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Selectivity between Faces in the Responses of a Population of Neurons in the Cortex in the Superior Temporal Sulcus of the Monkey

G. C. BAYLIS, E. T. ROLLS AND C. M. LEONARD*

University of Oxford, Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD (U.K.)

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There is a population of neurons in the cortex in the middle and anterior part of the superior temporal sulcus (STS) of the monkey with responses which are selective for faces. If, consistent with the effects of damage to the temporal lobe, these neurons are involved in face recognition or in making appropriate social responses to different individuals, then it might be expected that at least some of these neurons might respond differently to different faces. To investigate whether at least some of these neurons do respond differently to different faces, their responses were measured to a standard set of faces, presented in random sequence using a video framestore. It was found that a considerable proportion of the neurons with face-selective responses tested (34/44 or 77%) responded differently to different faces, as shown by analyses of variance. An index of the discriminability of the most and least effective face stimulus (d') ranged between 0.2 and 5.0 for the different neurons. Although these neurons often responded differently to different faces, they did not usually respond to only one of the faces in the set, so that information that a particular face had been shown was present across an ensemble of neurons, rather than in the responses of an individual neuron. These findings indicate that the responses of these neurons would be useful in providing information on which different behavioral responses made to different faces could be based. These neurons could thus be filters, the output of which could be used for recognition of different individuals and in emotional responses made to different individuals.

INTRODUCTION

A small proportion of the neurons in the temporal lobe visual cortex which respond to visual stimuli have responses which occur primarily to faces[6,17,23]. We have described one such population (48 of 497 cells recorded) in the cortex in the superior temporal sulcus (STS)[23]. The responses of these neurons to faces (real or projected, human or rhesus monkey) were selective in that they were 2–10 times as large to faces as to gratings, simple geometrical stimuli or complex three-dimensional (3-D) objects. The responses to faces were excitatory, sustained and were time-locked to the stimulus presentation with a latency of between 80 and 160 ms. The cells were unresponsive to auditory or tactile stimuli and to the sight of arousing or aversive stimuli. The magnitude of the responses of the cells was relatively constant despite isomorphic transformations such as rotation so that the face was inverted or horizontal, and alterations of color, size or distance. Rotation to profile substantially reduced the responses of 21 cells. Masking out or presenting parts of the face (i.e. eyes, mouth or hair) in isolation revealed that different cells responded to different features or subsets of features. For several cells, responses to the normal organization of cut-out or line-drawn facial features were significantly larger than to jumbled controls. These findings indicated that explanations in terms of arousal, emotional or motor reactions, simple visual feature sensitivity or receptive fields are insufficient to account for the selective responses to faces and face features observed in this population of STS neurons. It was suggested that these neurons are part of a system specialized to code for faces or features present in faces[23,25,26]. Similar findings have recently

* On leave from the Department of Neuroscience, University of Florida College of Medicine, Gainesville, FL, U.S.A.
Correspondence: E. T. Rolls, Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD U.K.

been reported by Desimone et al.[12]. It is possible[25–27,32] that damage to this system is related to prosopagnosia, or difficulty in face recognition, in man[5,10,21,36] and to the tameness and social disturbances which follow temporal lobe damage and are part of the Kluver–Bucy syndrome in the monkey[1,18–20].

If these neurons are involved in face recognition[31], or in making appropriate social responses to different individuals[14], then it might be expected that at least some of these neurons might respond differently to different faces. [In our previous study[23], the responses of the neurons were measured to only a few faces, but to a wide range of non-face stimuli, as one aim of that study was to investigate the extent to which these neurons responded differently to face as compared to non-face stimuli (see ref. 23)]. It was the aim of the study described here to test whether at least some of these neurons do respond differently to different faces. To investigate this, the responses of different neurons in this region to a standard set of faces were measured. In order to provide a completely standardized method of presenting the set of images repeatedly in a random sequence and to allow, in addition, quantitative manipulations of the images, the faces, together with a large range of non-face images, were digitized, stored on a computer disk and loaded in random sequence into a video framestore ready for presentation on a video monitor on each trial. This method of stimulus presentation also allowed the responses of the neurons to be measured to sine wave gratings and to boundary curvature descriptors[33], in order to provide evidence on whether these neurons could be activated by such stimuli varied systematically over a wide range of parameters.

MATERIALS AND METHODS

Recording techniques

The activity of single neurons was recorded with glass-insulated tungsten microelectrodes (after Merrill and Ainsworth[23], but without the platinum plating) in 3 alert macaque monkeys (*Macaca mulatta*) (weight 3.0–6.5 kg) seated in a primate chair using techniques that have been described previously[28]. The action potentials of single cells were amplified using techniques described previously[29], were converted into digital pulses using the trigger circuit of an oscilloscope and were analyzed on-line using a PDP11 computer. The computer collected peristimulus rastergrams of neuronal activity for each trial and displayed, printed and stored each trial, as well as computing the peristimulus time histogram by summing trials of a given type. To facilitate latency measurements, the cumulative sum distribution was calculated from the sum peristimulus time histogram. For each trial the number of action potentials occurring in a 500-ms period (and a 250-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 which were typically 100 ms or more, and the monkeys consistently fixated the stimuli for this period. Fixation of the stimuli was confirmed using permanently implanted silver–silver chloride electrodes for electrooculogram (EOG) recording. The EOG recordings provided eye position with an accuracy of 1–2°, and were sampled by the computer every 10 ms and saved with the action potentials for each trial.

