or removed from the full face. It is shown for example that for this neuron the mouth was neither necessary nor sufficient to elicit the response of the neuron to this threat face. The means and the standard errors of the responses measured over 7–12 presentations of each stimulus in random sequence are shown in this and subsequent figures.

than calm expressions on a variety of monkey faces presented on the video monitor. The rastergrams and peristimulus time histograms of the responses to 4 different faces with calm expressions and 4 faces with open-mouth expressions are shown in Fig. 2. The mean responses in spikes per second to these stimuli are shown in histogram form in Fig. 3. The response was not just due to the configuration of the mouth, since the mouth presented in isolation was not sufficient to elicit a response, as shown on the right of Fig. 3. The response was also elicited by a threat face with the mouth obscured.

Experiment 1

A total of 25 face-selective neurons from monkey NN and 20 neurons from monkey QQ were tested on the set of face stimuli shown in Fig. 1. Of these cells, 6 showed a consistently greater response to calm faces than to threat faces, and two showed a greater response to threat than to calm faces. The responses of an example of the first group are illustrated in Fig. 4a. This cell (NN0811) showed a stronger response to calm (C) or slight threat (t) expressions as compared to strong threat (T) expressions, and showed a similarity of response to yawn (Y) expressions for the two images tested. The responses of a cell (NN0826) showing a stronger response to threat expressions are illustrated in Fig. 4b. The response of this cell was considerably stronger to full open-mouth threat (T) expressions than to other expressions.

The responses of a neuron (NN0479) showing a consistent response dependent on identity are illustrated in Fig. 4c. The firing of this neuron was consistently higher to monkeys MM and LL than to monkey FF, regardless of expression. The responses of another cell (QQ0650) showing consistent response differences based on identity are shown in Fig. 4d. This cell showed little increase in response over baseline to face LL, with similar responses to FF and MM.

A two-way ANOVA was performed on the responses of each neuron to the 3 monkey faces for the 3 systematically varied expressions: calm (C), slight threat (t) and open-mouth threat (T). These ANOVAs gave an indication of how much variance was due to expression, how much to identity, and how much to an interaction of the two factors for each face. The results of these ANOVAs are shown in Table I.

