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# NEURONS IN THE AMYGDALA OF THE MONKEY WITH RESPONSES SELECTIVE FOR FACES

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To investigate the functions of the amygdala in visual information processing and in emotional and social responses, recordings were made from single neurons in the amygdala of the monkey. A population of neurons (40 of more than 1000 recorded in 4 monkeys) was investigated which responded primarily to faces. These neurons typically (1) responded to some human or monkey faces, which were presented to the monkey through a large aperture shutter so that response latencies could be measured, or were simply shown to the monkey, (2) responded to 2-dimensional representations of these faces, as well as to real 3-dimensional faces, (3) had no responses or only small (less than half maximum) responses to gratings, simple geometrical, other complex 3-D stimuli, or to arousing and aversive stimuli, (4) had response latencies of 110–200 ms, (5) were located in the basal accessory nucleus of the amygdala, (6) responded differently to different faces, as shown by measures of d′, and could thus over a population of such neurons code information useful for making different responses to different individuals, (7) could in some cases (9/11 tested) respond to parts of faces, and (8) in a few cases (4/19 tested) responded more to a face which produced an emotional response. A comparison made in three monkeys of the responses of these neurons with the responses of 77 neurons with face-selective responses recorded in the cortex of the superior temporal sulcus (STS) showed that the amygdaloid neurons had longer response latencies (110–200 compared to 90–140 ms), and were in some respects more selective in their responses to different faces. It is suggested that the deficits in social and emotional behavior produced by amygdala lesions could be due in part to damage to a neuronal system specialized in utilizing information from faces so that appropriate social and emotional responses can be made to different individuals.

## INTRODUCTION

One of the most dramatic constellations of behavioral changes that can be caused by brain damage is the Kluver-Bucy syndrome[19]. Rhesus monkeys with bilateral temporal lobe ablations respond inappropriately to visual stimuli by for example selecting and placing in their mouths non-food as well as food items, repeatedly fail to avoid noxious stimuli, display inappropriate social behavior, and have abnormal emotional behavior in that they become tame and are easy to handle[15,18,19]. The syndrome is produced by lesions of the temporal lobe which damage primarily the amygdala[45].

The changes in social behavior have been described in a series of investigations which show that they are produced by bilateral damage to the amygdala[9,18,35,42,45]. Thus, after amygdala lesions, monkeys lose their position in the dominance hierarchy[35]; are abnormally friendly to the experimenter[45]; attempt to enter alien troops, per-

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haps because they are 'retarded in their ability to foresee and avoid dangerous confrontations'[9]; and are 'slow in conforming to the social etiquette normally associated with a subordinate status and behave in ways that prolong the hostility directed at them'[42]. Thompson et al.[42] suggested that rather than becoming tame, or less fearful, monkeys with amygdala lesions simply respond inappropriately to social cues.

In order to obtain neurophysiological evidence on the functions of the amygdala in feeding and learning which have been suggested on the basis of lesion evidence[15,27–29,40,45], Rolls and his colleagues recorded the activity of single neurons in the amygdala while monkeys were feeding and were performing visual discrimination tasks[28,36]. A population of amygdaloid neurons was found which responded to visual stimuli with latencies of 100–190 ms. These latencies compared with latencies of 100–180 ms for neurons recorded in the same testing conditions in the inferior temporal visual cortex[31], which projects into the amygdala. 22% of these amygdaloid neurons with visual responses responded preferentially to the stimulus associated with positive reinforcement in the visual discrimination, or to the sight of foods. These results are consistent with the hypothesis that these neurons reflect processing in a system in which visual stimuli are becoming associated with reinforcement[28].

While making these recordings in the amygdala, a small number of neurons was observed which had visual responses which occurred selectively to faces[28]. These neurons were approximately 10% of those with visual responses (11/113). These neurons typically (1) responded to human or monkey faces, which were presented to the monkey through a large aperture shutter so that response latencies could be measured, or were simply shown to the monkey, (2) responded to 2-dimensional representations of faces, such as photographs or the sight of the monkey's own face in a mirror, as well as to real 3-dimensional faces, (3) had no responses or only small responses to gratings, simple geometrical, other complex 3-D stimuli, or to arousing and aversive stimuli and (4) had response latencies of 100–180 ms. Examples of these neurons were found in all 5 monkeys in which recordings were made in the amygdala. An additional 6 neurons in a category of neurons with possible or longer latency visual responses also responded selectively to faces[28]. This finding of face-responsive neurons in the amygdala is particularly interesting in view of the high importance that facial recognition and expression play in monkey social behavior[7,14,26,44]. In line with this, Rolls suggested that the deficits in social and emotional behavior produced by amygdala lesions could be due in part to damage to a neuronal system specialized in utilizing information from faces so that appropriate social and emotional responses can be made to different individuals[28].

In further investigations, other populations of neurons with responses selective for faces have been found[4,5,8,12,22,28,31,34]. These neurons are in the cortex in the anterior half of the superior temporal sulcus. It is of interest that this region of the cerebral cortex is known to send projections into the amygdala[1], and thus provides a route by which visual information specialized with respect to face-processing could reach the amygdala. This cortex itself receives projections from the inferior temporal visual cortex[16,38].

Given these previous findings, the present investigation was performed to obtain further information on the neurons in the amygdala which respond to faces. In particular, the aims were to investigate the regions of the amygdala in which neurons which responded to faces were found; to investigate how selective their responses were for faces as compared to non-face stimuli; to investigate whether they responded in any way differently to different faces, as might be expected of a system which would be useful in making differentiated behavioral responses to different faces; and to compare their responses with those of the neurons in the cortex of the superior temporal sulcus which respond to faces.

## MATERIALS AND METHODS

### *Recording techniques*

The activity of single neurons was recorded with glass-insulated tungsten microelectrodes (af-

ter Merrill and Ainsworth[20], but without the platinum plating) in 4 alert macaque monkeys (*Macaca mulatta*) (weight 3.0–6.5 kg) seated in a primate chair using techniques that have been described previously[30]. The action potentials of single cells were amplified using techniques described previously[32], 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 starting 100 ms after the stimulus onset was printed. This period was chosen because the neurons studied responded to visual stimuli with latencies 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 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. The position of cells was reconstructed from the X-ray co-ordinates taken together with serial 50 $\mu$m histological sections which showed the reference electrodes and micro-lesions 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, 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-dimensional stimuli such as real faces and 3-D objects which differed along a wide range of parameters such as size, shape, and color, and also allowed 2-D stimuli such as photographs of a wide range of faces to be presented. Second, stimuli were digitized, stored on computer disk, and displayed on a video monitor using a video framestore. The resolution of these images was 256 wide by 256 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.

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[32]. 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 10–13 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[37], and a complex visual image, to provide an indication of whether the neuron responded differently to face and to non-face stimuli. 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. An analysis of variance was then performed 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.

