Human Neurobiol (1984) 3:209–222

Human Neurobiology

Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces

E. T. Rolls

University of Oxford, Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD, UK

Summary. There are populations of neurons in the temporal lobe of the macaque which appear to be specialised to respond to faces. These neurons are relatively rare in the inferior temporal visual cortex, area TE, but are more common in the cortex in the middle and anterior parts of the superior temporal sulcus. In some cases these neurons can respond to parts of faces such as the eyes, and in other cases a fuller complement of the features present in faces, with even the correct configuration of these features, appears to be necessary for these neurons to respond. In experiments to investigate whether the responses of these neurons would be useful for recognition of an individual, it has been shown that in many cases (77% of one sample), these neurons are sensitive to differences between faces. In experiments designed to investigate the information required for these neurons to respond, it has been shown that these neurons can respond to blurred images of faces, and to faces with only the high spatial frequencies included. A population of neurons with face-selective responses has also been found in the amygdala, which receives inputs from the temporal lobe visual cortex. In many cases these neurons respond differently to different faces. It is suggested that the importance of this type of neuron may be in the different emotional and social responses which occur to different faces, and which are disrupted by damage to the amygdala.

Key words: Inferior temporal cortex – Amygdala – Face – Emotion – Recognition – Ensemble coding

There have been reports in the clinical literature for many years of deficits in face recognition (prosopagnosia) after damage to the brain in the occipito-temporal region in man (see Meadows 1974; Whiteley and Warrington 1977; Benton 1980; Damasio et al. 1982). It is also known that bilateral damage to the temporal lobe of the monkey leads to the Kluver-Bucy syndrome, in which the lesioned monkeys become tame, repeatedly fail to avoid noxious stimuli, and select and place in their mouths non-food as well as food items (Kluver and Bucy 1939; Jones and Mishkin 1972). The syndrome can be produced by lesions of the temporal lobe which damage primarily the amygdala (Weiskrantz 1956), and has also been described in man (Terzian and Dalle Ore 1955). Damage to the amygdala also leads to a failure of normal social interactions with other monkeys (Kling and Steklis 1976; Kling 1981). In this paper, recordings of the activity of single neurons in the temporal lobe which respond to faces, and which appear to be relevant to understanding the deficits in face recognition and in emotional and social responses to faces produced by brain damage in the primate are described. The recordings were made in a non-human primate, the rhesus monkey, in order to make them as relevant as possible to understanding these mechanisms and their defects in man.

Visual inputs reach the inferior temporal visual cortex (area TE of von Bonin and Bailey 1947; areas 20 and 21 of Brodmann 1909) on the inferior convexity of the monkey temporal lobe via a number of prestriate visual cortical areas, the inputs to which originate in the primary visual cortex (the striate cortex, area 17) (Jones and Powell 1970; Chavis and Pandya 1976; Streitfield 1980). In the dorsally adjacent cortex in the anterior and middle parts of the superior temporal sulcus there are a number of different cortical regions (Seltzer and Pandya 1978), as follows. Area TE itself extends across the ventral lip of the sulcus, there is an area in the ventral bank which receives from area TE, and in addition there are areas which receive from the parietal cortex (area 7) and from the superior temporal (auditory association) cortex. The amygdala of the primate receives major inputs from the temporal lobe cortex, including the inferior temporal visual cortex and the cortex in the superior temporal sulcus (Jones and Powell 1970; Herzog and Van Hoesen 1976; Aggleton et al. 1980; Turner et al. 1980).

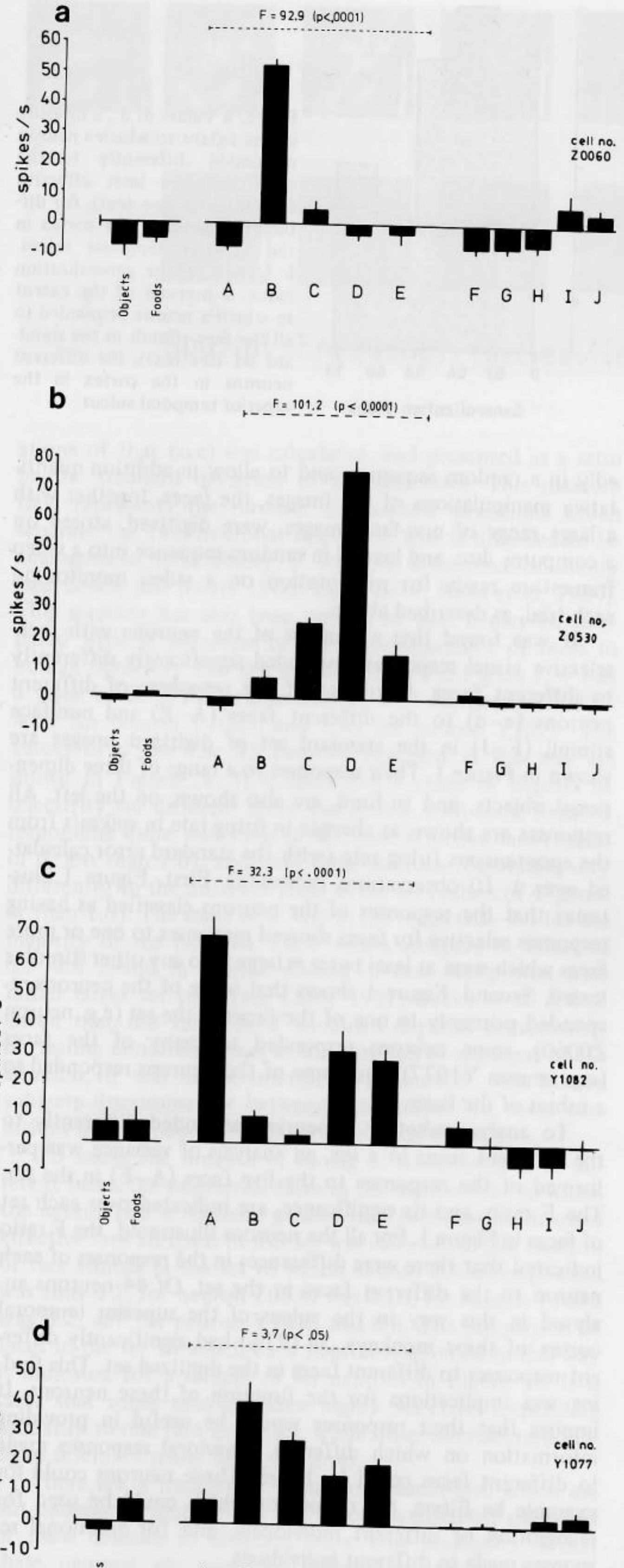
Given that damage to the inferior temporal visual cortex impairs visual discrimination learning (see Dean 1976), that visual inputs reach the amygdala via the temporal lobe visual cortex, and that many of the deficits produced by damage to the amygdala can be accounted for by a deficit in learning to associate stimuli with reinforcement (Jones and Mishkin 1972; Spiegler and Mishkin 1981; Rolls 1985), Rolls and his colleagues have analysed the activity of neurons in the inferior temporal visual cortex and amygdala during visual discrimination and feeding behavior (Rolls et al. 1977; Sanghera et al. 1979; Rolls 1981a, b, 1984). During these investigations, small populations of neurons were found which responded well to faces, but not to other stimuli. For example, Rolls et al. (1977) found some neurons in the temporal visual cortex which did not respond to the discriminanda, or to a range of three-dimensional objects, but did respond to faces. Bruce et al. (1981) also reported that 7 of 199 neurons tested in the cortex in the superior temporal sulcus had responses which appeared to be selective for faces. In the amygdala, a small number of neurons was also observed which had visual responses which occurred selectively to faces (Sanghera et al. 1979; Rolls 1981b). 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 stimuli, other complex 3-D stimuli, arousing and aversive stimuli such as the sight of the syringe from which the monkey was fed saline, or to tactile or auditory stimuli which produced arousal, and (4) had response latencies of 100–180 ms. Examples of these neurons were found in all five monkeys in which recordings were made in the amygdala. Nine of the neurons responded to faces by increasing their firing rates, and two neurons responded (by an increase of firing rate) to all stimuli shown except faces. An additional six neurons in the category of neurons with possible or longer latency visual responses also responded selectively to faces (Rolls 1981b).