X-radiographs were used to locate the position of the microelectrode on each recording track relative to permanently implanted reference electrodes and bony landmarks such as the posterior tip of the sphenoid bone[2]. The position of cells was reconstructed from the X-ray coordinates taken together with serial 50-μm histological sections which showed the reference electrodes and microlesions made at the end of some of the microelectrode tracks.

The monkey's behavioral reactions to the sight of the visual stimuli were monitored through a small hole in the side of the chair.

Stimulus presentation

The visual stimuli were presented in one of two ways. First, stimuli were digitized, stored on computer disk and displayed on a video monitor using a video framestore. The resolution of these images was 256 pixels wide by 256 pixels high with 256 gray levels. 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 stimuli as diverse as sine wave gratings and faces, and allowed

image processing techniques such as spatial frequency filtering and subregion extraction to be applied to the stimuli presented. Second, the stimuli were presented by the opening of a fast rise time (less than 15 ms), large aperture shutter (Compur Electronic 5FM, 6.4 cm aperture) which opened for 1.5 s after a 0.5-s signal tone (400 Hz) provided to allow the monkey to fixate before the shutter opened. The stimuli were presented against a uniform background (a large white screen). This method allowed the presentation of 3-D stimuli such as real faces and 3-D objects which differed along a wide range of parameter such as size, shape and color, and also allowed 2-D stimuli such as photographs of a wide range of faces to be presented.

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 (1.5-s) period in which the stimulus was on. This procedure was designed to ensure fixation of the stimuli[29]. If any other stimulus appeared (such as a grating, a 3-D object or a face), then if the monkey licked 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.

When digitized visual stimuli were being presented on the video monitor, one set of 5–20 visual stimuli were used at a time. Each set of stimuli was designed to provide neuronal response data relevant to one or several hypotheses. For example, one set included 5 different faces, to test whether the neuron responded differently to different faces, and some non-face stimuli such as a sine wave grating, a boundary curvature descriptor (see below) and a complex visual image (see Fig. 1), to provide an indication of whether the neuron responded differently to face and to non-face stimuli. Another set consisted of sine wave gratings with different spatial frequencies and another of boundary curvature descriptors (see below). The computer randomized the sequence in which the members of the set were presented, and after it had presented the sequence once, it restarted the set with another random sequence. The computer was allowed to repeat the set 4–10 times in order to provide sufficient data for an analysis of variance in order to determine whether the neuron responded differently to the different stimuli within the set. After data had been collected on one set, the experimenter then started a different set. Within each set, S− trials appeared with a probability which was usually specified as 0.25 but could be reduced.

Visual stimuli

Non-face stimuli

The responses of the cells were tested to a wide range of non-face stimuli, as follows.

Sine-wave gratings. A set of sine wave gratings with spatial frequencies of 1–64 cycles/image and with orientations spaced $\pi/4$ rad apart was presented on the video monitor in random sequence. Each image subtended 12° at the retina.

Boundary curvature descriptors. A set of boundary curvature descriptors with frequencies of 0–15 cycles, with amplitudes which ranged from 0.5 to 2.0 and with 4 different phases was presented[33].

Three-dimensional objects. Over 1000 3-D junk objects were collected, and 6–30 of these, chosen randomly, were used to test whether there was any indication that a neuron responded to a complex non-face stimulus. If there was any indication of a response, much more extensive testing with non-face stimuli was performed. The objects were chosen to differ from one another in size, shape, color, surface pattern and texture, but for convenience of storage the objects were less than 20 cm long. Since these junk objects varied along different visual dimensions, testing neuronal responses to several of them could potentially reveal selectivity for particular visual characteristics. Objects were held either by long forceps or by hand between 2 cm and 1 m behind the shutter, or they were placed on the surface of a matt black board tilted towards the monkey.