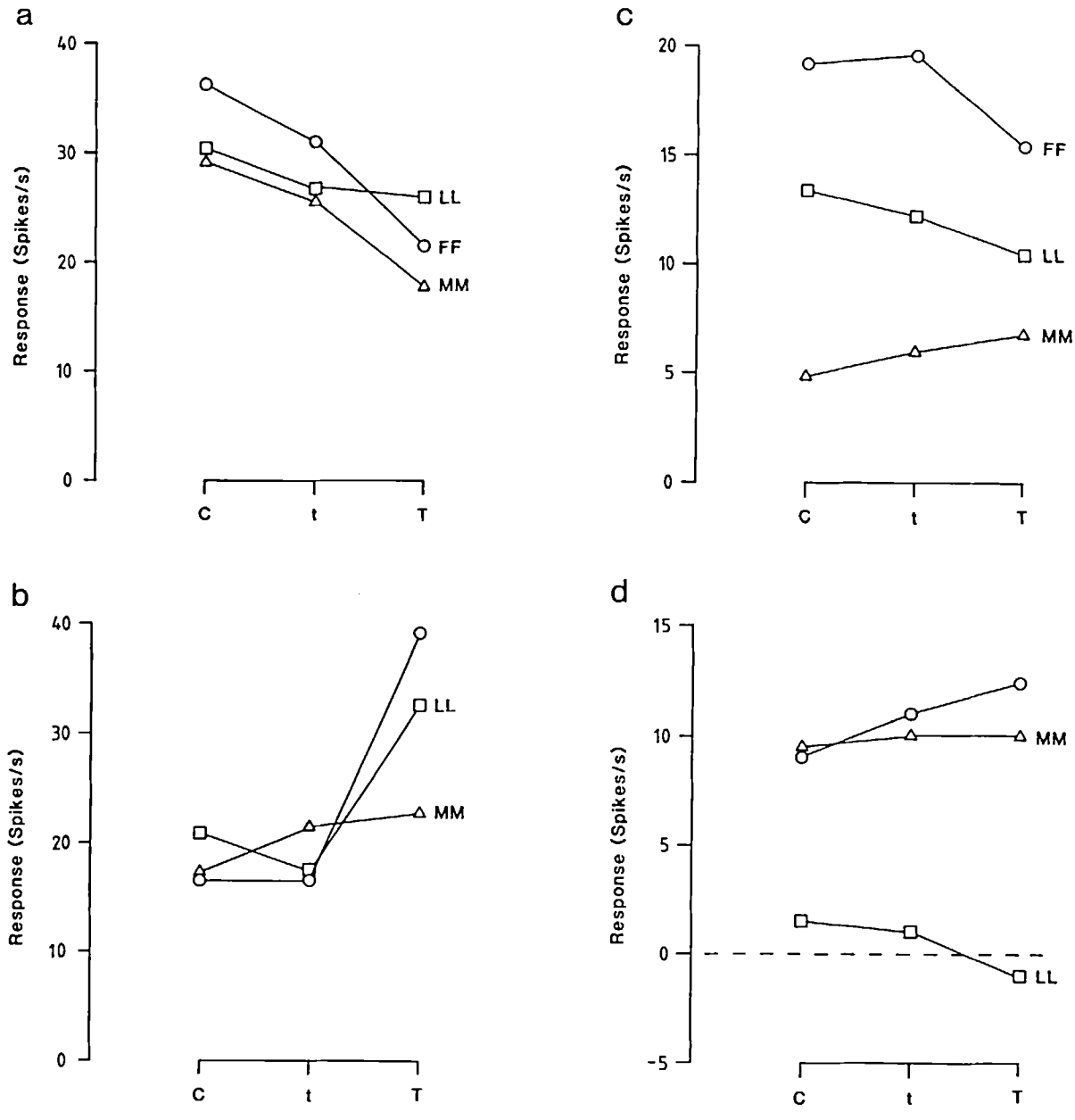


Fig. 4. The responses of 4 single cells to the set of 3 monkey faces (FF, MM, and LL), each with 3 expressions (C = calm; t = slight threat; T = threat). The neuronal response is shown in spikes per second. a: cell NN0811. The neuronal response was relatively consistent to the same expression on different faces, with partial or fully closed-mouth faces eliciting a consistently higher response than open-mouthed threat faces. b: cell NN0826. This cell responded better to full threat (T) than to other expressions. c: cell NN0479. This cell responded differently to different identities independently of expression. d: cell QQ0653. This cell responded to stimuli showing monkey FF or MM, but not to stimuli showing monkey LL.

Of the 45 neurons tested, 9 (20%) showed significant differences of response to expression independently of identity, and 15 (33.3%) showed significant differences of response to identity independently of expression (see Table I). There was little overlap between those showing significant effects of expression and those with significant effects of identity: only 3 neurons (6.7%) showed both effects. Only one neuron with a significant expression effect showed an inter-

TABLE I

Results of the two-way ANOVA performed for each neuron to analyse its responses to the 3 different faces (identity factor) each with 3 different expressions (expression factor)

The significant effects are in italics. Results from monkeys NN and QQ are shown. df = degrees of freedom; F = variance ratio; P = probability.