Having seen that neurons in the temporal lobe can respond apparently with some selectivity to faces, a more detailed analysis of their responses was performed (Perrett et al. 1979, 1982). Of 497 cells recorded in the cortex in the superior temporal sulcus, 48 responded selectively to faces. 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 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 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 rections, and 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 neurons in the cortex in the superior temporal sulcus (Perrett et al. 1982). Observations consistent with these findings have recently been published by Desimone et al. (1984), who described a similar population of neurons located primarily in the cortex in the superior temporal sulcus which responded to faces but not to simpler stimuli such as edges and bars or to complex non-face stimuli.

Methods and criteria used to identify neurons with responses selective for faces

In order to allow quantitatively defined visual stimuli to be presented, and the responses of the neurons to them to be measured fully objectively, the following methods have been developed and are being used for the studies described below (Baylis et al. 1985; Rolls et al. 1985; Leonard et al. 1985). The visual stimuli are presented in one of two ways. First, stimuli are digitized, stored on computer disc, and displayed on a video monitor using a video framestore. The resolution of these images is 256 pixels wide by 256 pixels high with 256 gray levels. A computer randomizes the order of presentation of these stimuli, switches the stimuli on and off for each trial, and synchronizes its data collection so that the stimulus is turned on at the start of the 21st bin of a peristimulus time histogram. This method allows completely standardized and randomized presentation of quantitatively specified stimuli as diverse as sine wave gratings and faces, and allows image processing techniques such as spatial frequency filtering and subregion extraction to be applied to the stimuli presented. Second, visual stimuli can be presented by the opening of a fast rise time (less than 15 ms), large aperture shutter (Compur Electronic 5FM, 6.4 cm aperture) which opens for 1.5 s after a 0.5 s signal tone (400 Hz) provided to allow the monkey to fixate before the shutter opens. The stimuli are presented against a uniform background (a large white screen). This method allows the presentation of three-dimensional stimuli such as real faces and 3-D objects which differ along a wide range of parameters such as size, shape, and color, and also allows 2-D stimuli such as photographs of a wide range of faces to be presented.

The monkeys are alert and perform a visual discrimination task during the testing to ensure that they look at the stimuli. [Although Bruce et al. (1981) have found neurons in the cortex in the superior temporal sulcus which respond to faces in the anesthetized monkey, the neuronal response latencies reported were long, in the range 200–300 ms, compared with typical latencies of 80–150 ms in the studies described here. Because of this possible interference by anesthetic with the activity of these neurons in this high order part of the visual system, and because the risk must be even greater in structures further on such as the amygdala, all the recordings described here are being made in the alert preparation.] 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 (Rolls et al. 1979). 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. Recordings of the electro-oculogram confirmed that this procedure resulted in consistent fixation of the stimuli.



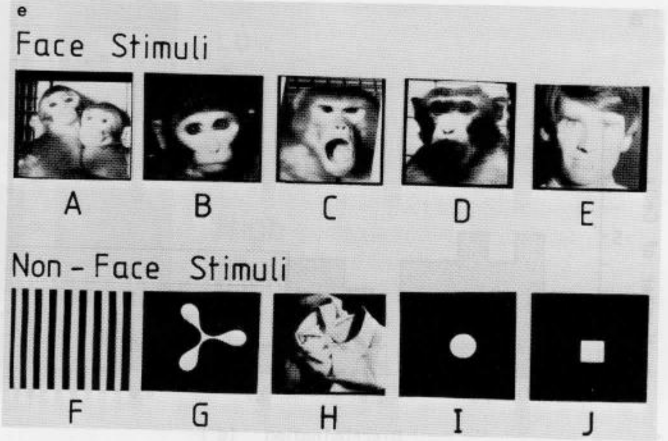


Fig. 1a–e. The responses of four cells (a–d) in the cortex in the superior temporal sulcus to a variety of face (A–E) and nonface (F–J) stimuli. Some of the stimuli are shown in e. A: Two infants; B: Juvenile; C: 5-year-old threat face; D: 10-year-old stare; E: Human experimenter; F: Complex texture; G: Spatial grating; H: Boundary descriptor; I: Circle (S^+); J: Square (S^-). The bar represents the mean response above baseline with the standard error calculated over 4 to 10 presentations. The F ratio for the analysis of variance calculated over the face sets indicates that the units shown range from very selective to relatively nonselective between faces. The responses to three-dimensional objects and to foods are shown on the left

When digitized visual stimuli were being presented on the video monitor, one set of 5–10 visual stimuli was 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 of stimuli included five 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 Figure 1e), 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 5–10 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.

Two main criteria are being used in these studies to select neurons with responses which occur primarily to faces for analysis. First, their responses to one or more faces had to be at least twice as large as to any other of the wide range of visual stimuli tested. (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 five times as large as to the most effective non-face stimulus, and for 25% of these neurons, the ratio was greater than 10:1.) Second, an analysis of variance performed over the set of face and non-

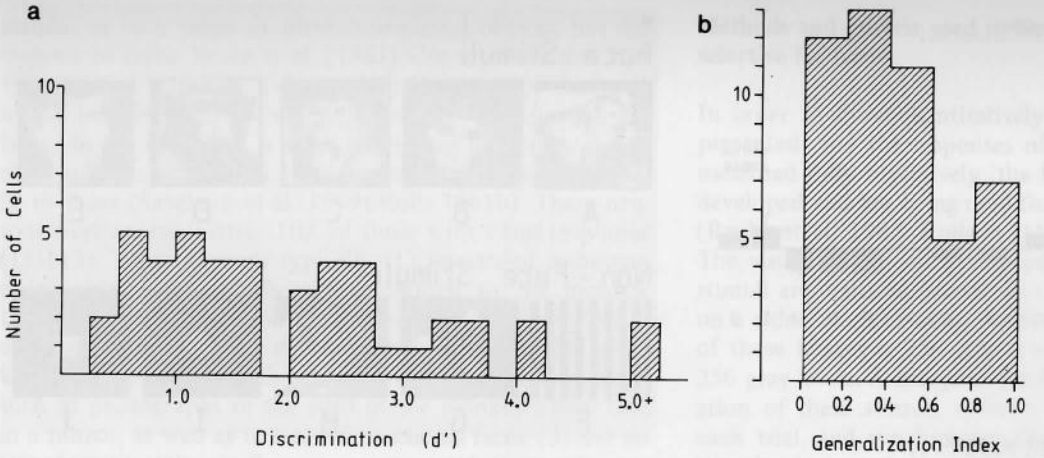


Fig. 2. **a** Values of d', a measure of the extent to which a neuron responded differently to the most and the least effective face stimulus (see text), for different neurons in the cortex in the superior temporal sulcus. **b** Values of the generalization index, a measure of the extent to which a neuron responded to all the face stimuli in the standard set (see text), for different neurons in the cortex in the superior temporal sulcus

face stimuli should show a significant effect of stimulus type, and subsequent multiple t, Tukey, and Newman-Keuls' analyses (see Bruning and Kintz 1977) should show that the response to the optimal face stimulus was significantly greater ($p < 0.05$) than the response to the optimal non-face stimulus. (In fact, the difference was significant at the 0.01 level for the great majority of the neurons described in this paper.) It should be noted that the neurons were tested on a wide range of non-face stimuli. These included a set of sine wave gratings with spatial frequencies of 1–64 cycles/image and with orientations spaced pi/4 radians apart; a set of boundary curvature descriptors with frequencies of 0–15 cycles, with amplitudes which ranged from 0.5–2.0, and with 4 different phases (Schwartz et al. 1983); and three-dimensional objects. Over one thousand of these three-dimensional objects were collected, and used to test whether responses could be obtained from neurons to a wide range of non-face complex stimuli. 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.