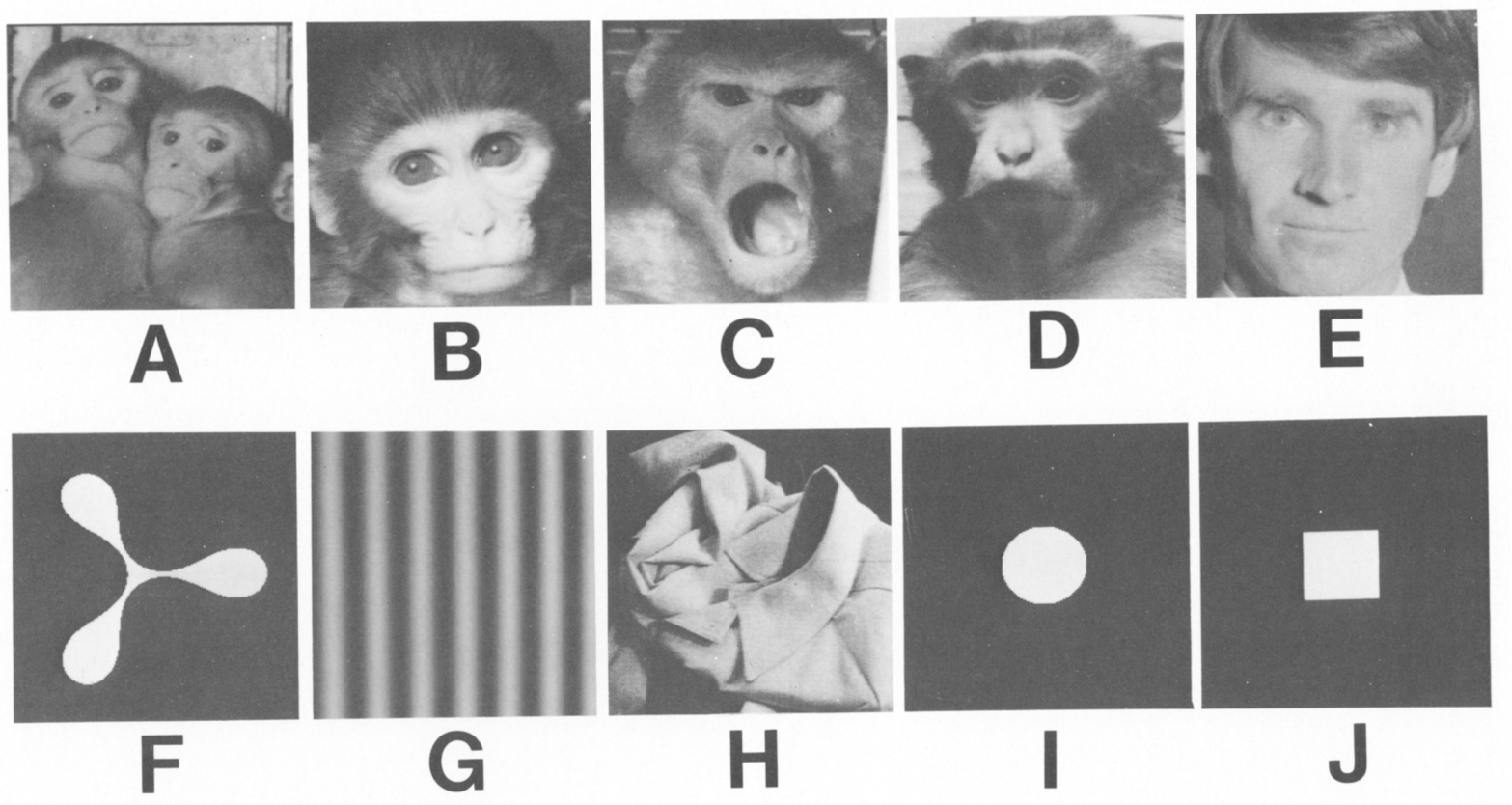

Fig. 1. The screening set of video images. A, two infants; B, juvenile; C, 5-year-old threat face; D, 10-year-old stare; E, human experimenter; F, grating; G, boundary descriptor; H, complex non-face image; I, circle (S+); J, square (S−).

Face stimuli

Photographs were prepared of macaque monkey faces (looking directly at the camera) and of human faces. The photographic negatives were digitized using a Scandig 3 (Joyce-Loebl, Gateshead, U.K.) scanning digitizer and stored in an image file with a resolution of 256 × 256 × 8 bits, ready for presentation on the Matrox (Quebec, Canada) QRGB 256 framestore. To determine whether a neuron responded differently to different faces, its responses were measured and compared to a standard subset of the digitized images of faces. The faces in this set are included in Fig. 1. In addition, a set of real faces and photographs of faces could be shown with the shutter method of presentation.

Arousing and aversive stimuli

Responses to a variety of arousing and aversive stimuli were tested to determine whether general arousal could account for the neuronal responses which occurred to faces.

Arousing auditory and tactile stimuli

To elicit general arousal (as indicated by the monkeys' behavioral responses such as movement), auditory and tactile stimuli were used. Auditory stimuli included various loud noises and human voices made out of sight of the monkey. (Screens limited the field of view of the monkey to the shutter through which visual stimuli were presented or to the video monitor.) The monkey's legs were touched out of sight to test the effects of tactile stimulation, which produced arousal.

Visually aversive stimuli

Stimuli that the monkey found aversive (as shown by the monkeys' behavioral responses such as open mouth threat) included an air puffer, a large brush and objects looming towards the monkey.

Other potentially arousing or interesting visual stimuli included food and reward-related stimuli (used in a visual discrimination task), stimuli that might be taken by the monkey to mean 'human' (e.g. hands or lab coats), and model animals (such as a large snake, a spider with dangling legs and a centipede).

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.

Analyses of variance were then performed on the responses of each cell to the different stimuli. If a significant difference between the responses to the different stimuli was indicated, then subsequent multiple t, Tukey and Newman–Keuls' analyses (see ref. 7) were performed to determine how the different stimuli differed in their efficacy. One analysis of variance was performed over the responses to a wide range of non-face and face stimuli, to determine whether a neuron responded differently to the face as compared to the non-face stimuli. Other analyses of variance were performed to analyze the differences of response to stimuli within one group, such as different faces. In the figures, the mean firing rate and its standard error to each stimulus based on typically 4–10 presentations of the stimulus are shown. The results of the analysis of variance are also usually indicated.