*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 between 2 cm and 1 m behind the shutter

*Face stimuli*

Both real faces and photographs of faces were used as stimuli with the shutter method of presentation. Real human faces together with a large toy monkey face were shown through the shutter in the same way as other objects. Photographs were prepared of macaque monkey faces (looking directly at the camera), and of human faces. Some of the photographic negatives were digitized using a Scandig 3 (Joyce-Loebl, Gateshead, England) 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 these real faces and photographs of faces, and when possible to a standard subset of the digitized images of faces.

The faces shown were chosen to include a number of different facial expressions, but all were frontal views with eye contact. When a real human face was shown, it was possible to determine the effect of different expressions, by comparing the neuronal response to a neutral face with that to an open-mouth threat. The latter was shown to be effective as a threat in that it frequently elicited a threat from the monkey.

To determine the extent to which responses to parts of the face could account for a cell's responses to the entire face, parts of the face were blanked out or left in isolation. For each of several faces, series of such parts of faces were stored on disk, and the parts of one face were shown in random series as video images by the computer. It was of interest to compare the responses of the neurons to parts of faces of monkeys which when the whole face was presented did or did not produce a large neuronal response.

*Arousing and aversive stimuli*

Responses to a variety of arousing and aversive stimuli were tested to determine whether arousal itself 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*

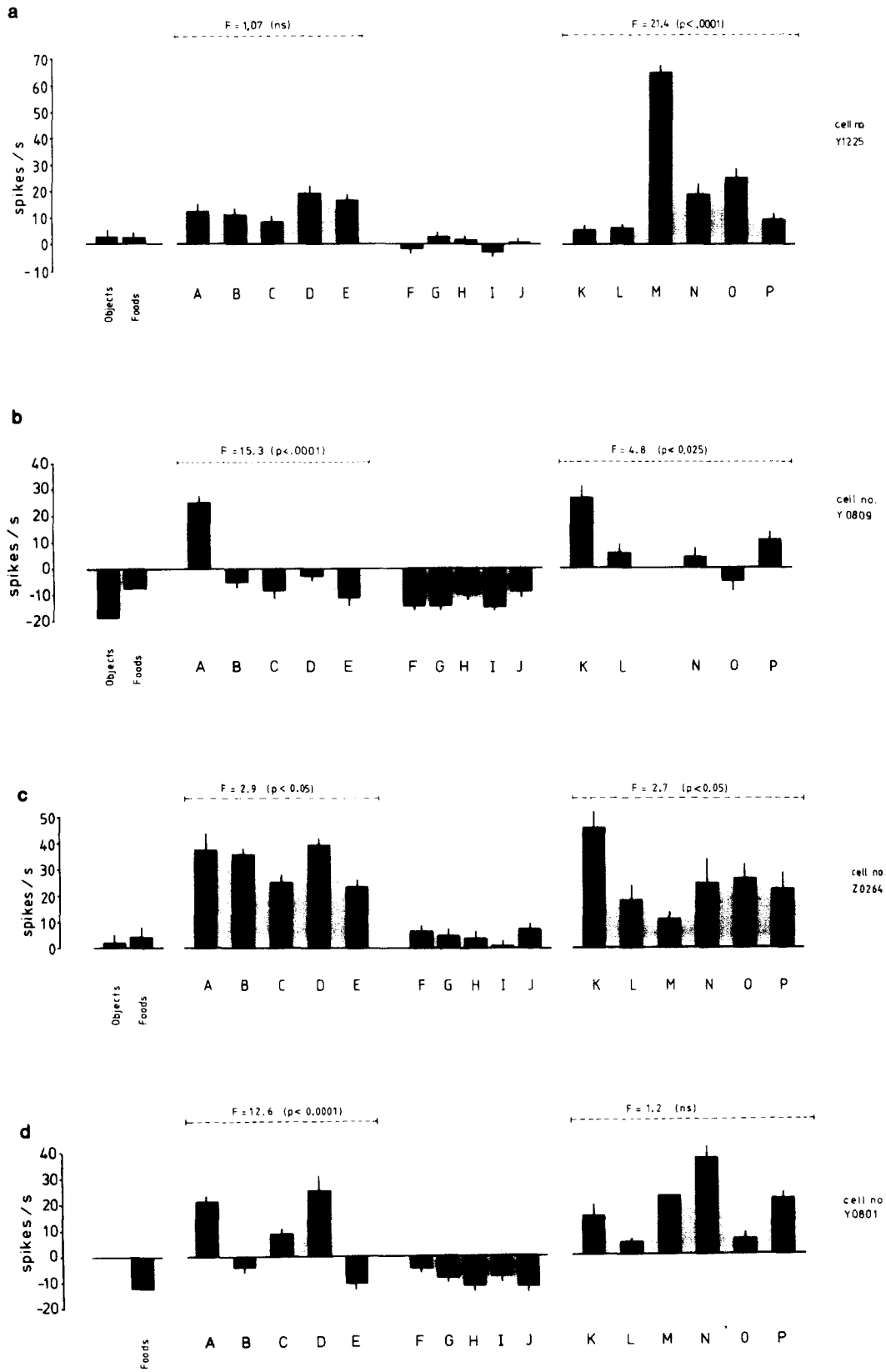
For each cell measures of responses were calculated from the total number of action potentials occurring on each trial in the period 100–600 ms following stimulus onset. This period was chosen because the cells studied typically responded to visual stimuli with latencies greater than 100 ms. Recordings 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 Bruning and Kintz, ref. 6) 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 analyse 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 calculated over typically 4–10 presentations are shown. The results of the analysis of variance are also usually indicated.

## RESULTS

Recordings were made from more than 1000 neurons in the amygdalas of 4 monkeys. Of these neurons, approximately 12% were found to have visual responses, using the criteria defined previously[36]. 40 of the visual neurons responded primarily to faces, and the responses of these neurons are the subject of this paper. In one monkey, Yasmin, extensive series of recordings were made in both the amygdala and the cortex in the superior temporal sulcus (STS) to provide a within-monkey comparison of the responses of neurons to faces in these two areas. For some comparisons, it was possible to use in addition data from two other monkeys in which results were obtained from both the amygdala and the STS under identical testing conditions. Observations of the responses of some of the other neurons in the amygdala with visual responses are described at the end of the results section.