Neurons in the cortex of the superior temporal sulcus with different responses to different faces

If these neurons in the cortex of the superior temporal sulcus with responses to faces 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. In the study by Perrett et al. (1982) 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 Perrett et al. 1982). It was the aim of the next study (Baylis et al. 1985) 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 disc, and loaded in random sequence into a video framestore ready for presentation on a video monitor on each trial, as described above.

It was found that a number of the neurons with face-selective visual responses responded significantly differently to different faces. 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 Figure 1. Their responses to a range of three dimensional 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, Figure 1 illustrates that the responses of the neurons classified 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, Figure 1 shows that some of the neurons responded primarily to one of the faces in the set (e.g. neuron Z0060), some neurons responded to many of the faces (e.g. neuron Y1077), and some of the neurons responded to a subset of the faces.

To analyse whether a neuron responded differently to the different faces in a set, an analysis of variance was performed of the responses to the five faces (A–E) in the set. The F ratio, and its significance, are indicated over each set of faces in Figure 1. 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 analysed in this way in the sulcus of the superior temporal cortex of three monkeys, 34 (77%) had significantly different responses to different faces in the digitized set. This finding was implications for the function of these neurons. It implies that their responses would be useful in providing information on which different behavioral responses made to different faces could be based. These neurons could for example be filters, the output of which could be used for recognition of different individuals, and for emotional responses made to different individuals.

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 present-

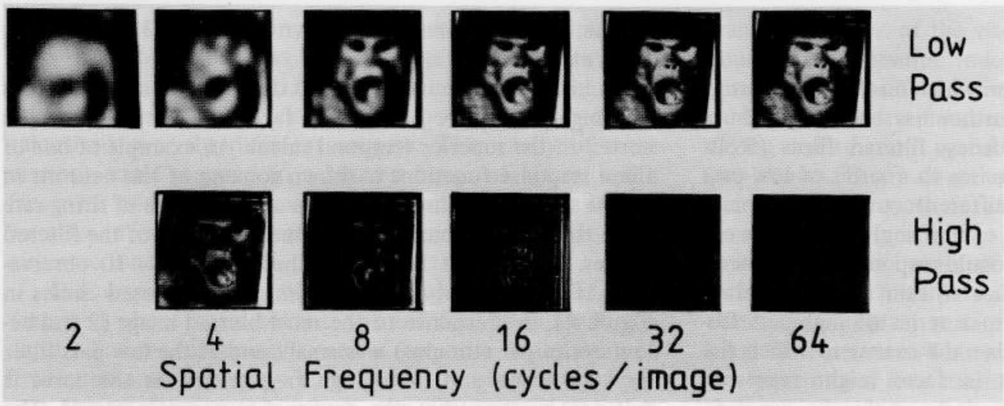


Fig. 3. Examples of the low-pass and high-pass spatial frequency filtered face stimuli

ations of that 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 Green and Swets 1966; Egan 1975; Rolls et al. 1984). This measure has also been chosen so that it may be compared with d′ measures of the discriminability of faces to human observers. For the neurons shown in Figure 1, 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 45 neurons analysed in this way are shown in Figure 2a. 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). The value of d′ was in the range 0.2–5.0 for the majority of the neurons. These values compare to values of 0.5–2.4 found in human studies of face recognition with rather larger set sizes (see Carey 1981; Davies et al. 1981). 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 same conditions used in neurophysiological investigations.

To assess the breadth of tuning of these neurons to different faces, 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. The fraction of face stimuli in the set to which neuron Z0060 responded was thus 0.2, for neuron Z0530 was 0.16, for neuron Y1082 was 0.2, and for neuron Y1070 was 0.6. The proportion of faces in the set to which each neuron responded in this way is indicated for a sample of 48 neurons in Figure 2b. 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.

There are a number of possible explanations, which are not necessarily mutually exclusive, of the different responses of these neurons to different faces. 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 face making an open-mouth threat, whereas another had the mouth closed. However, 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). This makes it unlikely that differences in expression accounted for the differences in the responses of the majority of the neurons recorded in this particular population. 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. 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 (see Baylis et al. 1985), and in addition fixation of the different faces in the set was shown by the electro-oculogram 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 to different faces is raised by the finding that in different monkeys some faces were more often optimal stimuli for the neurons than other faces. For example, 9/17 cells in one monkey, Yasmin, responded best to stimulus A (the two weanling monkeys, see Figure 1), whereas only 1/28 of the cells in the other two monkeys in which recordings were made in this study responded best to stimulus A (Baylis et al. 1985). 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, to resolve the contributions of age and experience to the tuning of these neurons, detailed longitudinal studies in animals of different ages and with different experience are required. The findings described here do raise the possibility that these factors do influence the tuning of these neurons in the cortex in the superior temporal sulcus which respond primarily to faces.

Spatial frequency

One way in which the information which leads these neurons to respond has been analysed further has been to measure their responses to spatial frequency filtered faces (Rolls et al. 1985). For example, responses to a series of low-pass frequency filtered faces with different cutoff frequencies (i.e. faces with different degrees of blurring) showed the extent to which different neurons could respond to the general configuration of features in a face without any fine detail. Responses were also measured to a series of high-pass frequency filtered faces to determine the extent to which the sharp edge information present in faces might represent sufficient information for the responses of these neurons to occur. Spatial frequency filtering in fact provided a way to parametrically alter the information present in a face and thus to obtain evidence on the type of information to which these neurons respond. In addition to allowing analysis of the information which leads these neurons to respond, these experiments (Rolls et al. 1985) allowed comparisons to be made between the spatial frequencies in faces to which these neurons respond and the spatial frequencies necessary for face recognition by humans. Thus Harmon and Julesz (1973) and Harmon (1973) have shown that frequencies below 10 cycles/face image are sufficient for humans to recognize faces to at least some extent. Fiorentini et al. (1984) have extended this by showing that spatial frequencies above 8 cycles/face, as well as those below 8 cycles/face, are adequate for recognizing different individuals' faces. It was thus of interest to determine how the responses of these neurons compared to those found to be important for face recognition.

In order to provide a completely standardized method of presenting a set of precisely spatial frequency filtered images repeatedly in a random sequence, faces, together with a large range of non-face images, were digitized, spatially frequency filtered on a PDP11 computer, stored on the computer disc, and loaded in random sequence into a video framestore ready for presentation on a video monitor on each trial. Examples of the filtered stimuli are shown in Figure 3 (see further Rolls et al. 1985).