RESULTS

Examples of the responses of different neurons (a–d) to the different faces (A–E) and non-face stimuli (F–J) in the standard set of digitized images are shown in Fig. 2. Their responses to a range of 3-D objects, and to food, are also shown, on the left. All responses are shown as changes in firing rate in spikes/s from the spontaneous firing rate (with the standard error calculated over 4–10 observations indicated). First, Fig. 2 illustrates that the responses of the neurons classified here as having responses selective for faces showed responses to one or more faces which were at least twice as large as to any other stimulus tested. Second, Fig. 2 shows that some of the neurons responded primarily to one of the faces in the set (e.g. neuron Z0060), some neurons responded to

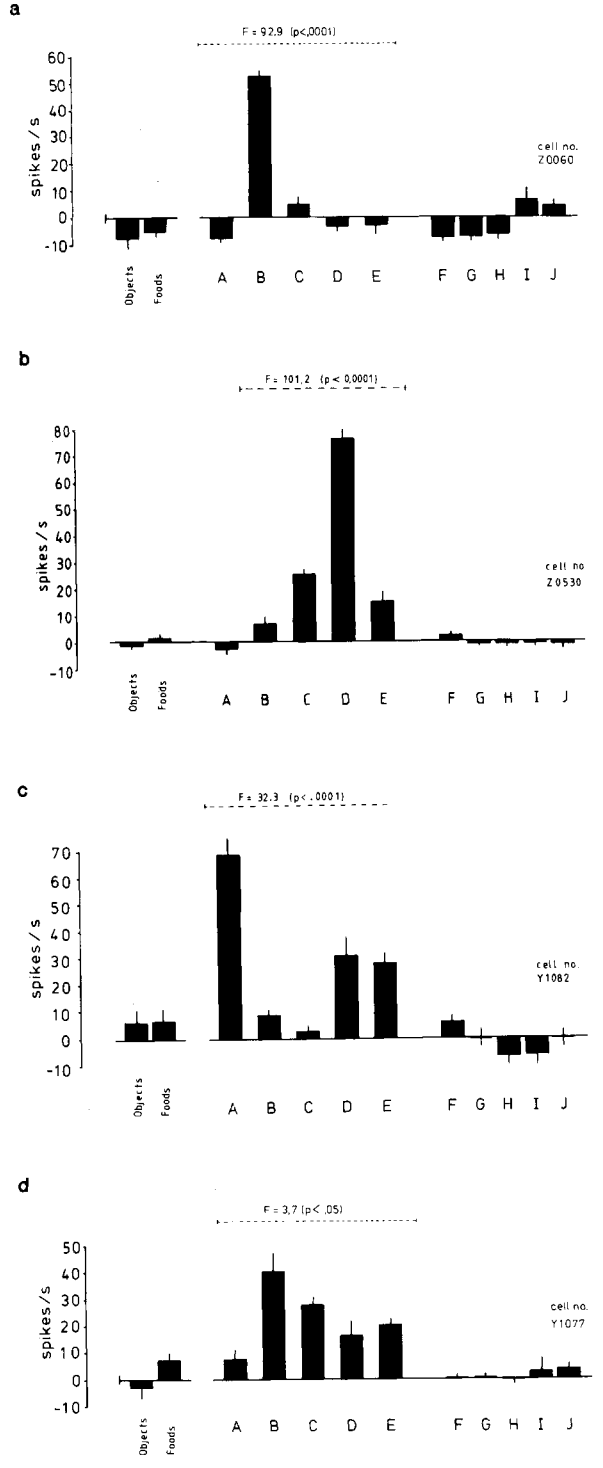

Fig. 2. The responses of 4 cells (a–d) in the cortex in the STS to a variety of face (A–E) and non-face (F–J) stimuli, which are illustrated in Fig. 1. The bar represents the mean firing rate response above the spontaneous baseline firing rate with the standard error calculated over 4–10 presentations. The F ratio for the analysis of variance calculated over the face sets indicates that the units shown range from very selective (Z0060) to relatively non-selective (Y1077).

many of the faces (e.g. neuron Y1077) and some of the neurons responded to a subset of the faces.

Examples of the responses of these neurons on individual trials are shown in the raster displays and peristimulus time histograms of firing rate in Fig. 3. The figure shows that even on individual trials these neurons responded differently to different faces. Fig. 3 also shows that the response to the different faces became differential to different faces near the beginning of the neuronal response, i.e. with a latency of approximately 110 ms for this neuron. It is also shown that while responding with an increase of firing rate to an effective face, these neurons can decrease their firing rate below the spontaneous level to other faces. This implies active filtering.

To analyze whether a neuron responded differently to the different faces in a set, an analysis of variance was performed of the responses to the 5 faces (A–E) in the set. The F ratio, and its significance, are indicated over each set of faces in Fig. 2. For all the neurons illustrated, the F ratio indicated that there were differences in the responses of each neuron to the different faces in the set. Of 44 neurons analyzed in this way in the cortex of the STS of 3 monkeys, 34 had significantly different responses to different faces in the digitized set.