Examples of the responses of neurons recorded in the amygdala which responded preferentially to faces are shown in Fig. 1. The responses of 4 different neurons (a–d) to the different faces (A–E) and non-face stimuli (F–J) in a set of digitized images are shown. These stimuli are illustrated in Fig. 1e. The responses to a range of 3-D objects, and to food, are also shown, on the left of Fig. 1a–d. In addition, responses to other faces (K–P) are shown on the right, because many amygdaloid neurons did not respond very well to the faces which happened to be in the digitized series, but could respond well to other faces (e.g. neuron Y1225). The faces in this second set were photographs of monkeys or were real human faces, and they were presented in random order when a large aperture shutter opened. All responses are shown as mean changes in firing rate in spikes/s from the spontaneous firing rate (with the standard error calculated over 4–10 observa-


a
F = 1,07 (ns)
F = 21,4 (p<.0001)
spikes / s
cell no
Y1225
Objects
Foods
A B C D E F G H I J K L M N O P
b
F = 15.3 (p<.0001)
F = 4.8 (p< 0,025)
spikes / s
cell no.
Y 0809
Objects
Foods
A B C D E F G H I J K L N O P
c
F = 2.9 (p < 0.05)
F = 2.7 (p<0.05)
spikes / s
cell no.
Z0264
Objects
Foods
A B C D E F G H I J K L M N O P
d
F = 12.6 (p< 0.0001)
F = 1.2 (ns)
spikes / s
cell no
Y0801
Foods
A B C D E F G H I J K L M N O P

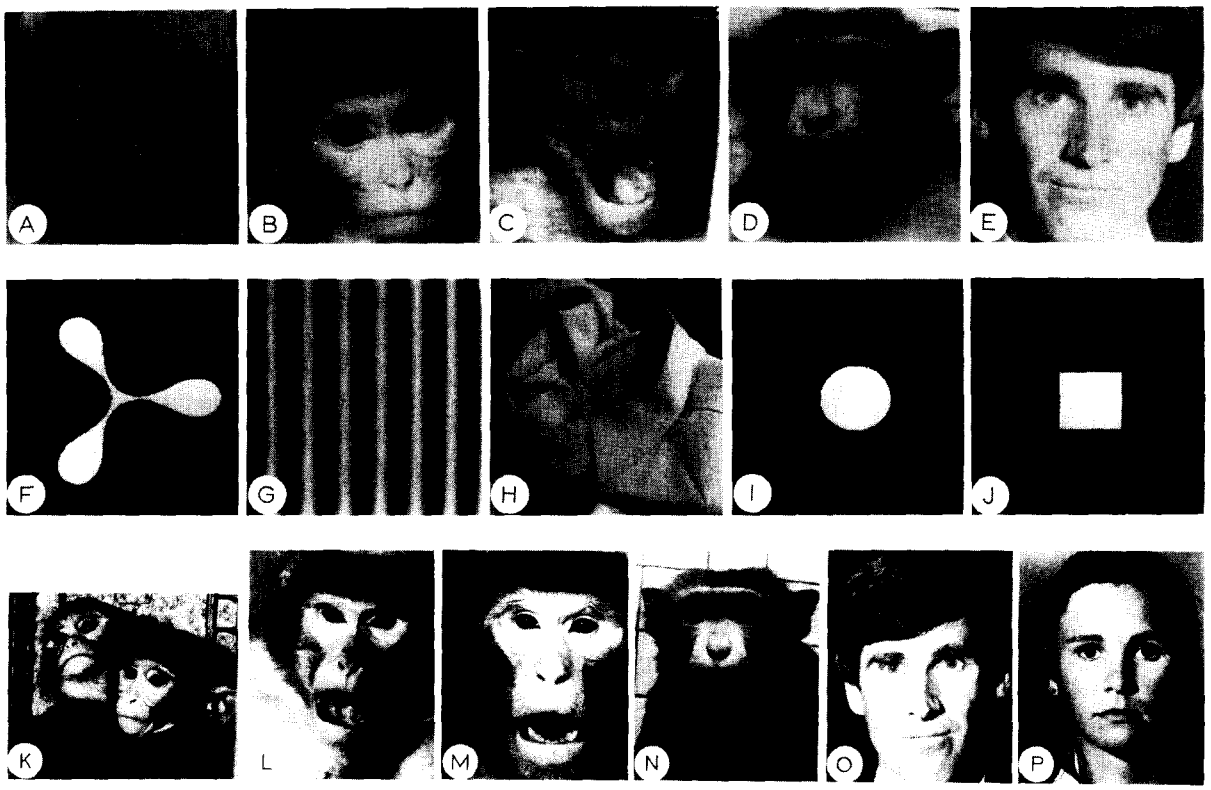



Fig. 1. The responses of 4 cells (a–d) in the amygdala to a variety of face (A–E) and non-face (F–J) stimuli, which are illustrated in e. The set A–J is the screening set of TV images. A: two infants. B: juvenile. C: 5-year-old threat face. D: 10-year-old stare. E: human experimenter. F: boundary descriptor. G: spatial grating. H: complex texture. I: circle (S + ). J: square (S − ). Stimuli K–P in f are samples of photographs shown when the TV images did not evoke a response. The bar represents the mean response above baseline 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 (Y0809) to relatively nonselective (Z0264). Note that cells Y0801 and Y0809 both inhibit to some faces and non-face stimuli.

tions indicated). Examples of the responses of one of these neurons are shown as peristimulus time histograms and rastergrams for each trial in Fig. 2.

First, Fig. 1 shows that the responses of these neurons to one or more faces were at least twice as large as to any other of the wide range of visual stimuli tested. This illustrates the application of one of the criteria by which the neurons described here were classified as having visual responses selective for faces. In fact, the majority of these neurons responded much more specifically than this. For half these neurons, their response to the most effective face was more than five times as large as to the most effective non-face stimulus, and for 10% 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 second criterion was that an analysis of variance performed over the set of face and non-face stimuli should show a significant effect of stimulus type, and that subsequent multiple $t$, Tukey, and Newman–Keuls' analysis (see ref. 6) should show that the response to the optimal face stimulus was significantly greater ($P < 0.05$) than the response to the optimal non-face visual stimulus. (In fact, the difference was significant at the 0.01 level for each of the neurons described in this paper.) It should be noted that the neurons were tested on a wide range of non-face stimuli, which included many three dimensional objects, the mean response to which is shown under 'objects'.

Second, Fig. 1 shows that some of the neurons responded primarily to one of the faces in the set (e.g. neuron Y1225, Fig. 1a), some neurons re-

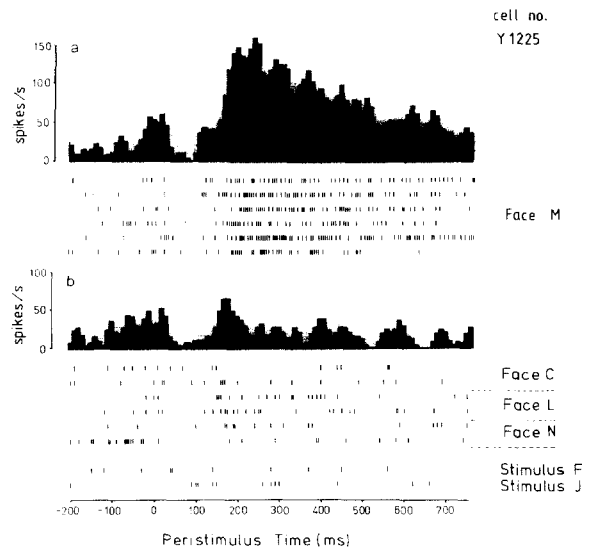



Fig. 2. A raster plot showing the response to selected stimuli for cell Y1225. Each vertical stroke represents one spike. These data are from the neuron whose response histogram is shown in Fig. 1a and are representative of the data from which Fig. 1. was calculated.

sponded to many of the faces (e.g. neuron Z0264, Fig. 1c), and some of the neurons responded to a subset of the faces (e.g. neuron Y0801, Fig. 1d).