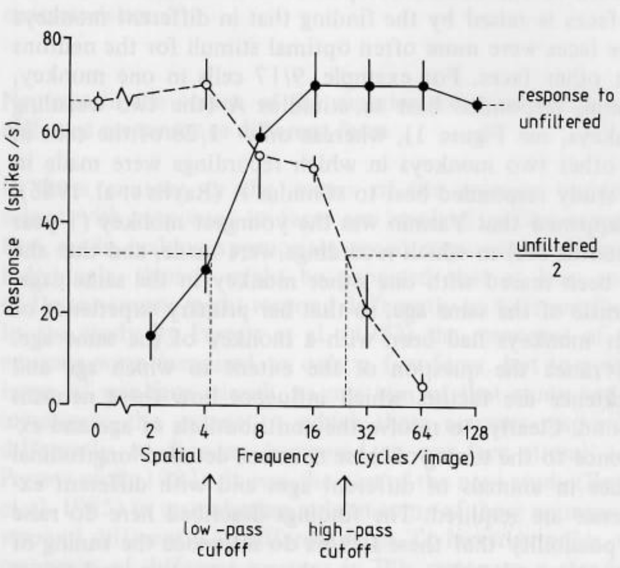


Fig. 4. The responses of a neuron in the cortex in the superior temporal sulcus to the low-pass (closed circles) and high-pass spatial frequency filtered images of a face

It was possible to measure the responses to low-pass and high-pass filtered images of faces of 32 neurons in the cortex in the superior temporal sulcus. An example of one of these response functions is shown for one of the neurons in Figure 4. The responses are shown as the change of firing rate from the spontaneous value produced by each of the filtered images. Each point represents the mean of 4–10 observations. For the low-pass filtered images (see closed circles in Figure 4), the response to the most blurred image (2 and below cycles per stimulus) was small, and as the low-pass filter included more and more high frequencies (as the curve is followed to the right), the neuronal response increased. The unfiltered image is plotted at the 128 cycles per stimulus point on the low-pass graph, as this represented all frequencies in the 256 by 256 pixel image. For the highpass filtered images (see open circles in Figure 4), the response to the image with only the highest frequencies included (64 and above cycles per image) was small, and increased as the high-pass filter included more and more low frequencies (as the curve is followed to the left). The unfiltered image is plotted at the 0 cycles per stimulus point on the low-pass graph, as this represented all frequencies in the 256 by 256 pixel image.

To enable the response functions of the different neurons to be compared, high-pass and low-pass cutoff frequencies were obtained from the curves as follows. The cutoff frequencies were measured from the curves as the frequencies at which the response had decreased to half its value to the unfiltered stimulus. Interpolation was used along the logarithmic frequency axis. Thus for the neuron illustrated in Figure 4, the low-pass cutoff frequency was 4.3 Hz, and the high-pass cutoff frequency was 24.3 Hz. The difference between these cutoff frequencies was also calculated to give an estimate of the bandwidth of the neuron, and for the example shown in Figure 4 was 4.6–2.1 (i.e. 2.5) octaves. The distribution of these cutoff frequencies for the low-pass and the high-pass filtered stimuli is shown for the different neurons in Figure 5. It is clear from Figure 5 and the response functions of the different neurons (see Rolls et al. 1985) that the cutoff frequencies and the pattern of the responses to the filtered stimuli were different for the different cells. The mean value of the low-pass cutoff frequency was 3.3 Hz, and for the high-pass cutoff frequency was 29.7 Hz.

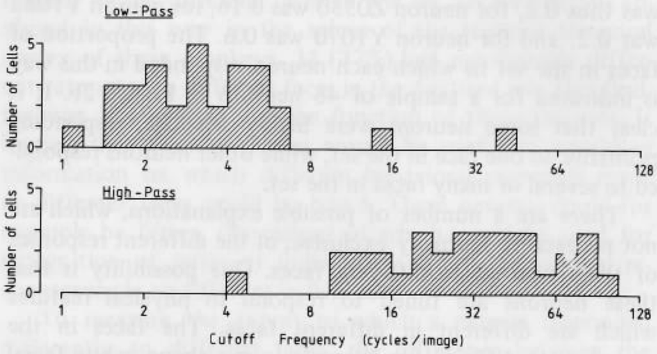


Fig. 5. The low-pass and high-pass cutoff frequencies to spatial frequency filtered faces of different neurons in the cortex in the superior temporal sulcus

It was found that many of the neurons could respond to a low-pass and a high-pass filtered image of a face even when the filtered images had no frequencies in common. The mean separation between the cutoff frequencies was 3.0 octaves, calculated over the different neurons. Thus many of these neurons could respond to a blurred image of a face, and a face with primarily edge information in it, when these images were so different that their nearest common spatial frequencies were 3 octaves apart.

The responses to low-pass and high-pass filtered faces described above were to the optimal face stimulus in the digitized series. Different types of response were obtained if the neuronal response was measured to low-pass and high-pass images from a face which was not optimal for that neuron (see Rolls et al. 1985). For example, some neurons responded less or not at all to most of the filtered stimuli of the non-optimal face as compared to the optimal face. On the other hand, more interestingly, other neurons responded to some but not to other of the filtered stimuli of the non-optimal face stimulus. This is consistent with the possibility that information relevant to some aspects of the neuron's criteria for responsiveness were met by some of the filtered stimuli, but that introducing further frequencies from the non-optimal face introduced information which produced inhibition and was normally responsible for the lack of response of the neuron to the non-optimal face.

The responses of these neurons to low-pass and high-pass filtered faces show that these neurons can in many cases respond to simplified images of faces, that is to faces in which considerable information has been removed. The responses to these filtered images also indicate the type of information necessary to activate these neurons. For example, many of the neurons responded to low-pass filtered faces which included frequencies up to 4 cycles/face (see Figures 4 and 5 and Rolls et al. 1985). These images are very blurred (see Figure 3) and contain relatively little information. This opens the way for further analyses of the minimal stimulus configuration necessary to activate these neurons. For example, it will be of interest to determine how rearrangement of different parts of these low-pass filtered images of faces influences the responses of these neurons, to determine how sensitive these neurons are to the configuration of the features present in these images. Many of the neurons also responded to high-pass filtered images of faces which included only frequencies above 16 cycles/face (see Figures 4 and 5 and Rolls et al. 1985). Thus low frequencies are not essential for the activation of these neurons, and edge information is sufficient. It is of interest that in many cases a neuron could be activated by either low frequencies or high frequencies present in a face (see Figures 4 and 5 and Rolls et al. 1985), even when these frequencies were separated by 3 octaves. This could be useful in a system in which responses to a face should occur irrespective of whether the face was blurred or was presented as edges, as in a line drawing. It may be noted here that it is a property of human perception that objects including faces can be recognized even when an object is blurred, and even when a line drawing of an object containing only edge information is presented.

The tuning of the neurons to the different low-pass and high-pass filtered faces was different for the different neurons (see Rolls et al. 1985), so that an explanation for the tuning in terms of a single function such as the overall modulation transfer function of the visual system is not sufficient to account for the results. Indeed, the fact that the neurons responded differently to the different frequencies is further evidence that these neurons could act as filters useful in conveying information useful in distinguishing between faces (see above). The finding that the response of the neurons was not always a smooth function of frequency, but could for example decrease as higher frequencies were included in the low-pass filtered images of faces or as low frquencies were included in the high-pass filtered images of faces, indicates that information in certain frequency bands was able to inhibit these neurons. This was particularly likely to occur for the non-optimal face stimulus for a given neuron, indicating that the selectivity of these neurons to different faces was a combination of the excitation produced by some aspects of faces and inhibition produced by others. Such inhibition was particularly likely to occur for high spatial frequencies, implying that these frequencies might be particularly important in distinguishing between individual faces.

Harmon and Julesz (1973) and Harmon (1973) have shown that low spatial frequencies, below for example 10 cycles/face, are sufficient for the recognition of the faces of different individuals in man. Fiorentini et al. (1984) have extended this work, and shown that the spatial frequencies above 8 cycles/face present in a face can also provide the basis for face recognition. It is of interest that the great majority of the cells described here had low-pass cutoff frequencies below 8 cycles per face, that is they responded well to faces containing only frequencies below 8 cycles/face (see Figure 5). Similarly, the great majority of the cells described here had high-pass cutoff frequencies above 8 cycles per face (and even above 16 cycles/face), that is they responded well to faces containing only frequencies above 8 cycles/face (see Figure 5). Thus almost all of the cells described here responded well to both the low frequencies shown by Harmon and Julesz (1973) to be sufficient for face recognition, and to the high spatial frequencies shown by Fiorentini et al. (1984) to be sufficient for face recognition. The responsiveness of these neurons to both low and to high spatial frequencies present in faces could thus provide a basis for these psychophysical findings.