Cell	*df*	*Expression*		*Identity*		*Interaction*	
		F	*P*	*F*	*P*	*F*	*P*
NN							
0331	35	5.27	*0.016*	0.39	0.68	1.56	0.22
0333	44	1.26	0.30	1.36	0.29	1.57	0.21
0344	35	0.32	0.72	5.28	*0.030*	1.24	0.38
0347	44	0.22	0.80	3.82	0.051	0.42	0.72
0374	44	0.55	0.58	34.93	*0.00005*	1.14	0.36
0423	35	7.14	*0.005*	0.16	0.85	0.51	0.72
0426	44	0.81	0.53	10.96	*0.002*	1.20	0.33
0444	35	0.64	0.54	0.03	*0.97*	0.45	0.77
0443	35	0.36	0.70	4.98	*0.034*	1.09	0.39
0479	35	1.41	0.26	66.19	*0.00004*	1.33	0.29
0515	44	0.84	0.55	4.75	*0.029*	2.87	0.044
0658	35	4.33	*0.029*	1.81	0.27	1.42	0.28
0768	35	0.06	0.94	7.62	*0.012*	0.89	0.59
0783	35	9.66	*0.002*	0.4	0.82	2.23	0.16
0786	53	0.06	0.94	3.80	*0.045*	0.84	0.51
0802	44	9.82	*0.001*	1.58	0.24	1.48	0.23
0807	35	0.13	0.87	2.27	0.15	1.09	0.39
0811	62	11.68	*0.0002*	0.67	0.52	3.97	*0.009*
0817	35	3.62	*0.047*	0.11	0.89	2.19	0.11
0826	44	4.69	*0.019*	2.40	0.13	0.55	0.70
0839	44	0.74	0.50	0.07	0.93	0.45	0.77
0857	35	2.23	0.13	0.06	0.94	4.53	*0.011*
0870	35	2.64	0.097	1.37	0.30	1.29	0.31
0893	35	0.91	0.57	0.54	0.60	1.15	0.36
0925	44	2.86	0.075	8.10	*0.006*	3.64	*0.019*
QQ							
0108	65	1.61	0.21	7.59	*0.004*	0.25	0.91
0216	53	3.73	*0.036*	18.66	*0.0002*	3.39	*0.025*
0247	53	1.67	0.21	4.78	*0.025*	1.36	0.44
0346	53	2.60	0.088	10.31	*0.0018*	0.93	0.53
0391	35	0.02	0.98	1.00	0.41	1.36	0.29
0624	35	0.44	0.65	6.59	*0.017*	1.33	0.29
0637	26	0.83	0.22	0.03	0.97	1.96	0.16
0650	35	0.13	0.88	10.44	*0.0048*	0.28	0.89
0653	26	0.10	0.90	3.05	0.12	0.43	0.79
0661	35	0.03	0.97	3.06	0.096	1.86	0.16
0685	44	2.22	0.13	2.33	0.14	1.08	0.39
0694	35	0.81	0.54	0.24	0.79	0.67	0.62
0723	53	0.30	0.75	0.54	0.59	0.25	0.91
0725	44	0.28	0.76	0.35	0.73	0.88	0.51
0736	35	0.66	0.53	9.79	*0.003*	0.74	0.58
0738	35	6.18	*0.0093*	8.34	*0.0092*	6.22	*0.0028*
0747	38	7.34	*0.004*	7.39	*0.011*	1.90	0.15
0828	44	3.54	*0.044*	2.82	0.098	2.60	0.060
0862	44	0.08	0.92	2.82	0.098	1.19	0.34
0962	53	0.03	0.97	1.18	0.33	3.53	*0.018*

action, while two neurons with a significant identity effect showed an interaction. Two of the 3 neurons significant on both factors showed an interaction, and two neurons showed an interaction effect without any other significant effect. (In only one case was there any indication that these interactions were due to the fact that the T face of monkey FF included a fear component.) All cells significant for identity on the two-way ANOVA were tested on a further one-way ANOVA pooling responses to the full range of expressions for each face. Most cells ($^{11}/_{15}$) showed consistent response differences to identity across all expressions as indicated. When cells showed any overlap it was the yawn expression which was inconsistent. This may be due to the great distortion of facial features produced by the yawn. It may also be noted that it was the identity of individual monkeys, rather than their species, which accounted for the differences between the responses of these neurons to the faces of different monkeys (see for example Fig. 4d).