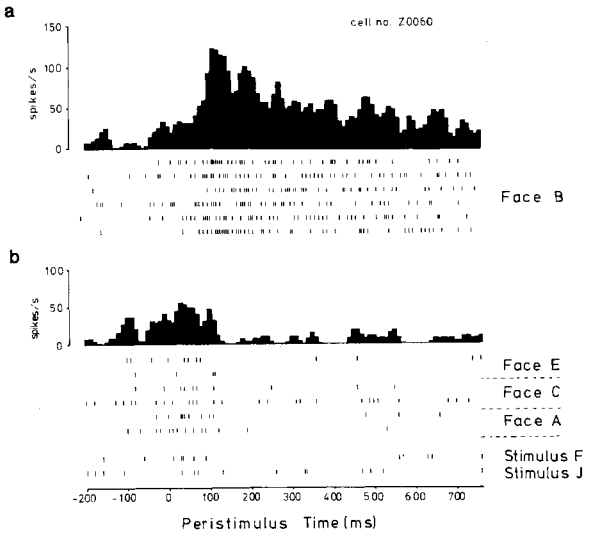

Fig. 3. A raster plot showing the response to some stimuli for cell Z0060. Each vertical line represents one action potential. These data are from the neuron whose response histogram is shown in Fig. 1a and are representative of the data from which Fig. 2 was calculated.

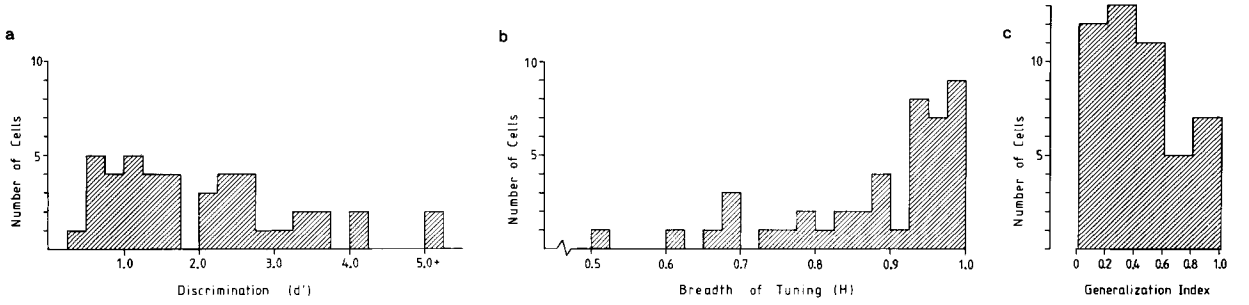

Fig. 4. a: the discriminability indices (d'). b: the breadths of tuning. c: generalization indices calculated across the standard set of faces for the cells recorded in the cortex in the STS.

To measure the extent to which a neuron responded differently to different faces, the difference between the response to the most effective face stimulus and the least effective face stimulus (both averaged over all 4–10 presentations of the face) was calculated and presented as a ratio to the standard deviation of the responses. This measure thus represents the number of standard deviations which separate the two neuronal responses and is intended to be analogous to detectability, d', in signal discrimination theory (see refs. 13, 16 and 30). This measure has also been chosen so that it may be compared with d' measures of the discriminability of faces to human observers. As we did not wish to assume that the standard deviations of the responses to the two stimuli were equal, a measure of the joint standard deviation was calculated (by summing the two variances and taking the square root, see Green and Swets[16]). For the neurons shown in Fig. 2, d' had a value of 8.77 for neuron Z0060, 6.35 for neuron Z0530, 4.03 for neuron Y1082 and 2.62 for neuron Y1077. The values of d' for the neurons tested in this way are shown in Fig. 4a. It is clear that a range of degrees of selectivity for different faces was found, with some neurons responding quite well even to the least effective face (values of d' less than 1.0), and with some neurons responding very differently to the different faces in the set (values of d' greater than 1.0).

To assess the breadth of tuning of these neurons to different faces using a measure derived from information theory, the breadth of tuning metric developed by Smith and Travers[35] was calculated. 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 set was 0.52 for neuron Z0060, 0.67 for neuron Z0530, 0.77 for neuron Y1082 and 0.94 for neuron Y1077. The breadth of tuning of the population of neurons analyzed in this way is shown in Fig. 4b.

To provide a measure of the proportion of the faces to which a given neuron responded, 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 this set was calculated. This is named the generalization index. The fraction of face stimuli in the set to which neuron Z0060 responded was thus 0.2, for neuron Z0530 it was 0.2, for neuron Y1082 it was 0.2 and for neuron Y1077 it was 0.6. The proportion of faces in the set to which each neuron responded in this way is indicated for each neuron in Fig. 4c. It is clear that some neurons were highly selective, responding primarily to one face in the set, while other neurons responded to several or many faces in the set.

The value of d' for each neuron is shown as a function of its breadth of tuning in Fig. 5. Neurons which had a high degree of discriminability (d') between the response to the most and the least effective face

* $H = -k \sum_{i=1}^{n} p_i \log p_i$, 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) and p_i = the response to stimulus i expressed as a proportion of the total response to all the stimuli in the set.