One series of investigations which would provide useful further evidence on this neural system would be to determine to what extent these neurons can distinguish between different faces when these are low-pass or high-pass filtered with cutoff frequencies of 8 cycles per face. There is some evidence that even when frequencies below 8 cycles/face are included in the stimulus, the neurons still respond differently to different faces. Although more experiments on this are needed, this preliminary evidence suggests a very close parallel between the ability of the human observer to distinguish between the faces of different individuals when only for example low spatial frequencies are present, and a corresponding property of the neurons described here.

The relatively wide range of frequencies within which information can activate these neurons is of interest in relation to the hypotheses that there are tuned spatial frequency channels at earlier stages of the visual system. The width of these channels has been estimated as 1.5 octaves (Campbell 1983; Kulikowski et al. 1982). Insofar as the neurons described here can respond to information from a wider frequency range than this, if there are spatial frequency chan-

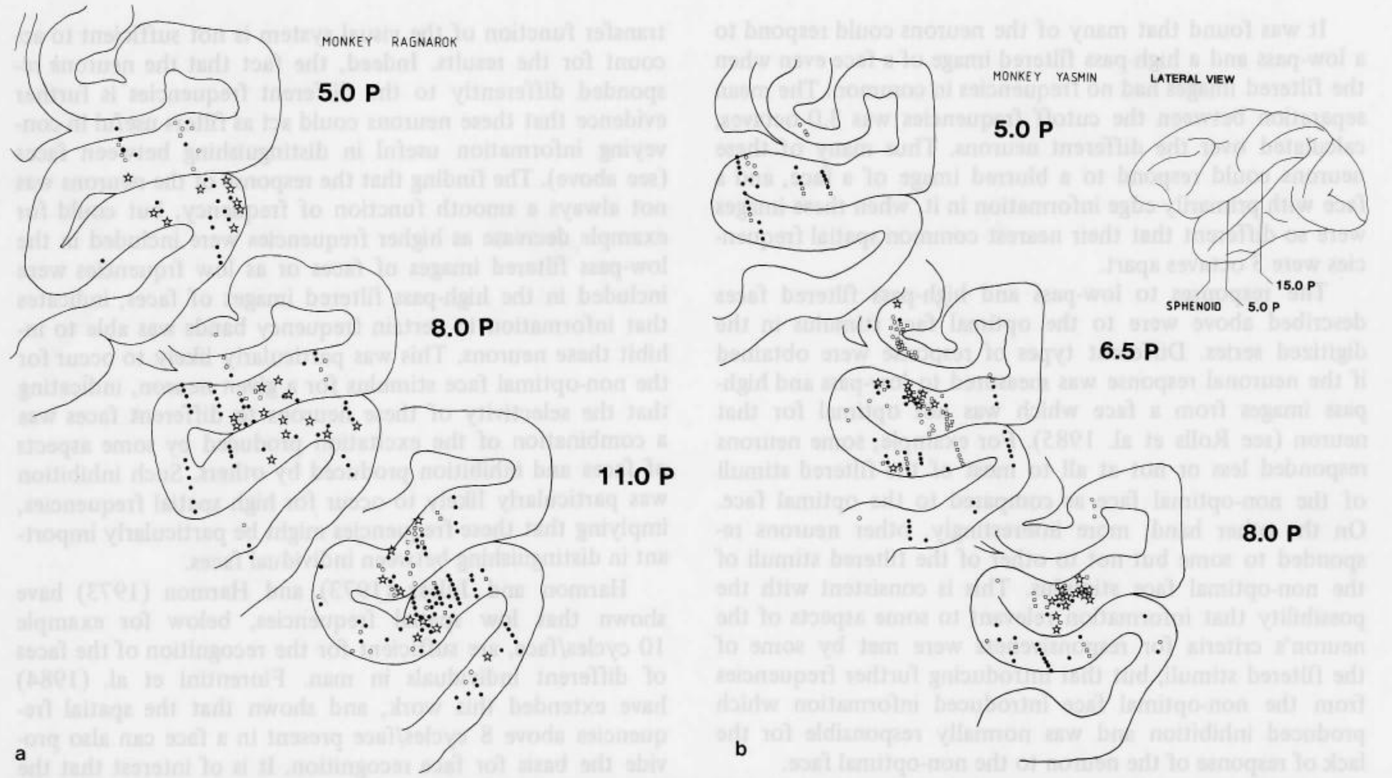


Fig. 6a and b. The locations of neurons with responses selective for faces (stars) and of other responsive neurons in the cortex in and near the superior temporal sulcus. Squares: neurons selective for moving visual stimuli; closed circles: neurons with other visual responses; open circles: neurons responding to sounds, movements made by the monkey, or arousal. **a** and **b** show the recording sites in two different monkeys. The inset to **b** shows where the coronal sections are taken, in mm posterior to the sphenoid process, which was 18–21 mm anterior to the external auditory meatus in these rhesus monkeys

nels earlier in the visual system, than information from these channels would need to be recombined (in a particular way) in order to account for the width of tuning of the neurons described here. It is also worth noting here that although the neurons described here are tuned to accept information in a certain range of spatial frequencies, this does not mean that any power in this frequency band will activate these neurons. Indeed, the contrary is the case, in that these neurons were activated by only some of the face stimuli and not by non-face stimuli such as gratings or complex stimuli, so that to the extent that their response properties depend on the spatial frequency of the stimulus, an additional constraint is that the phase information within this frequency band must also be appropriate.

Location of these neurons in the temporal visual cortex

The sites at which these neurons were recorded are shown in Figure 6. The majority of the neurons with face-selective responses were in the cortex in the middle to anterior part of the superior temporal sulcus, in for example cytoarchitectonic area TPO (Seltzer and Pandya 1978), and on the ventral lip of the sulcus. It should be noted that although these neurons are in the cortex in the superior temporal sulcus, they are very far anterior to area MT (Newsome and Wurtz 1982).

Neurons in the amygdala of the monkey with responses selective for faces

Bilateral damage to the temporal lobe of primates leads to the Kluver-Bucy syndrome, in which the lesioned monkeys select and place in their mouths non-food as well as food items, repeatedly fail to avoid noxious stimuli, and are tame (Kluver and Bucy 1939; Jones and Mishkin 1972). The syndrome is produced by lesions of the temporal lobe which damage primarily the amygdala (Weiskrantz 1956). Damage to the amygdala also leads to a failure of normal social interactions with other monkeys (Kling and Steklis 1976; Kling 1981).

Given that damage to the amygdala alters emotional and social responses to faces (see Introduction), and that some neurons have been found in the amygdala which respond to faces (Sanghera et al. 1979; Rolls 1981b), a more detailed investigation has been performed to obtain further information on the neurons in the amygdala which respond to faces (Leonard et al. 1985). 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, and 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.

Recordings were made from more than 1000 neurons in the amygdalas of 4 monkeys (Leonard et al. 1985). Of these neurons, approximately 12% were found to have visual responses, using the critera defined previously (Sanghera et al. 1979). 36 of the visual neurons responded primarily to faces, and the responses of these neurons are described next.