The relative independence of expression and identity is suggested by Fig. 5. This figure shows the *F*-values from the two-way ANOVAs for identity graphed against the *F*-values for expression. Data from monkeys NN and QQ are combined here. The data points tended to lie close to one of the axes, indicating that high *F*-values on one factor tended to be associated with low *F*-values on the other. The different symbols in Fig. 5 represent cells recorded in different areas. Cells marked with open circles were recorded in the inferior temporal gyrus, while cells marked with filled circles were recorded in the cortex in the superior temporal sulcus. Half-filled circles represent cells recorded in area TEm on the border of the superior temporal sulcus and inferior temporal gyrus. Cells recorded in area TE tended to cluster along the identity axis, while cells recorded within the cortex in the superior temporal sulcus tended to cluster along the expression *F*-value axis. Cells recorded in area TEm on the lip of the sulcus were most likely to show effects of both identity and expression. This distribution reflects the anatomical distribution of cells responsive to expression and identity.

The anatomical distribution of the cells is

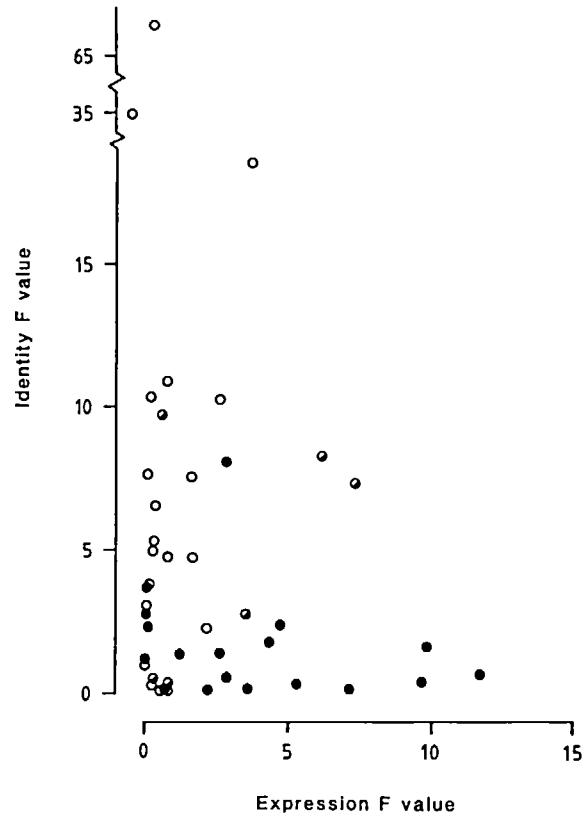


Fig. 5. Graph of *F*-values for identity factor versus *F*-values for expression factor from the two-way ANOVAs performed on the responses of each neuron to the faces of 3 different monkeys each with 3 different expressions. Each point indicates the values of *F* for the two factors for one neuron. Filled circles, neurons recorded from the cortex in the superior temporal sulcus; open circles, neurons recorded from the cortex on the inferior temporal gyrus; half-filled circles, neurons recorded from the cytoarchitectonic area TEm on the ventral lip of the superior temporal sulcus.

shown in Fig. 6. The locations of the cells recorded in monkeys QQ and NN in relation to the structure of the superior temporal sulcus and inferior temporal gyrus are represented schematically. Different symbols indicate the results of the two-way ANOVA. Open circles represent cells which showed a significant effect of expression in the test, and filled circles represent cells showing a significant effect of identity. Half-filled circles showed a significant effect of both expression and identity, while open squares represent cells showing only an interaction of the two factors. Cells without any significant effect on the test are marked with small triangles. Cells responsive to