To analyze whether a neuron responded differently to the different faces in a set, an analysis of variance was performed on the responses to the 5 faces (A–E) in the digitized set, and to the set of real and photographic faces. The *F* ratio, and its significance, are indicated over each set of faces. For all the neurons illustrated, the *F* ratio indicated that there were differences in the responses of each neuron to the different faces in one of the sets. Of 32 neurons analysed in this way in the amygdala of 4 monkeys, 26 had significantly different responses to individual faces.

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 that face) was calculated, and divided by 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[10,11,33]. 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 ref. 11). For the neurons shown in Fig. 1, d′ had a value of 2.21 for neuron Y1225, 1.42 for neuron Y0809, 1.25 for neuron Z0264, and 0.79 for neuron Y0801. These values are for the photographic set of faces K–P as indicated in Fig. 1. The d′ values for the population of neurons in the amygdala are shown in Fig. 3a. The discriminability (d′) values shown in Fig. 3 were calculated over the photographic and real set of (5–8) monkey and human faces, in order to have comparable values for all neurons. 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 (d′ of less than 1.0), and with some neurons responding very differently to the different faces in the set (d′ of 1.0 and above).

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[39] 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 6 face stimuli in the photographic set (K–P) was 0.80 for neuron Y1225, 0.79 for neuron Y0809, 0.95 for neuron Z0264, and 0.88 for neuron Y0801. The breadth of tuning of the population of neurons analyzed in this way is shown in Fig. 3b.

To provide a measure of the proportion of the faces to which a given neuron responded, the number of faces in the same set (K–P) to which the neuron had a response greater than half that

* $H = -k \sum_{i=1}^{n} p_i \log p_i$ 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.

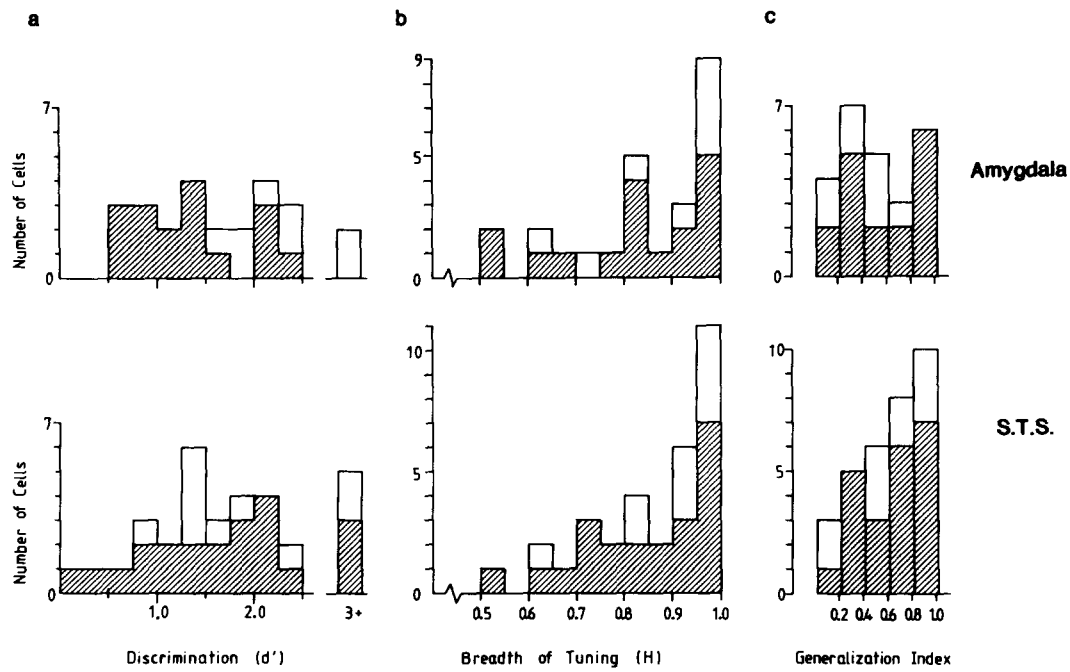



Fig. 3. The discriminability indices (d'), breadth of tuning (H) and generalization indices for cells recorded in the amygdala and cortex in the superior temporal sulcus (S.T.S.). Data obtained in both structures within monkey Y (to allow a within-monkey comparison) are shown hatched.

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 Y1225 responded was thus 0.17, for neuron Y0809 was 0.17, for neuron Z0264 was 0.5, and for neuron Y0801 was 0.67. The proportion of faces in the set to which each neuron responded in this way (the 'generalization index', again calculated over the set of real and photographic faces) is indicated for each neuron in Fig. 3b. 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.

Further evidence on the nature of the tuning of these amygdaloid neurons to faces was obtained. First, it was found that although some neurons did respond to the set of 5 digitized video faces (see Fig. 1 stimuli A–E), the majority of neurons in the amygdala tested with this set (17/22) were relatively unresponsive to the images in this set. This is why it was necessary to introduce the second set of images, which included photographs of monkey faces and real human faces. In that it was only when the number of face stimuli available were extended in this way that good responses were obtained from these amygdaloid neurons, they appeared to be able to differentiate between a considerable range of different faces. (It may be noted that it was not that digitized video images per se were ineffective for these neurons, as shown by similar responses to the same face in a number of cases if it was included in both the digitized and photographic sets. For the 27 such cases, the mean response to the digitized face was 23.9 and to the photograph of the same face was 21.1 spikes/s.)

Second, it was found that while increasing their firing rate to effective stimuli, some neurons in the amygdala (7/24) decreased their firing rates to non-effective stimuli, sometimes including some faces (see for example cells Y0801 and Y0809 in Fig. 1).

Third, it was found that inputs from other modalities could sometimes activate neurons in the amygdala which responded to faces. For example, 7 of 17 face-responsive neurons tested with auditory stimuli responded to complex

sounds. For these 7 cells, the auditory response averaged 32% of the response to the most effective face stimulus. Also, 3 of 17 neurons with face-selective visual responses responded to touch to the abdomen or leg. The somatosensory response of these 3 cells averaged 30% of that to the most effective face stimulus.

Fourth, it was found that the responses of these neurons did not simply reflect arousal, in that the majority did not respond during behavioral arousal and movements induced by touch to the leg or abdomen (14/17), and none responded to aversive non-face visual stimuli out of 28 tested.

*Responses to parts of faces*

Some of these neurons in the amygdala could respond to parts of faces, which were extracted from the optimal face stimulus. For example, it was found that 9/11 neurons tested in this way responded well (with a response comparable to that to a whole face) to the eyes presented alone. The mouth alone was less effective, causing a measurable response in only 4 of 7 cases. For 4 of the above cells a set of digitized parts of stimulus A was randomly presented. The results in all four cases demonstrated that either the right or the left face or the eyes of only one face could produce a response equivalent to that of the two faces together. A representative example is shown in Fig. 4. It was found that removing the mouth and nose had little effect on the response, while removing the eyes caused a significant decrement.