Examples of the responses of neurons recorded in the amygdala which responded preferentially to faces are shown

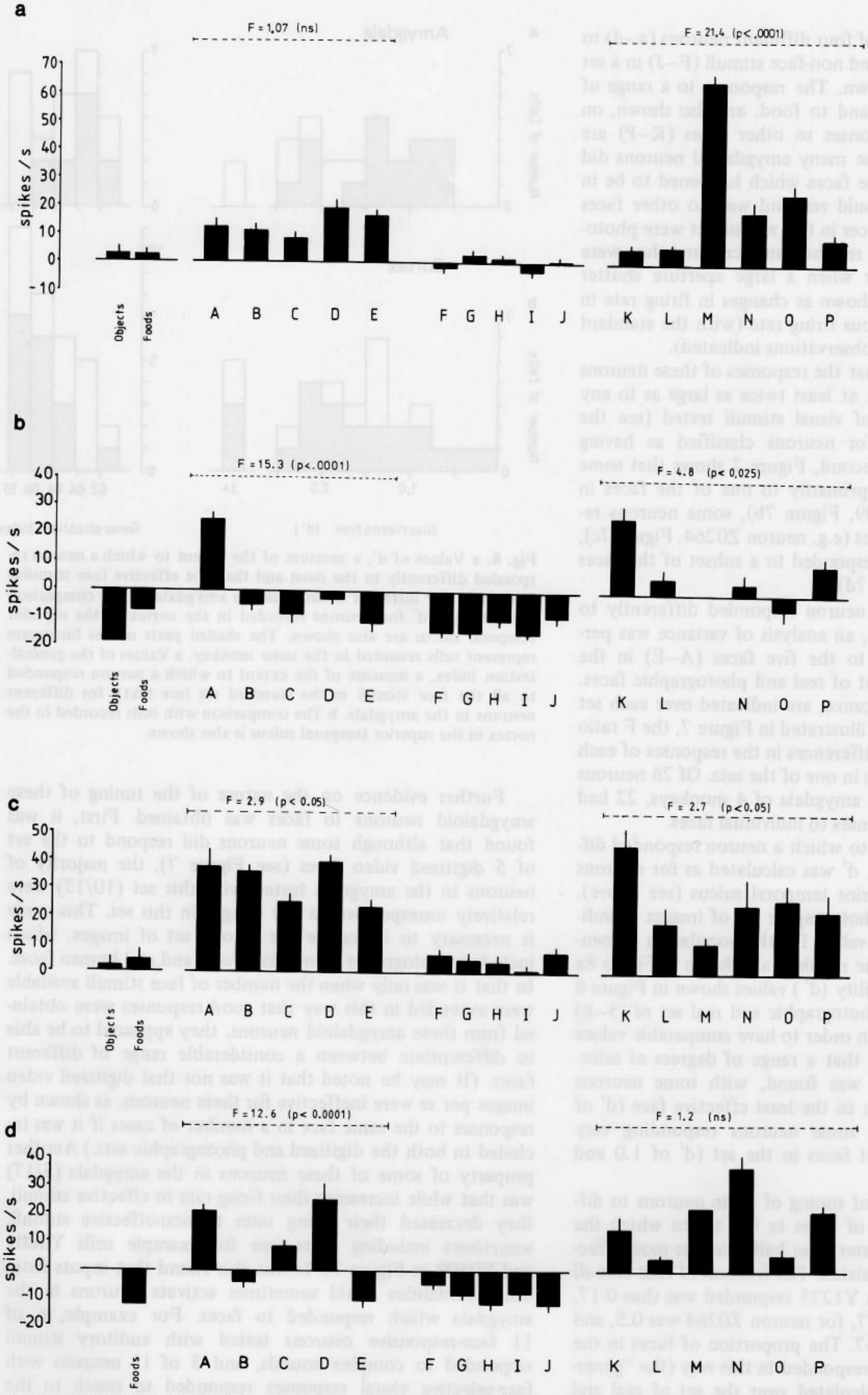


Fig. 7. The responses of four cells in the amygdala to a variety of face (A–E) and nonface (F–J) stimuli, as in Figure 1. Stimuli K–P are samples of face photographs shown as the TV images (A–E) did not always evoke a response. The bar represents the mean response above baseline with the standard error calculated over 4 to 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) between faces. Note that cells Y0801 and Y0809 both inhibit to some faces and nonface stimuli

in Figure 7. The responses of four different neurons (a–d) to the different faces (A–E) and non-face stimuli (F–J) in a set of digitized images are shown. The responses to a range of three dimensional objects, and to food, are also shown, on the left. 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 changes in firing rate in spikes/s from the spontaneous firing rate (with the standard error calculated over 4–10 observations indicated).

First, Figure 7 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 (see the criteria described above for neurons classified as having face-selective responses). Second, Figure 7 shows that some of the neurons responded primarily to one of the faces in the set (e.g. neuron Y0809, Figure 7b), some neurons responded to many of the faces (e.g. neuron Z0264, Figure 7c), and some of the neurons responded to a subset of the faces (e.g. neuron Y0801, Figure 7d).

To analyse whether a neuron responded differently to the different faces in a set, an analysis of variance was performed on the responses to the five 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 in Figure 7, the F ratio indicated that there were differences in the responses of each neuron to the different faces in one of the sets. Of 26 neurons analysed in this way in the amygdala of 4 monkeys, 22 had significantly different responses to individual faces.

To measure the extent to which a neuron responded differently to different faces, d′ was calculated as for neurons in the cortex in the superior temporal sulcus (see above). These values are for the photographic set of images as indicated in Figure 7. The d′ values for the population of neurons in the amygdala of one monkey are shown in Figure 8a (top left). The discriminability (d′) values shown in Figure 8 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, the number of faces in the set to which the neuron had a response greater than half that the most effective face stimulus was calculated. 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 Figure 8b (top right). 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.

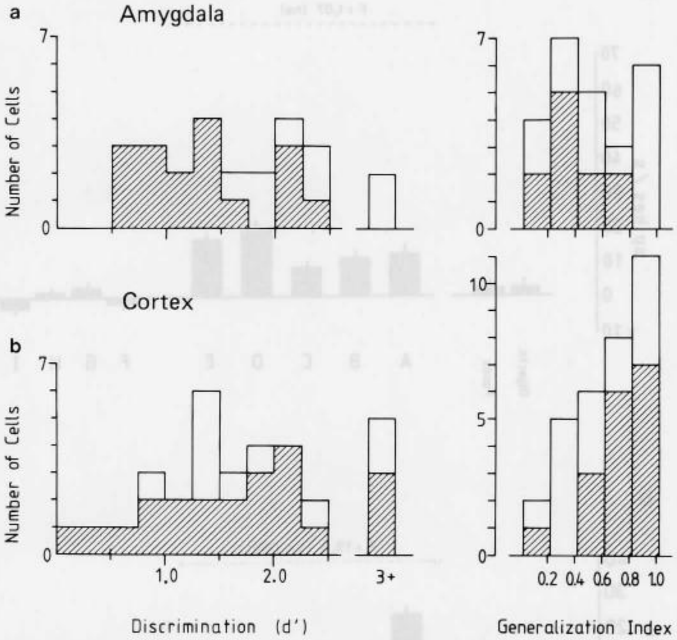


Fig. 8. **a** Values of d′, a measure of the extent to which a neuron responded differently to the most and the least effective face stimulus (see text), for different neurons in the amygdala. **b** For comparison the values of d′ for neurons recorded in the cortex in the superior temporal sulcus are also shown. The shaded parts of the histogram represent cells recorded in the same monkey. **a** Values of the generalization index, a measure of the extent to which a neuron responded to all the face stimuli in the standard set (see text), for different neurons in the amygdala. **b** The comparison with cells recorded in the cortex in the superior temporal sulcus is also shown

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 Figure 7), the majority of neurons in the amygdala tested with this set (10/13) were relatively unresponsive to the images in this set. This made is 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 responses to the same face in a number of cases if it was included in both the digitized and photographic sets.) Another property of some of these neurons in the amygdala (5/17) was that while increasing their firing rate to effective stimuli, they decreased their firing rates to non-effective stimuli, sometimes including faces (see for example cells Y0801 and Y0809 in Figure 7). It was also found that inputs from other modalities could sometimes activate neurons in the amygdala which responded to faces. For example, 6 of 11 face-responsive neurons tested with auditory stimuli responded to complex sounds, and 3 of 11 neurons with face-selective visual responses responded to touch to the abdomen or leg.