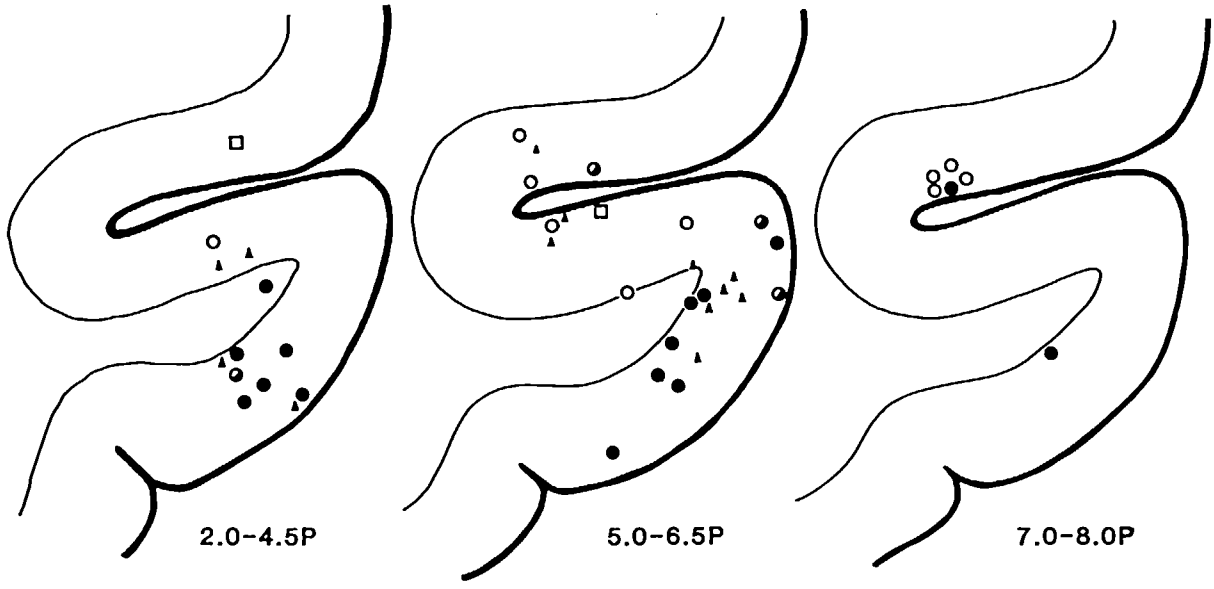


Fig. 6. The locations of cells recorded in monkeys QQ and NN shown on coronal sections. The large sulcus is the superior temporal sulcus. The numbers represent the distances posterior to the sphenoid reference within which the cells were found (see ref. 2). Open circles, neurons with significant responses to expression; filled circles, neurons responding on the basis of identity; half-filled circles, neurons responding to both expression and identity; squares, neurons showing an interaction of the two factors only; triangles, neurons showing no significant differential response to the variations in expression and identity contained in the stimulus set. Cells responsive to expression were located mainly in the upper and lower banks of the superior temporal sulcus, and with cells responsive to identity were located mainly in the inferior temporal cortex.

expression were found primarily in the cortex in the sulcus, while cells responsive to identity were found primarily in area TE.

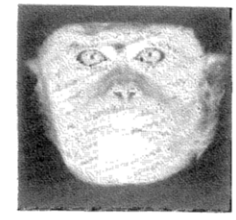
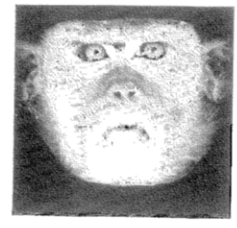
The strongest evidence for this difference in distribution of cells selective for expression and identity was found in monkey NN. In this monkey, face-responsive neurons were recorded in relatively even proportions between the two areas. Seven cells significant for identity on the two-way ANOVA were found in the inferior temporal cortex and two cells in the cortex in the superior temporal sulcus, while all 9 of the cells significant on the expression factor of the two-way ANOVA were found in the cortex in the superior temporal sulcus. A χ^2-test was performed on these data, showing a highly significant difference of distribution from chance ($\chi^2 = 14.96$, df = 1, $P < 0.001$), although we note that because cells in this region are frequently clumped together, a much larger sample of neurons might be required to be sure that there is across the whole population significant segregation between cytoarchitectonic areas of these different types of neuron.