In two other cases the response evoked by parts was particularly noteworthy. In P303, a cell that was significantly excited by only one face, that of a young female experimenter, a series of masking experiments was performed. Although masking the nose and mouth or nose, mouth and eyes had little effect (responses of 26 and 22 spikes/s compared to 32 spikes/s to the whole face), masking the hairline dramatically lowered the neuronal response (to 12 spikes/s). The back of the head elicited a response of only 7 spikes/s. In the other case, that of a cell presented in Fig. 1 (cell Y1225), there was no digitized set of images available for the most effective face, so a set of parts from face D (the calm adult) was used. The forehead, eyes, and mouth alone all caused significant responses ($F = 4.57$, df = 43, $P < 0.001$), 29, 32 and 36 spikes/s respectively, compared to 17 spikes/s for the complete face. This suggests that some inhibitory component might have been contributed by the combination of the parts into the whole, or by the face outline itself. This possibility will be considered further in the discussion.

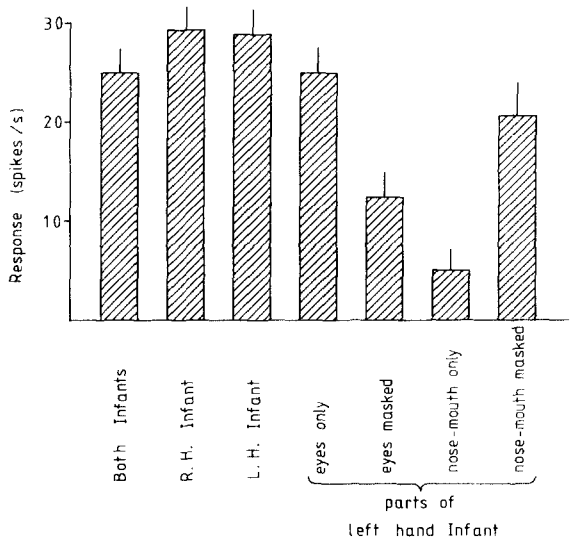



Fig. 4. The response to digitized parts of faces for cell Y1299. The parts were presented randomly 4–7 times. The eye of one infant evoked a response equivalent to that evoked by the original infant, while masking the eyes caused a significant decrement in response ($t = 3.1$, $P < 0.05$). Masking the mouth had little effect on the response.

*Neuronal response latencies*

The latencies of the responses of the neurons in the amygdala which responded selectively to faces are shown in Fig. 5a. The majority of the latencies were in the range 110–200 ms. These response latencies were somewhat longer (and also more variable) than the response latencies of neurons with face-selective responses recorded in the cortex of the superior temporal sulcus (see Fig. 5b). the hatched parts of Fig. 5 compare the response latencies of neurons recorded in the amygdala and the cortex in the superior temporal sulcus in the same monkeys in the same testing conditions. Some of these neurons had responses which did not last for the full 1.5 s duration of presentation of the stimulus, but it was possible to show for a number of neurons which had sustained re-

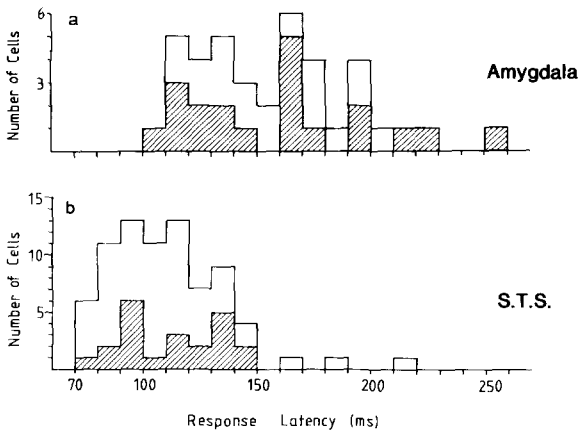



Fig. 5. The response latencies for cells with responses to faces in the amygdala and cortex in the superior temporal sulcus (S.T.S.) of 5 monkeys. Data obtained in both structures within monkey Y (to allow a within-monkey comparison) are shown hatched.

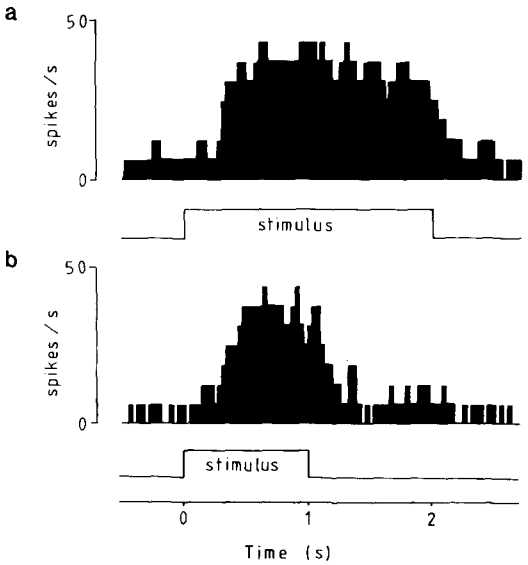



Fig. 6. A peristimulus histogram showing the effect of stimulus duration on response for cell Y0066. In a, the electronic shutter opened for 2 s displaying the optimal face stimulus. In b, the shutter closed after 1 s.

sponses that the response of the neuron stopped sharply at stimulus offset. An example of this is shown in Fig. 6.

*Responses related to affect*

In order to test the possibility that cells in the amygdala respond to the emotional aspects of faces, the neuronal response to a face making an open mouth threat was compared to the same face with mouth closed. Four of 19 cells tested in this way in 3 monkeys had greater responses when presented with an open mouth threat. These cells did not respond to generalized arousal caused by touch to the leg or by the sight of an aversive puffer or snake.

*Comparisons with responses of neurons in the cortex in the superior temporal sulcus*

As the analysis illustrated in Fig. 3 showed that sharp tuning of these amygdaloid neurons to particular faces in the set was common, with a number of neurons responding primarily to one face in the set, comparisons were made to obtain evidence on whether this fineness of tuning was characteristic of the amygdala. These comparisons were with the fineness of tuning of neurons in the superior temporal sulcus recorded in the same monkey to the same range of faces. One such comparison is shown in the Fig. 3a, in which the values of d′ calculated over the real and photographic set for 31 neurons in the superior temporal sulcus are shown. These values of d′ were not different for the population of neurons analyzed in the amygdala and the superior temporal sulcus (as shown in Fig. 3a and by a Kolmogorov–Smirnov test). This indicates that these neurons in the amygdala and cortex in the superior temporal sulcus are similar in the extent to which they discriminate between the most effective and the least effective face in the photographic/real set. It was notable however that the change of firing rate to the optimal face stimulus was generally smaller for neurons in the amygdala than in the cortex in the superior temporal sulcus (means 26 and 40 spikes/s respectively). (The mean spontaneous firing rates of the neurons in the amygdala and STS were not significantly different, means 14.3 and 12.7 respectively.)

A second comparison is shown in Fig. 3b in which the breadth of tuning for 32 neurons recorded in the superior temporal sulcus are shown. The breadth of tuning of neurons in the amygdala and STS shown in this way was similar (as shown in Fig. 3b and by a Kolmogorov–Smirnov test).