The latencies of the responses of the majority of these neurons in the amygdala which responded selectively to faces were in the range 110–200 ms. These response latencies were

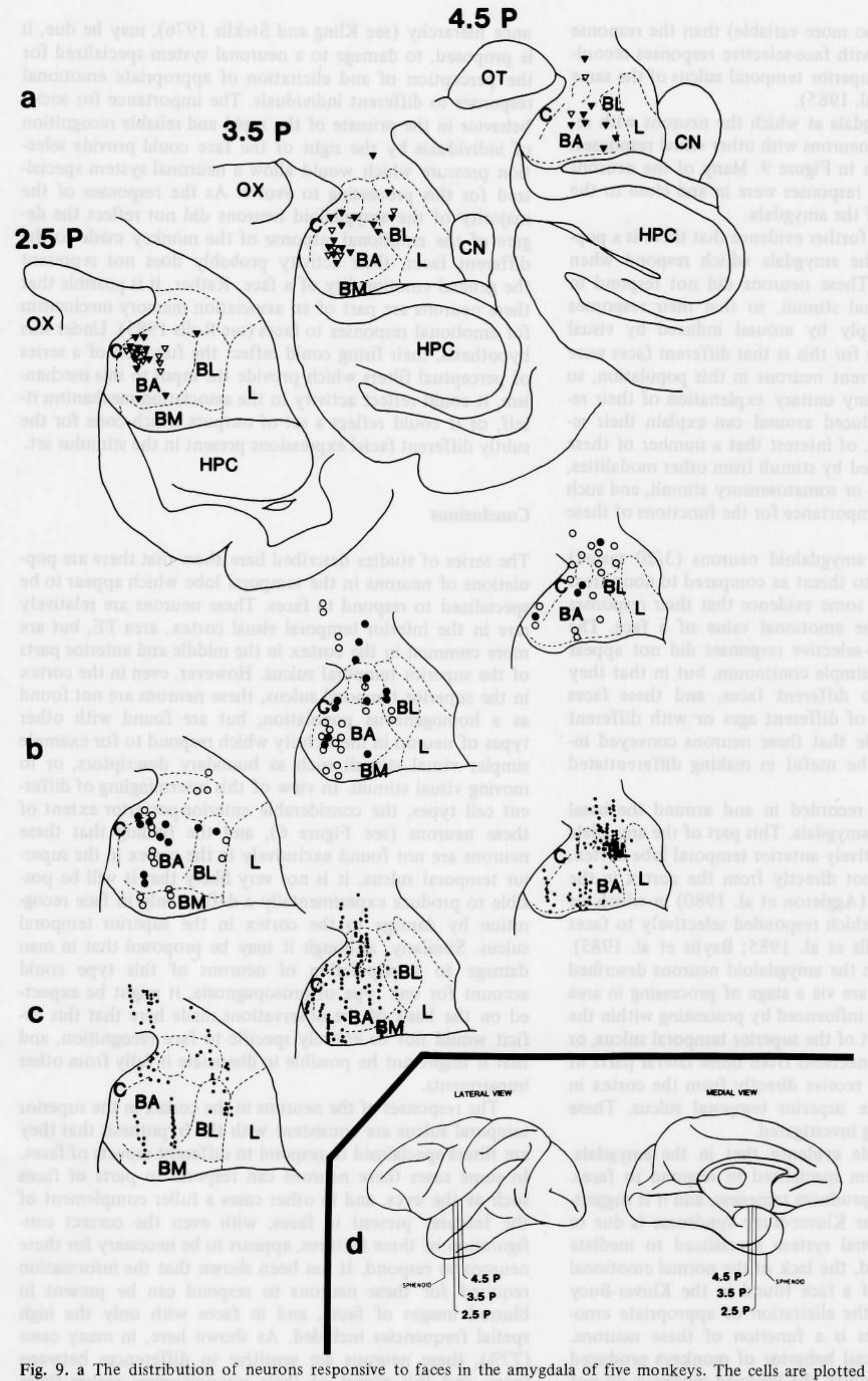


Fig. 9. a The distribution of neurons responsive to faces in the amygdala of five monkeys. The cells are plotted on three coronal sections at different distances (in mm) posterior (P) to the sphenoid. Filled triangles: cells selective for faces; open triangles: cells responding to face and hands. b Other responsive neurons. Closed circles: cells with other visual responses; open circles: cells responding to cues, movement, or arousal. c The locations of nonresponsive cells

somewhat longer (and also more variable) than the response latencies of 22 neurons with face-selective responses recorded in the cortex of the superior temporal sulcus of the same monkey (see Leonard et al. 1985).

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 Figure 9. Many of the neurons with face-selective visual responses were in and close to the basal accessory nucleus of the amygdala.

These results provide further evidence that there is a population of neurons in the amygdala which respond when a monkey sees a face. These neurons did not respond to arousing or aversive 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.

A small number of amygdaloid neurons (3/20 tested) responded differentially to threat as compared to non-threat faces, and this provided some evidence that their responses reflected decoding of 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.

These neurons were recorded in and around the basal accessory nucleus of the amygdala. 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 (Aggleton et al. 1980) in which we have described neurons which responded selectively to faces (Perrett et al. 1982; Rolls et al. 1985; Baylis et al. 1985). 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 superior temporal sulcus. These possibilities are now being investigated.

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 it is suggested that this aspect of the Kluver-Bucy syndrome is 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 (see Kling and Steklis 1976), 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 an association memory mechanism for emotional responses to faces (see Rolls 1985). 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.

Conclusions

The series of studies described here show that there are populations of neurons in the temporal lobe which appear to be specialized to respond to faces. These neurons are relatively rare in the inferior temporal visual cortex, area TE, but are more common in the cortex in the middle and anterior parts of the superior temporal sulcus. However, even in the cortex in the superior temporal sulcus, these neurons are not found as a homogeneous population, but are found with other types of neuron in the vicinity which respond to for example simpler visual stimuli such as boundary descriptors, or to moving visual stimuli. In view of this intermingling of different cell types, the considerable anterior-posterior extent of these neurons (see Figure 6), and the finding that these neurons are not found exclusively in the cortex in the superior temporal sulcus, it is not very likely that it will be possible to produce experimentally a deficit only in face recognition by damage to the cortex in the superior temporal sulcus. Similarly, although it may be proposed that in man damage to a population of neurons of this type could account for one type of prosopagnosia, it might be expected on the basis of the observations made here that this deficit would not be entirely specific to face recognition, and that it might not be possible to dissociate it fully from other impairments.

The responses of the neurons in the cortex in the superior temporal sulcus are consistent with the hypothesis that they are filters specialized to respond to different aspects of faces. In some cases these neurons can respond to parts of faces such as the eyes, and in other cases a fuller complement of the features present in faces, with even the correct configuration of these features, appears to be necessary for these neurons to respond. It has been shown that the information required for these neurons to respond can be present in blurred images of faces, and in faces with only the high spatial frequencies included. As shown here, in many cases (77%), these neurons are sensitive to differences between faces, and this aspect of their responsiveness makes them particularly appropriate as filters to be used in the recognition of individuals by their faces. However, in that these neurons did not usually respond exclusively to one of the faces, we do not consider them as "grandmother" neurons (Barlow 1972). Rather, the activity of a particular subset of these neurons, each firing at a particular level, could convey the information necessary to individuate a face. Thus, they may be a set of neurons particularly useful in face perception, in that they are specialized as filters which could provide an input, appropriate for distinguishing between faces, to a recognition system. Such a system of neurons which respond primarily to faces may be particularly useful because of the importance of rapid and reliable identification of individuals by their faces for primates, and because the differences which are useful in distinguishing between individual faces may be quite subtle and require fine tuning.