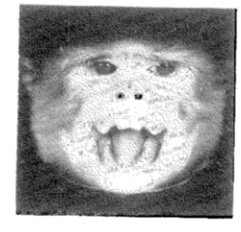
Cells in monkey QQ were recorded primarily in the cortex forming the inferior temporal gyrus, and the predominance of identity responses among these cells may be related to this sampling of area TE. Conversely, cells in monkey II were recorded primarily in the cortex in the superior temporal sulcus. The cells showing strong specificity for particular expressions were clustered in close proximity on the lower bank of the sulcus (as shown in Fig. 6).

The data from the neuronal responses to the stimulus set with 3 expressions of each of 3 different faces were used to compute a multidimensional space as shown in Fig. 7. The capability of separate subpopulations of neurons to discriminate different factors is represented here. Data from the 18 cells showing responses significant for identity were used to compute the stimulus space shown in Fig. 7A. It was found that this population of neurons effectively divides the stimulus space into 3 groups corresponding to different identities. Data from the 12 cells showing significant responses to expression were used to

A





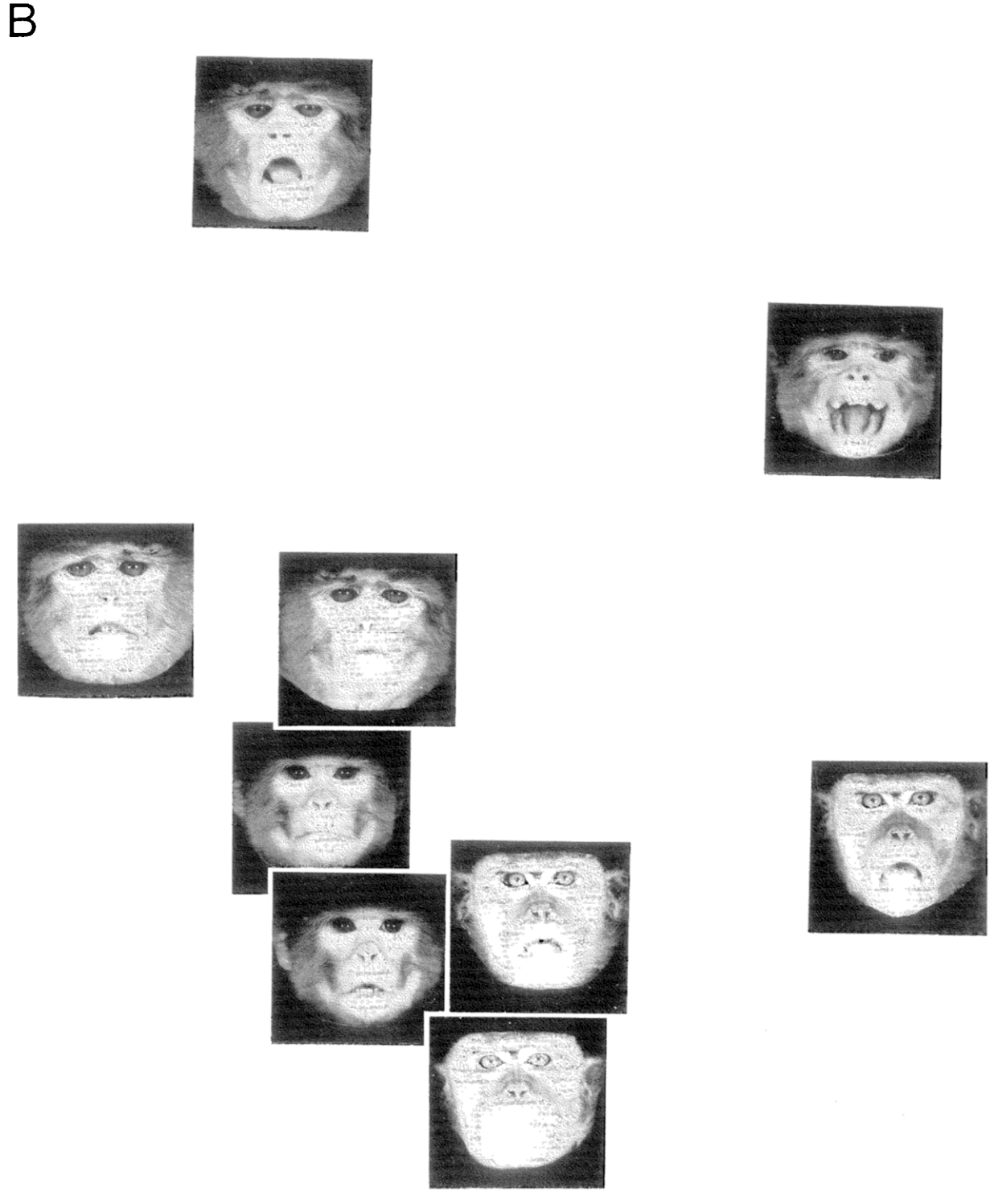


Fig. 7. Stimulus spaces based on the responses to 3 faces each with 3 different expressions for the cells tested in monkeys QQ and NN. A: the stimulus space computed with the data from 18 neurons whose responses were significantly related to identity. B: the stimulus space computed with data from 12 neurons whose responses were significantly related to the expression factor.

compute the stimulus space shown in Fig. 7B. This subpopulation of neurons effectively separated the strong threat expressions (placed away from the lower left of the space shown in Fig. 7B) from the other expressions (placed towards the lower left of the space). These other less discriminable calm and slight threat expressions are mixed together, with faces of different identity clustered in close proximity.

DISCUSSION

The results of these experiments show quantitatively that in the monkey the responses of one population of neurons reflect facial identity independently of expression, and the responses of a separate population reflect facial expression independently of identity. Cells responsive to identity were found primarily in the cortex forming the inferior temporal gyrus (area TE), while cells responsive to expression were found primarily in the cortex in the superior temporal sulcus.