A third comparison is shown in Fig. 3c, in which the generalization indices for 32 neurons

recorded in the superior temporal sulcus are shown. The generalization of neurons in the amygdala and STS shown in this way was similar (as shown in Fig. 3c and by a Kolmogorov–Smirnov test). However, a difference in the way in which neurons in the amygdala and STS generalized to different faces is indicated in Fig. 7. It is shown in Fig. 7b that a majority of neurons in the STS generalized over all humans shown (a generalization index over humans of 1), whereas neurons in the amygdala often responded differentially (or not at all) to different human faces (Fig. 7b). (This comparison was significant at the 0.01 level as shown by a Kolmogorov–Smirnov test, d = 0.57.) The hatched parts of Fig. 7 compare the data obtained from neurons recorded in the amygdala and the cortex in the superior temporal sulcus in the same 3 monkeys in the same testing conditions.

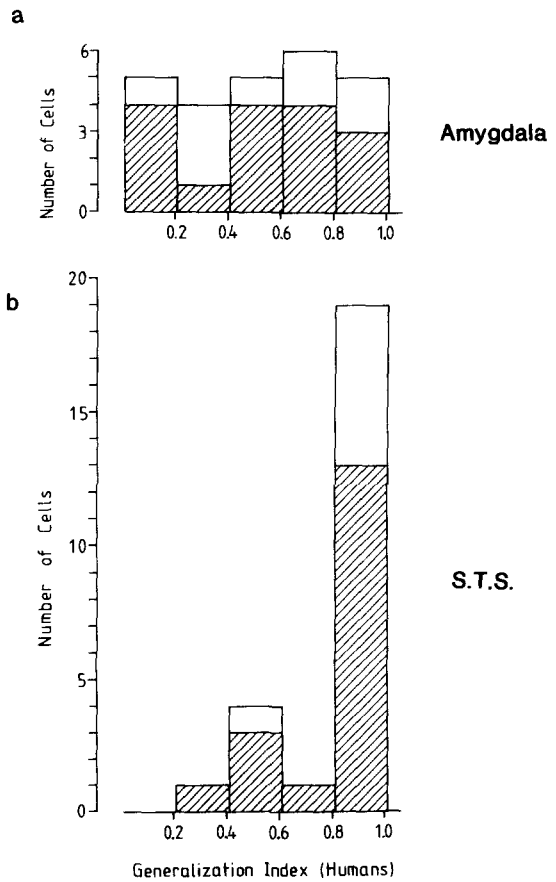



Fig. 7. The generalization indices across human faces for cells in the amygdala and STS. Cells in the amygdala rarely had responses that generalized over all humans shown. In contrast, a majority of cells in STS generalized over all humans shown. Data obtained in both structures in monkey Y (to allow a within-monkey comparison) are shown hatched.

Another difference between neurons in the amygdala and STS with responses selective for faces was that the majority of neurons in the amygdala did not happen to respond well to the set of 5 digitized faces presented on the video monitor (see Fig. 1), whereas the majority of neurons in the STS did respond (with a change of firing rate greater than twice that to the most effective non-face stimulus) to one or more of these images (5/22 tested for the amygdala compared to 56/77 for the STS in the same 3 monkeys).

*Neurons with other responses*

Many neurons in the amygdala responded to visual stimuli with latencies of 110–190 ms, and although they responded to faces, their responses were not selective for faces, as defined by the criteria given above. For example, in one monkey (Yasmin), 22 of 68 visually responsive cells in the amygdala could be excited by hands as well as or better than by faces (cf. ref. 12). In a first subgroup of 11 of these 22 cells, there was no response to a variety of 3-D objects and aversive visual stimuli. They responded to hands held in different positions, gloves, and in 3 cases, to a single finger. Of 7 of these cells tested, 2 habituated to repeated presentations of these visual stimuli, and all 7 cells tested responded to complex auditory stimuli and to touch. The second subgroup of 11 cells with responses to faces and hands were even less selective, exhibiting in addition some response to foods, 3-D stimuli and aversive stimuli. All 7 cells in this subgroup tested habituated to repeated presentations of visual stimuli, and responded to complex auditory stimuli and to touch. Although the cells in these subgroups were relatively non-specific they still showed considerable discrimination between faces. The mean generalization indices were 0.48 and 0.57, respectively for the two groups, with mean d′ of 1.78 and 1.89. The selectivity in the responses of these neurons arose because they had poor responses to monkey photographs but

good responses to at least one real human face or a model of a monkey.

*Recording sites*

The sites in the amygdala at which the neurons with responses to faces, and the neurons with other visual responses, were recorded, are shown in Fig. 8a. Examples of lesions made to mark the recording sites are shown in Fig. 9. Most of the neurons with face-selective visual responses were in and close to the basal accessory nucleus of the amygdala. The sites of other responsive neurons are shown in Fig. 8b, and the non-responsive neurons are shown in Fig. 8c to indicate the regions of the amygdala sampled.

## DISCUSSION

These results provide evidence that there is a population of neurons in the amygdala which respond when faces are shown to a monkey. The selectivity of these neurons for faces, the differences in their response properties from neurons in the overlying temporal lobe visual cortex, and the possible functions of these neurons are considered.

The population of neurons with visual responses categorized as selective for faces satisfied the following criteria. First, their responses to one or more faces were at least twice as large as to any other of the wide range of visual stimuli tested. As noted above, for half of this population of neurons, the response to the most effective face stimulus was more than five times as great as to the most effective non-face visual stimulus. The neurons were tested on a wide range of non-face visual stimuli, which included many 3-D objects, photographs and digitized images of complex non-face stimuli, aversive and arousing visual stimuli, and foods. The second criterion was that an analysis of variance performed over the set of face and non-face stimuli should show a significant effect of stimulus type, and that subsequent multiple *t*, Tukey, and Newman–Keuls' analysis (see ref. 6) should show that the response to the optimal face stimulus was significantly greater ($P < 0.05$) than the response to the optimal non-face visual stimulus. The responses of these neurons were moderately well locked to the onset of the visual stimuli (see example in Fig. 2) with latencies of 110–200 ms (compared to latencies of 90–140 ms of the neurons with face-selective visual responses in the anterior part of the cortex in the superior temporal sulcus), so that their responses reflected the visual input quite closely. These neurons did not respond to arousing or aversive non-face visual stimuli, so that their responses were not produced simply by arousal induced by visual stimuli. Further evidence for this is that different faces were optimal stimuli for different neurons in this population, so that it is unlikely that any unitary explanation of their responsiveness such as induced arousal can explain their responses. It was, however, of interest that a number of these neurons could be activated by stimuli from other modalities, for example by auditory or somatosensory stimuli, and such convergence may be of importance for the functions of these neurons.