The population of neurons with face-selective responses in the amygdala also in many cases respond differently to different faces, and it is suggested above that the importance of this type of neuron may be in the different emotional and social responses which occur to different faces, and which are disrupted by damage to the amygdala.

Acknowledgements. The author has worked on some of the experiments described here with G.C. Baylis, C.M. Leonard, W. Caan, S. Judge, D.I. Perrett, M.K. Sanghera, and F.A.W. Wilson, and their collaboration is sincerely acknowledged. Support was received from the Medical Research Council.

References

Aggleton JP, Burton MJ, Passingham RE (1980) Cortical and subcortical afferents to the amygdala in the rhesus monkey (Macaca mulatta). Brain Res 190:347–368

Barlow HB (1972) Single units and sensation: a neuron doctrine for perceptual psychology? Perception 1:371–394

Baylis GC, Rolls ET, Leonard CM (1985) Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. Brain Res (in press)

Benton A (1980) The neuropsychology of facial recognition. Am Psychol 35:176–186

Bonin G von, Bailey P (1947) The neocortex of Macaca mulatta. University of Illinois Press, Urbana, Illinois

Brodman K (1909) Vergleichende Localisationslehre der Großhirnrinde in ihren Prinzipien dargestellt aufgrund des Zellenbaues. Barth, Leipzig

Bruce C, Desimone R, Gross CG (1981) Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. J Neurophysiol 46:369–384

Bruning JL, Kintz BL (1977) Computational handbook of statistics, 2nd edn. Scott, Foresman, Glenview, Illinois

Campbell FW (1983) Why do we measure contrast sensitivity? Behav Brain Res 10:87–97

Carey S (1981) The development of face perception. In: Davies G, Ellis H, Shepherd J (eds) Perceiving and remembering faces, Ch 2. Academic Press, London, pp 9–38

Chavis DA, Pandya DN (1976) Further observations on cortico-frontal connections in the monkey. Brain Res 117:369–386

Damasio AR, Damasio H, Van Hoesen GW (1982) Prosopagnosia: anatomic basis and behavioral mechanisms. Neurology 32:331–341

Davies G, Ellis H, Shepherd J (eds) (1981) Perceiving and remembering faces. Academic Press, London

Dean P (1976) Effects of inferotemporal lesions on the behavior of monkeys. Psychol Bull 83:41–71

Desimone R, Albright TD, Gross CG, Bruce C (1984) Stimulus-selective properties of inferior temporal neurons in the macaque. J Neurosci 4:2051–2062

Egan JP (1975) Signal detection theory and ROC analysis. Academic Press, New York

Fiorentini A, Maffei L, Sandini G (1984) Role of high spatial frequencies in face perception. Perception 12:195–201

Green DM, Swets JA (1966) Signal detection theory and psychophysics. Wiley, New York

Harmon LD (1973) The recognition of faces. Sci Am 229(5):70–82

Harmon LD, Julesz B (1973) Masking in visual recognition: effects of two-dimensional filtered noise. Science 180:1194–1197

Herzog AG, Van Hoesen GW (1976) Temporal neocortical afferent connections to the amygdala in the monkey. Brain Res 115:57–69

Jones B, Mishkin M (1972) Limbic lesions and the problem of stimulus-reinforcement associations. Exptl Neurol 36:362–377

Jones EG, Powell TPS (1970) An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain 93:793–820

Kling A (1981) Influence of temporal lobe lesions on radio-telemetered electrical activity of amygdala to social stimuli in monkey. In: Ben-Ari Y (ed) The amygdaloid complex. Elsevier, Amsterdam, pp 271–280

Kling A, Steklis HD (1976) A neural substrate for affiliative behavior in nonhuman primates. Brain Behav Evol 13:216–238

Kluver H, Bucy PC (1939) Preliminary analysis of functions of the temporal lobes in monkeys. Arch Neurol Psychiatr 42:979–1000

Kulikowski JJ, Marcelja S, Bishop PO (1982) Theory of spatial position and spatial frequency relations in the receptive fields of simple cells in the visual cortex. Biol Cybern 43:187–198

Leonard CM, Rolls ET, Wilson FAW, Baylis GC (1985) Neurons in the amygdala of the monkey with responses selective for faces. Behav Brain Res (in press)

Meadows JC (1974) The anatomical basis of prosopagnosia. J Neurol Neurosurg Psychiatr 37:489–501

Newsome WT, Wurtz RH (1982) Identification of architectonic zones containing visual tracking cells in the superior temporal sulcus of macaque monkeys. Invest Ophthalmol Vis Sci 22:238

Perrett DI, Rolls ET, Caan W (1979) Temporal lobe cells of the monkey with visual responses selective for faces. Neurosci Letters S3:S358

Perrett DI, Rolls ET, Caan W (1982) Visual neurons responsive to faces in the monkey temporal cortex. Exptl Brain Res 47:329–342

Rolls ET (1981a) Processing beyond the inferior temporal visual cortex related to feeding, memory, and striatal function. In: Katsuki Y, Norgren R, Sato M (eds) Brain mechanisms of sensation, Ch 16. Wiley, New York, pp 241–269

Rolls ET (1981b) Responses of amygdaloid neurons in the primate. In: Ben-Ari Y (ed) The amygdaloid complex. Elsevier, Amsterdam, pp 383–393

Rolls ET (1984) Connections, functions and dysfunctions of limbic structures, the prefrontal cortex, and hypothalamus. In: Swash M, Kennard C (eds) The scientific basis of clinical neurology. Churchill Livingstone, London

Rolls ET (1985) Neural systems involved in emotion in primates. In: Plutchik R, Kellerman H (eds) Biological foundations of emotion. Academic Press, New York

Rolls ET, Judge SJ, Sanghera MK (1977) Activity of neurones in the inferotemporal cortex of the alert monkey. Brain Res 130:229–238

Rolls ET, Sanghera MK, Roper-Hall A (1979) The latency of activation of neurons in the lateral hypothalamus and substantia innominata during feeding in the monkey. Brain Res 164:121–135

Rolls ET, Thorpe SJ, Boytim M, Szabo I, Perrett DI (1984) Responses of striatal neurons in the behaving monkey. 3. Effects of iontophoretically applied dopamine on normal responsiveness. Neuroscience 12:1201–1212

Rolls ET, Baylis GC, Leonard CM (1985) Responses of neurons in the cortex in the superior temporal sulcus of the monkey to low-pass and high-pass spatial frequency filtered stimuli. Vision Res (in press)

Sanghera MK, Rolls ET, Roper-Hall A (1979) Visual responses of neurons in the dorsolateral amygdala of the alert monkey. Exp Neurol 63:610–626

Schwartz EL, Desimone R, Albright TD, Gross CG (1983) Shape recognition and inferior temporal neurons. Proc Natl Acad Sci 80:5776–5778

Seltzer B, Pandya DN (1978) Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. Brain Res 149:1–24

Spiegler BJ, Mishkin M (1981) Evidence for the sequential participation of inferior temporal cortex and amygdala in the acquisition of stimulus-reward associations. Behav Brain Res 3:303–317

Streitfield B (1980) The fiber connections of the temporal lobe with emphasis on the rhesus monkey. Intern J Neurosci 11:51–71

Terzian H, Dalle Ore G (1955) Syndrome of Kluver and Bucy reproduced in man by bilateral removal of the temporal lobes. Neurology 5:373–380

Turner BH, Mishkin M, Knapp M (1980) Organization of the amygdalopetal modality-specific cortical association areas in the monkey. J Comp Neurol 191:515–543

Weiskrantz L (1956) Behavioral changes associated with ablation of the amygdaloid complex in monkeys. J Comp Physiol Psychol 49:381–391

Whiteley AM, Warrington EK (1977) Prosopagnosia: a clinical, psychological, and anatomical study in three patients. J Neurol Neurosurg Psychiatr 40:394–430