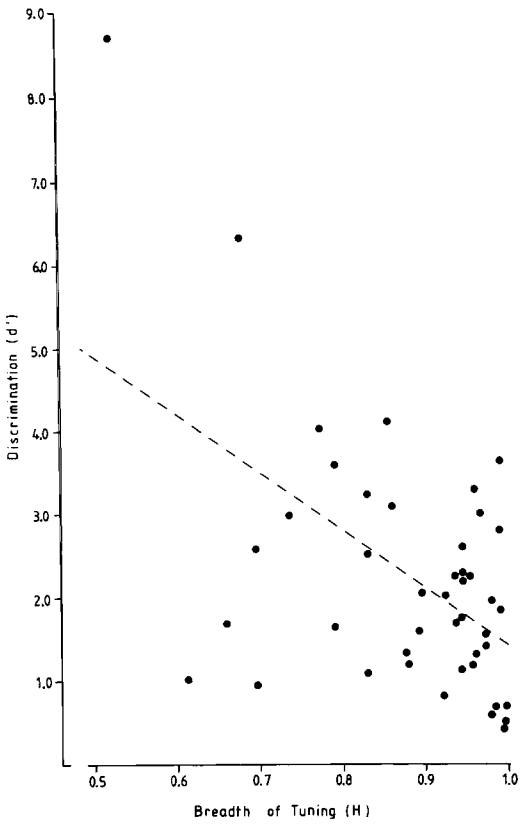

Fig. 5. The discrimination index (d') is shown as a function of the breadth of tuning metric (H). Each point represents the values of the indices for one neuron.

tended to respond to few faces, i.e. to have a low breadth of tuning value.

The latencies of the responses of these neurons are shown in Fig. 6. The majority of the neurons had response latencies between 70 and 150 ms. A comparison of the latency at which a neuron responded with its selectivity for different faces as shown by its value for d' and for the generalization index did not reveal that the neurons in this population which responded more selectively to different faces had longer response latencies.

To analyze whether different neurons tended to respond best to the same face, the number of neurons which responded best to each face in the digitized series is shown in Table I separately for each monkey. The table shows that different neurons recorded responded best to different faces, although in one monkey one of the faces was particularly effective. The possible reasons for and significance of this relative

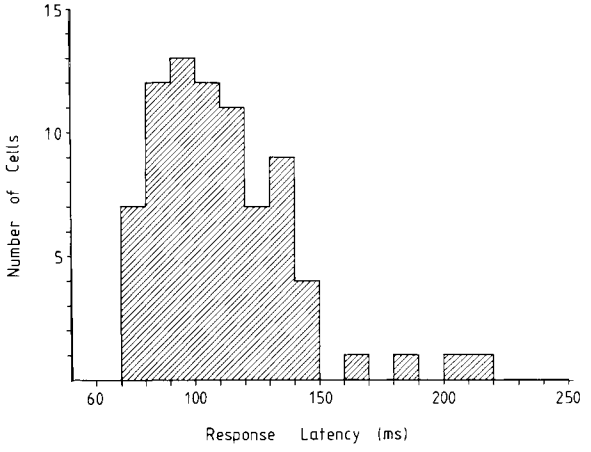

Fig. 6. The response latencies of the neurons in the cortex in the STS with responses selective for faces.

preponderance of best responses to one of the faces in the series found in one of the monkeys is considered in the discussion.

The sites at which these neurons were recorded are shown in Figs. 7 and 8. The majority of the neurons with face-selective responses were in the cortex in the anterior part of the STS and on the ventral lip of the sulcus. Many of the neurons were found in the dorsal bank of the STS, in area TPO as defined cytoarchitectonically and myeloarchitectonically[34].

DISCUSSION

These results show that neurons in the cortex in the STS which respond to faces can respond differently to different faces. A considerable proportion (34/44 or 77%) of the neurons with face-selective visual responses had this type of differential response (as shown by an analysis of variance) to different faces.

TABLE I

The number of neurons in each of 3 monkeys for which the different faces in the standard set of faces was the optimal stimulus

If two of the faces were equally and optimally effective, the neuronal count for each stimulus was increased by 0.5.

Monkey	*Face*				
	A	*B*	*C*	*D*	*E*
Y	9.5	2	0	3.5	1
Z	0	6.5	2.5	3	3
R	0.5	2.5	2.5	1.5	1