Fifteen of the 45 neurons (33.3%) whose responses to 3 different monkeys with 3 expressions each were analysed by an ANOVA showed significant effects due to identity, as summarized in Table I. The individual neuronal responses are illustrated in Fig. 4. Out of a total of 45 face-selective neurons analysed, 9 (20%) showed effects of expression without any significant effect due to identity. Strong responses to particular expressions were found in some cells, such as the cell in Fig. 4a which responded strongly to calm, closed-mouth monkeys, or the cells illustrated in Figs. 4b and 3 which had strong responses to threat and open mouth expressions. There was little overlap between the groups, with only 3 out of 45 neurons (6.7%) showing significant effects of both expression and identity. The plot of identity *F*-values against expression *F*-values in Fig. 4 shows clustering of data points along the axes, indicating that high sensitivity to one factor tended to be associated with low sensitivity to the other factor (i.e. that when one factor accounted for a large amount of the variance, the other factor tended to account for a small amount of the variance). The fact that fewer cells were found which encoded expression independently of identity than vice versa may reflect the fact that many different identities must be stored, and also that identity is frequently important in reacting to particular expressions. For example, a threat expression may elicit fear in a subordinate monkey, but aggression in a monkey higher in the group hierarchy.

The investigation described here shows that the different neuronal responses produced by different faces reported previously[1] can be ascribed to specific factors such as for some neurons the expression and for other neurons the identity of a face. This work provides a systematic study of the independent effects of such factors which was suggested by findings of individual cells with strong specificity for faces of particular expression or identity[21]. It will be of interest in future to examine quantitatively all the ways in which different facial features contribute to the expression-related responses of the neurons described here.