It was found that these neurons often responded differently to different faces. It should be noted that the different faces were all frontal views with eye contact. Further, 9 of 12 cells tested responded similarly to different frontal views of the same monkey. Thus, differences in for example eye contact, to which some neurons in the cortex in the superior temporal sulcus are sensitive[23], or in the particular view of a monkey, do not appear to account for the different responses shown by these neurons to different faces. Seven neurons (in a relevant sample of 21 neurons) responded best to human faces, and 5 of these were very selective in that they responded to only one of the human faces. Three of the 10 cells responding to monkey faces had very selective responses, two responding to the photograph of the weanling monkeys (photograph K). The third cell (Y1225) responded to photographs of monkeys with the mouth slightly open. The neuron did not respond to monkeys with their mouths closed and monkeys with their mouths wide open. Thus the response of this neuron depended on the expression on a monkey's face. This property might be expected of cells functioning to regulate social behavior. A small number of amygdaloid neurons (4/19 tested) responded differentially to

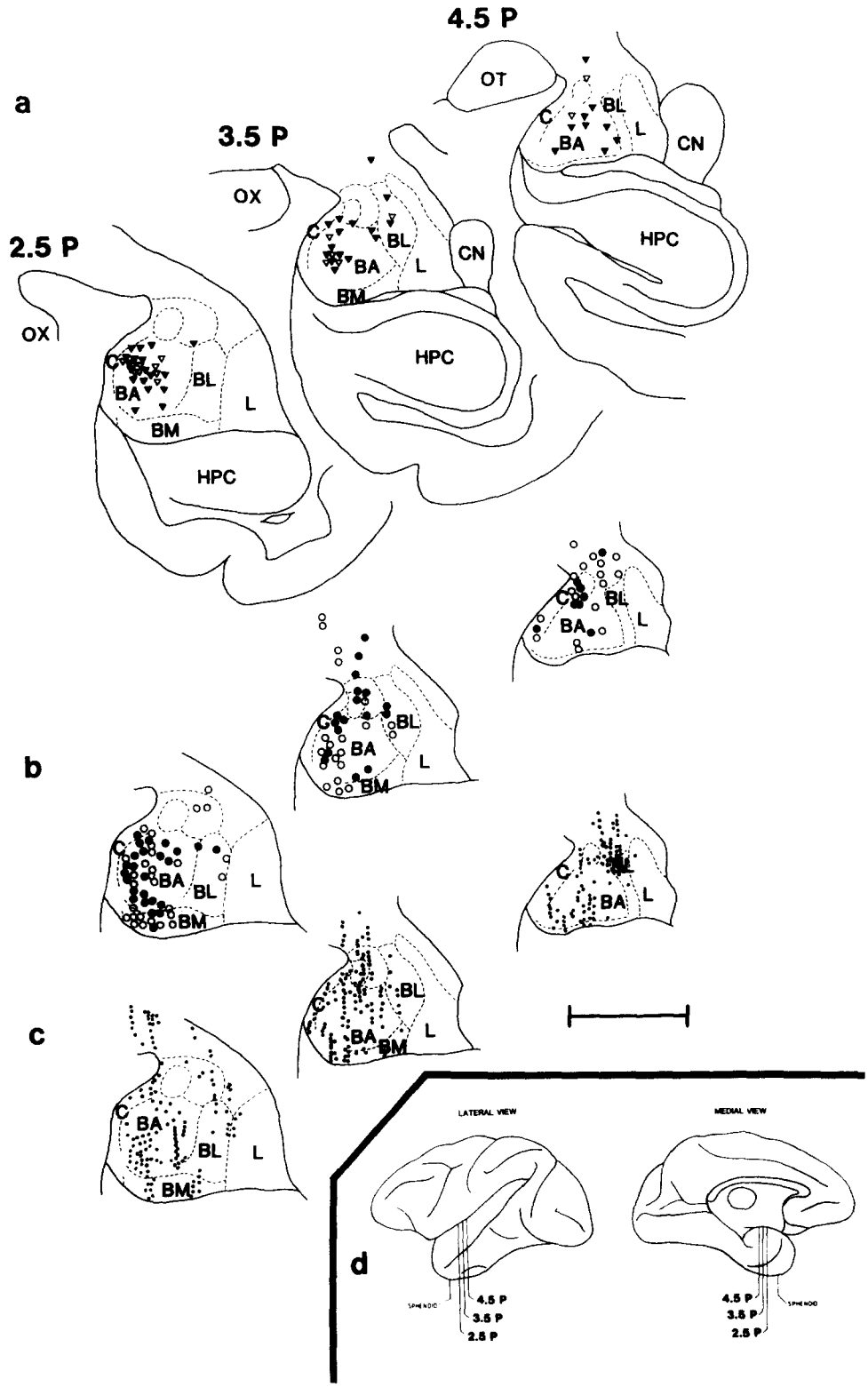



Fig. 8. a: The distribution of neurons responsive to faces in the amygdala of the four monkeys. The cells are plotted on three coronal sections at different distances (in mm) posterior (P) to the sphenoid. Filled triangles: cells selective for faces; open triangles: cells responding to face and hands. b: Other responsive neurons. Closed circles: cells with other visual responses; open circles: cells responding to cues, movement, or arousal. c: The locations of non-responsive cells. Abbreviations: BA, basal accessory nucleus of the amygdala; BL, basolateral nucleus of the amygdala; BM, basomedial nucleus of the amygdala; C, cortical nucleus of the amygdala; CN, tail of the caudate nucleus; HPC, hippocampus; L, lateral nucleus of the amygdala; OT, optic tract; OX, optic chiasm.