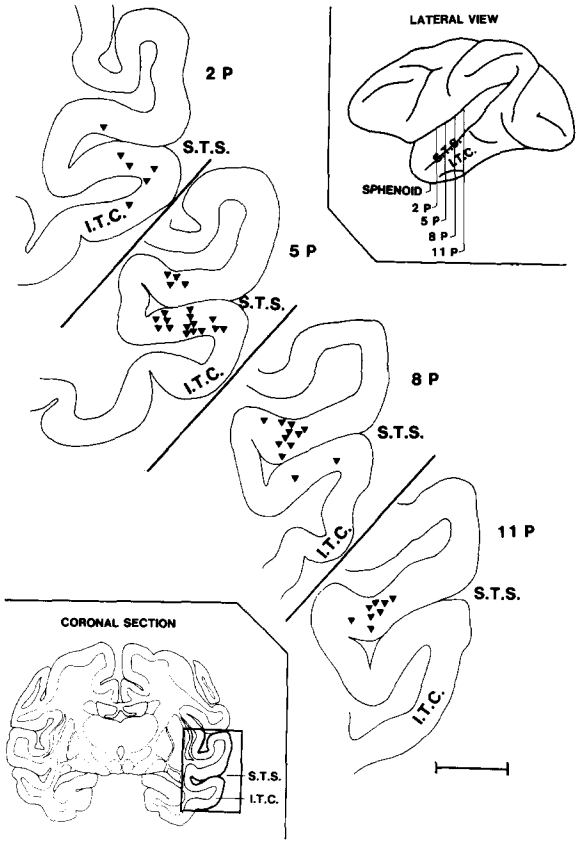

Fig. 7. The locations of neurons with responses selective for faces are shown by triangles. The upper inset shows the levels at which these coronal sections were taken. The position at which the sections were taken is indicated in millimeters posterior to the sphenoid process[2], which was 18–21 mm anterior to the external auditory meatus in these rhesus monkeys. The lower inset shows a coronal section of the whole brain to indicate the area shown in the enlarged sections at the middle of the region. Scale bar = 5.0 mm.

These results extend our previous study of neurons in the STS[23], in which the majority of the neurons with face-selective responses responded well to at least one monkey face presented as a photograph and one real human face but were not tested routinely on an extensive series of different faces.

In both this study and our previous study[23], the neurons classified as having face-selective responses were tested on a wide range of non-face stimuli. In the present study these included sine wave gratings and series of boundary descriptors presented on a video screen, a large number of 3-D junk objects and complex images digitized from the television which were presented as novel and familiar for a particular day as part of a recognition memory experiment[4]. To be classified as a face-selective neuron in this study, the neuron had to respond to the optimal face stimulus with a change of firing rate which was at least twice that to any non-face stimulus tested. In fact, the majority of the neurons in the cortex in the STS 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. Indeed, we view them as a population which, in that they respond well to faces but generally poorly to other stimuli, and in that they can respond differently to different faces, conveys information which could be useful in recognition of different faces. Some further evidence which suggests that they may perform a common computation is that they appear to be grouped together in the cortex in the STS rather than spread uniformly throughout the inferior temporal cortex, as shown by our earlier observations[23], by the results presented here and by Desimone et al.[12].

The values of the discriminability of the different faces as shown by the estimate of d′ between the most and least effective face had values in the range 0.2 to 5.0, as shown in Fig. 4. These values compare to values of 0.5–2.4 found in human studies of face recognition with rather larger set sizes[8,11]. Given that the value of d′ obtained depends considerably on testing conditions such as the duration of exposure of the stimulus, it will be of interest to measure d′ with human subjects discriminating between faces under the conditions used in this neurophysiological study. It is worth noting that the period of neuronal firing from which d′ was estimated in the present study finished 600 ms after stimulus onset.

Given that it has been shown in this study that neurons in the cortex in the anterior part of the STS can respond differently to different faces, a number of explanations of this, which are not necessarily mutually exclusive, are considered next. Further investigations will be needed to determine how these different factors contribute to the face selectivity found.