We were able to extend previous studies by analysing how specifically the neurons in our present sample, which had been shown in the ANOVA to reflect the identity (and not the expression) of the face shown, responded to one only of the faces, or in contrast responded to more than one face, but with differential responses to the different faces. To do this we took the subset of 15 neurons which reflected the identity of the face (see Table I), and measured the breadth of tuning of these neurons. To assess this we used, as in our earlier study[1], the breadth of tuning metric developed by Smith and Travers[33] from information theory. This is a coefficient of entropy (H) for each cell which ranges from 0.0, representing total specificity to one stimulus, to 1.0 which indicates an equal response to the different stimuli*. The breadth of tuning calculated over the 5 face stimuli in the standard set of faces (see Baylis et al.[1]) had a mean value of 0.89 for the

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* $H = -k \sum_{i=1}^{n} p_i \log p_i$ where H = breadth of responsiveness, k = scaling constant (set so that H = 1.0 when the neuron responds equally well to all stimuli in the set of size *n*), p_i = the response to stimulus i expressed as a proportion of the total response to all the stimuli in the set.

population of 13 neurons (range 0.71–0.99). Thus even the neurons which reflected the identity of the faces shown were not tuned so finely that they responded to only one of the faces in the stimulus set. This is also shown by the number of faces in the digitized set to which the neuron had a response greater than half that to the most effective face stimulus in the set. This is named the generalization index (see Baylis et al.[1]). The mean generalization index was 0.62 (range 0.20–1.00). Given that each of the neurons responded differently to the different members of the set of stimuli, there is sufficient information across an ensemble of such neurons, but not in the response of a single neuron, to identify a particular face. The point here is that these neurons do respond differently to different faces[1], and are thus not responding just for example to the presence of eyes, yet their responses reflect information about identity using ensemble and not grandmother cell encoding. The advantages of this type of encoding of information in neuronal networks are discussed by Rolls[27]. It may be noted that there are at present no quantitative measures of the breadth of tuning of neurons available to support the grandmother cell method of encoding information in these populations of neurons (Perrett et al.[23a]).

As shown in Figs. 5 and 6, cells responsive to expression and identity may appear in different cortical regions, with identity represented by cells primarily in the inferior temporal cortex, and expression represented primarily by cells in the cortex in the superior temporal sulcus. Impairment of the function of cells responsive to identity in the inferior temporal cortex may explain the deficits of face discrimination found with cooling of the anterior temporal lobe cortex[14]. The location of expression-sensitive cells in the cortex in the superior temporal sulcus places them near cells sensitive to direction of gaze[23], which may contribute to the encoding of important social signals. For example, lesions of the cortex in the superior temporal sulcus impair the discrimination of gaze direction in faces at different angles without impairing face discrimination learning (A. Cowey and C. Heywood, personal communication). Their location in the cortex in the superior temporal sulcus also places expression-responsive cells close to cells which respond to moving visual stimuli[2,6,22]. This may reflect the importance of the dynamic aspects of face expression. The necessity for rapid orientation to particular expressions may explain the location of expression-sensitive cells in an area where connections of the dorsal and ventral visual pathways converge.

The multi-dimensional scaling techniques showed that populations of neurons distribute the set of stimuli in an information space according to interpretable factors of expression and identity. The different cell populations from monkeys QQ and NN separated the stimuli along the expected dimensions of expression or identity (Figs. 7a and 7b). Multi-dimensional scaling techniques thus appear to be useful for the analysis of population encoding of complex stimuli.

The results described here support the hypothesis that the deficits in social behaviour found after anterior temporal lobe lesions in monkeys[8,12,14] are due to an impairment of the ability to perceive factors such as the identity of a face and its expression[16,25,26,28]. Moreover, the results described here, that there are separate neurons which code for the expression and identity of faces, and that these are at least partly separated into different locations in the temporal lobe cortex, are supported by the evidence from cognitive psychology that the mechanisms in man for matching face identity and expression are different, in that they are differently affected by whether the faces are familiar[35,36], and by the neurological evidence that there can be dissociable deficits in face recognition and in decoding the expression on a face[9,12].

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