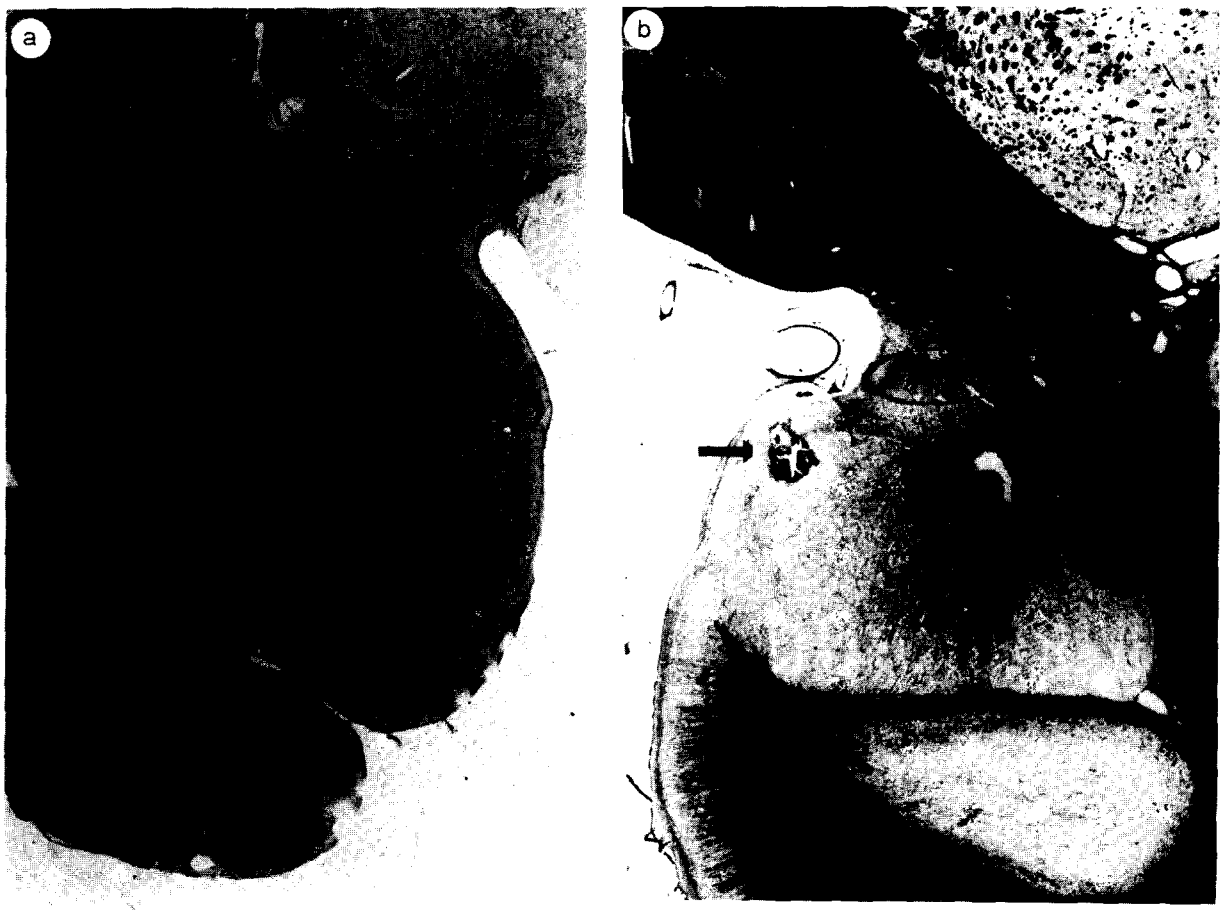



Fig. 9. Examples of histological sections to show the recording sites, marked by lesions, of neurons in the amygdala which responded to faces. a: a lesion on the medial edge of the basal accessory nucleus of monkey R. Cresyl violet stain. b: a lesion on the edge of the basal accessory nucleus of monkey Y. Myelin stain.

threat as compared to non-threat faces, and thus their responses could have reflected the emotional value of a face. The other neurons with face-selective responses did not appear to respond along such a simple continuum, but in that they responded differently to different faces, and these faces were often of monkeys of different ages or with different expressions, it is possible that these neurons conveyed information which could be useful in making differentiated emotional responses. We thus conclude that the responses of these neurons are consistent with the hypothesis that they could be used to produce different emotional and social responses to faces, but that in only a few cases (4/19 neurons tested) was there any evidence that these neurons could reflect emotionality in a simple test in which the expression on a face was changed to a threat. Further tests to investigate how the responses of these neurons depend on eye contact would be of interest, for this is an important determinant of the emotionality of a face.

In that each of these amygdaloid neurons did not usually respond to only one face even in the limited set of faces tested, and in that a particular face activated 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 different responses, including different emotional responses, to be made to different faces or to different expressions.

It was notable that this population of neurons was a relatively small proportion of the sample of neurons recorded in the amygdala (21/312 for example in one monkey, or 30/488 in 3 monkeys in which all amygdaloid neurons were tested for responses to faces). Other neurons recorded often responded to some but not other visual stimuli without any clear categories being apparent, but one group of neurons responded particularly well to faces and to hands. Eleven of 22 of these neurons recorded in one monkey responded only to these stimuli from the wide range tested.

These neurons were recorded in and around the basal accessory nucleus of the amygdala, a nucleus prominent in the primate but probably absent in the rodent[2,25,41]. This part of the amygdala receives inputs from relatively anterior temporal lobe cortex, area TG, but probably not directly from the cortex in the superior temporal sulcus[1] in which we have described neurons which responded selectively to faces[4,22,34]. Possible routes by which the amygdaloid neurons described here receive their inputs are via a stage of processing in area TG which in turn may be influenced by processing within the cortex in the anterior part of the superior temporal sulcus, or via intra-amygdaloid connections from more lateral parts of the amygdala, which do receive directly from the cortex in the anterior part of the STS. These possibilities are now being investigated.

The neurons responsive to faces exhibited a wide range of selectivity (see Fig. 3). The selectivity was frequently more marked between (real) human faces than between (photographic) monkey faces, whereas in the cortex in the superior temporal sulcus the majority of cells generalized among (real) human faces (see Fig. 7). This relatively greater selectivity of amygdaloid neurons was shown when real faces were used, and it is possible that the amygdaloid neurons were sensitive to subtle differences present in the real faces. This study was not designed to define all the differences, but to determine if a population of face responsive neurons could be identified in the amygdala. It will be of interest in future to investigate how potentially important factors such as the age and experience of the monkey, and subtle differences in facial expression, affect the responses of these neurons in the amygdala.

The latencies of the visual responses in the amygdala were longer and frequently more variable than those found in the STS to the same stimuli. This suggests that additional neuronal processing is occurring between the cortical response to faces and that seen subcortically. Presumably the response to the face is being integrated with a variety of information from the internal and external environment. The basal accessory nucleus is appropriately placed to receive such information by ascending pathways from the brainstem and hypothalamus and descending information from the cortex. One of the major projections of this nucleus is to the medial orbitofrontal cortex[24]. It is thus of interest that this cortical region has been implicated in the control of social behavior[18]. A problem for future research would be to determine whether information about faces, or information about the appropriate response to faces is transmitted from the amygdala to this cortical region.

These findings provide evidence that in the amygdala, there is a neuronal system specialized to respond to faces. Damage to the amygdala produces tameness and socially inappropriate behavior, and it is suggested that these aspects of the Kluver–Bucy syndrome are due to disruption of this neuronal system specialized to mediate responses to faces. Indeed, the lack of the normal emotional responses to the sight of a face found in the Kluver–Bucy syndrome suggests that the elicitation of appropriate emotional responses to faces is a function of these neurons. Similarly, the altered social behavior of monkeys produced by amygdala lesions, in which the lesioned monkeys do not respond appropriately to other monkeys in the group and so are unable to maintain their normal position in the dominance hierarchy[18], may be due, it is proposed, to damage to a neuronal system specialized for the perception of and elicitation of appropriate emotional responses to different individuals. The importance for social

behavior in the primate of the rapid and reliable recognition of individuals by the sight of the face could provide selection pressure which would allow a neuronal system specialized for this processing to evolve. As the responses of the majority of the amygdaloid neurons did not reflect the degree of the emotional response of the monkey made to the different faces, their activity probably does not represent the general emotionality of a face. Rather, it is possible that these neurons are part of a lookup or association mechanism for emotional responses to faces. Under this hypothesis, their firing could reflect the function of a series of perceptual filters which provide the input to this mechanism, it could reflect activity in the association mechanism itself, or it could reflect a set of outputs which code for the subtly different facial expressions present in the stimulus set.

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