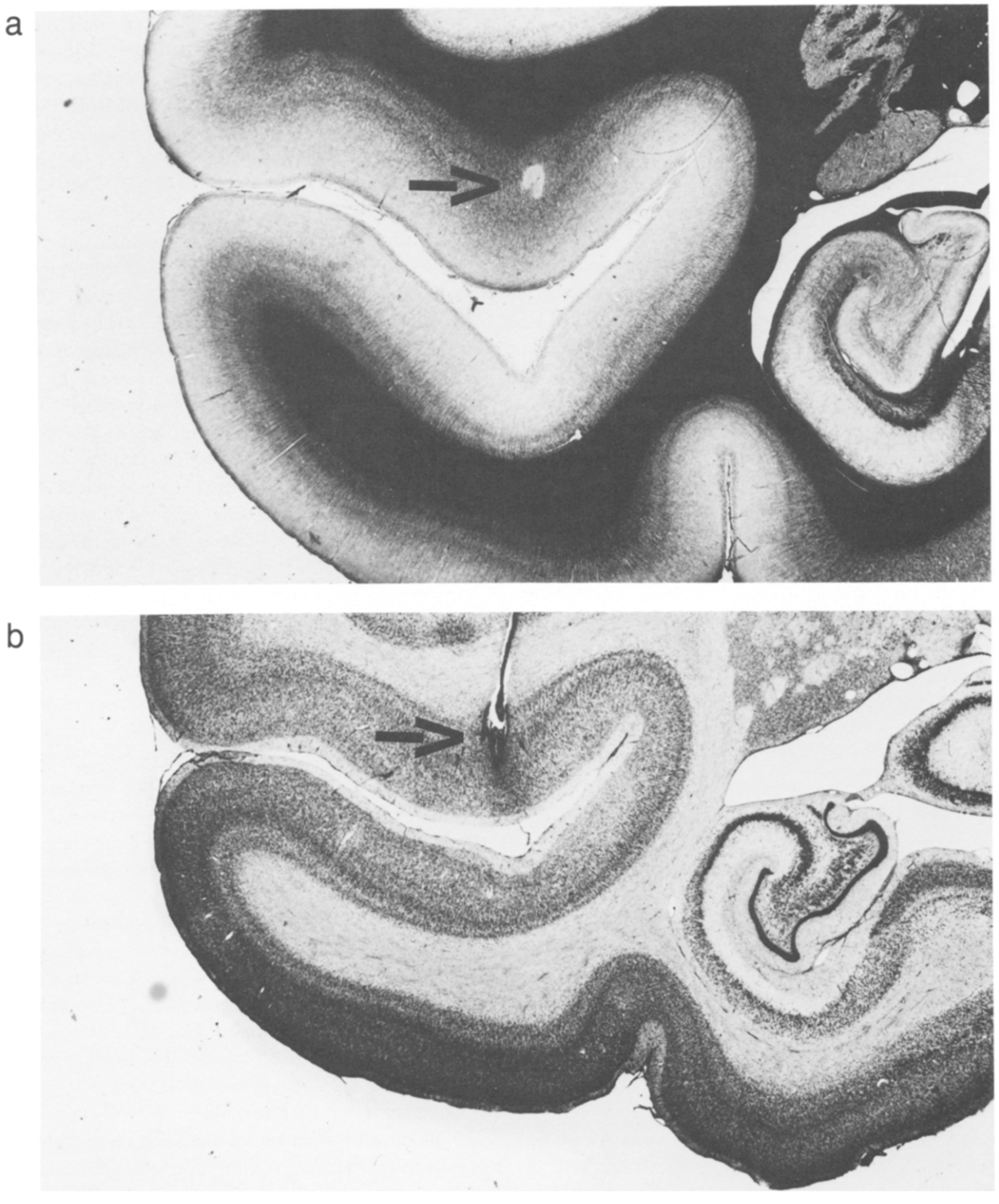

Fig. 8. Recording sites (marked by small lesions) in the cortex in the STS of neurons which responded selectively to faces. The section in a was stained by the Gallyas[15] method to show myeloarchitecture and in b with cresyl violet to show cytoarchitecture. Section a is from monkey R and b from monkey Y. The lesions are in area TPO[34].

One possibility is that these neurons are tuned to respond to physical features which are different in different faces. The faces in the stimulus set differed for example in eye shape, white facial markings, etc. Another possibility is that the expression on the face provided the basis for the cells' responses. One face in the set was for example a threat face, whereas another had the mouth closed. However, there is little evidence so far that differences in expression accounted for the differences in the responses of the majority of the neurons recorded in this particular population, for when the facial expression was altered on a human face to which these neurons responded, this usually did not alter the responses of these neurons (in 9/12 cases). Another possibility is that the responses of these neurons reflected the attention shown by the monkey to the different faces in the set. It is known for example that in a monkey group, different individuals pay different amounts of attention to each other, and that the information conveyed by some faces is more important than that conveyed by others[9,24]. It is unlikely, however, that differential attention accounted for the differences in the neuronal responses studied here, for different single neurons recorded on the same track were found to respond preferentially to different faces in the set, and in addition fixation of the different faces in the set was shown by the EOG recordings to be equally good in the 500-ms period in which the neuronal responses were measured.

Another interesting set of factors which could have contributed to the different responses of the neurons described here is suggested by the data shown in Table I. This shows that 9/16 cells in one monkey, Yasmin, responded best to stimulus A (the two weanling monkeys), whereas only 1/28 of the cells in the other two monkeys did. It happened that Yasmin was the youngest monkey (1 year, 6 months old) in which recordings were made, and that she had been reared with one other monkey in the same cage, a female of the same age, so that her primary experience of other monkeys had been with a monkey of the same age. This raises the question of the extent to which age and experience are factors which influence how these neurons respond. Clearly, in order to resolve the relative contributions of age, experience and sex in the tuning of these neurons, detailed longitudinal studies in animals with different experience are required.

In that the responses of these neurons were different to the different face stimuli presented in this study, it is likely that these neurons would be useful for distinguishing between different individuals. Further evidence consistent with this is that when different (though primarily frontal) views of the face of an individual monkey were used as stimuli, the neurons typically responded similarly to the different views. It is also known that the responses of these neurons to a given face are relatively constant over a number of physical transformations such as size and contrast (ref. 25 and experiments of Rolls and Baylis, unpublished), so that the differences in the responses to the different face stimuli used here are more likely to be related to the different individual rather than to the slightly different size, contrast and angle at which each photograph is taken. However, we do not believe that these neurons respond to a face regardless of view, as shown by the observation that their responses can decrease if the face is shown in profile[23].

The findings described here show that the responses of each of these neurons in the cortex in the STS do not uniquely code for the face of a particular individual. However, the findings do show that across a population of such cells information is conveyed which would be useful in making different behavioral responses to different faces. Thus information which specifies an individual face is present across an ensemble of such cells. In that each neuron does not respond to only one face, and in that a particular face can activate many neurons, these are not 'grandmother' cells[3]. However, in that their responses are relatively specialized both for the class 'faces' and within this class, they could contribute to relatively economic coding of information over relatively few cells[3]. It may be noted that even if individual neurons in this population are not tuned to respond completely specifically to only face stimuli, it is nevertheless the case that the output of such an ensemble of neurons would be useful for distinguishing between different faces. The appropriateness of these neurons for such a function is enhanced by the findings that their responses to a face are somewhat resistant to physical transforms. These findings lead us to consider these neurons as filters, the output of which could be used for recognition of different individuals and in emotional responses made to different individuals.

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