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Responses of neurons in the inferior temporal cortex in short term and serial recognition memory tasks

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Summary. Gaffan and Weiskrantz (1980) and Mishkin (1982) have shown that lesions to the inferior temporal visual cortex can impair the performance of serial visual recognition memory tasks. In order to provide evidence on whether the inferior temporal visual cortex contains a mechanism which enables memory to span the intervening items in a serial recognition task, or whether the inferior temporal cortex is merely afferent to such recent memory mechanisms, we analysed the activity of single neurons in the inferior temporal visual cortex and the adjacent cortex in the superior temporal sulcus in both delayed match to sample and serial recognition memory tasks. In the serial recognition task, various numbers of stimuli intervened between the first and second presentations of a stimulus. A considerable proportion (64/264 or 26%) of visually responsive inferotemporal neurons showed a different response to the "novel" and "familiar" presentations of a stimulus in the serial recognition memory task, and often a corresponding difference in response between the sample and match presentations of a stimulus in the delayed match to sample task. For the majority of neurons this difference was not sustained across even one intervening stimulus in the serial recognition task, and no neurons bridged more than 2 intervening stimuli. These results show that neurons in the inferior temporal cortex have responses which would be useful for a short term visual memory for stimuli, but would not be useful in recency memory tasks in which more than one stimulus intervenes between the first and second presentations of a stimulus. In this investigation, neurons were recorded both in the cortex on the inferior temporal gyrus (commonly called inferior temporal visual cortex, and consisting of areas TE3,TE2 and TE1 of Seltzer and Pandya 1978), and in the cortex in the adjacent anterior part of the superior temporal sulcus, in which a number of different temporal cortical visual areas have now been described (see Baylis et al. 1986).

Key words: Inferior temporal cortex – Temporal lobe cortex – Serial recognition task – Konorski task – Short term memory – Memory – Amnesia – Primate

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Introduction

One of the deficits produced by bilateral damage to the inferior temporal cortex of the monkey (see Dean 1976) is an impairment in visual memory tasks. For example, there is a deficit in a delayed match to sample task in which a sample is shown, and then after a delay the monkey must choose the stimulus which matches the sample shown previously, after lesions or cooling of the inferior temporal visual cortex (e.g. Fuster et al. 1981; Sahgal et al. 1983; Sahgal and Iversen 1983). The inferotemporal cortex has been also implicated in short-term memory processes by the findings of Gross et al. (1979), Mikami and Kubota (1980), Fuster and Jervey (1981) and Ashford and Fuster (1985) that single neurons in this area code information useful for the performance of delayed match to sample (Konorski) tasks. For example, some neurons respond more to the first (sample) than to the second (match) stimulus. Further, Gaffan and Weiskrantz (1980) and Mishkin (1982) have shown that the performance of serial visual recognition tasks (in which many stimuli intervene between the novel and familiar presentations of a given stimulus) is impaired by inferotemporal lesions. It may be noted that the deficit is not purely sensory, in that the impairment is much less at short delays. However, the findings of Gaffan and Weiskrantz (1980) and Mishkin (1982) do not provide

information on whether the inferior temporal visual cortex contains a mechanism which enables memory to span the intervening items in a serial recognition task, or whether the inferior temporal cortex is merely afferent to such recent memory mechanisms. In order to provide evidence on this, we analysed the activity of single neurons in the inferior temporal visual cortex in both delayed match to sample and serial visual recognition memory tasks, to determine whether inferior temporal cortex neurons have a memory which enables them not only to bridge the simple time delay of a delayed match to sample task, but also the longer delay with intervening stimuli used in recency memory tasks such as serial visual recognition tasks.

Methods

Recording techniques

The activity of single neurons was recorded with glass-insulated tungsten microelectrodes (after Merrill and Ainsworth 1972, but without the platinum plating) in two alert rhesus macaque monkeys (Macaca mulatta) (weight 3.0 and 6.5 kg) seated in a primate chair using techniques that have been described previously (Rolls et al. 1976). The action potentials of single cells were amplified using techniques described previously (Rolls et al. 1979), were converted into digital pulses using the trigger circuit of an oscilloscope, and were analysed 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 which were typically 100 ms or more, and the monkeys constantly fixated the stimuli for this period. Fixation of the stimuli was confirmed using permanently implanted silver/silver chloride electrodes for electro-oculogram (EOG) recording. The EOG recordings provided eye position with an accuracy of 1–2 degrees, and were sampled by the computer every 10 ms and saved with the action potentials for each trial. Data from trials during which the monkey was not already fixating the screen when the stimulus was switched on or during which eye movements of more than 3 degrees occurred in the first 600 ms (while the firing rate was being measured) were rejected.

X-radiographs were used to locate the position of the microelectrode on each recording track relative to permanently implanted reference electrodes and bony landmarks. The position of cells was reconstructed from the X-ray co-ordinates taken together with serial 50 μm histological sections which showed the reference electrodes and micro-lesions made at the end of some of the microelectrode tracks. These reconstructions were performed by making for each monkey large scale drawings of histological sections at intervals of 250 μm throughout the temporal lobe. On these the positions of all cyto- and myelo-architectonic transitions were marked. In this way the architectonic subregion within which each neuron was located could also be determined (see further Baylis et al. 1986).

Visual responsiveness was assessed in three ways. First, stimuli were stored in digital form on a computer disk, and displayed on a video monitor (Microvitec) using a video framestore (Matrox QRGB 256). The resolution of these images was 256 wide by 256 high with 256 grey levels. A large number of complex video images were collected by digitization from television broadcasts. These were intended to be analogous to 3D junk objects (see below) and were selected to differ along a large number of dimensions to be readily distinguishable. Second, 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 1.0 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 three-dimensional junk objects which differed along a wide range of parameters such as size, shape and color. A large number of neurons were found to have selectivity for particular visual stimuli, including spatial frequency, particular shapes, colors etc (see Baylis et al. 1985, 1986). Any cell showing a significantly different response ($p < 0.01$) to different stimuli was included in this category.

Tasks

1. Delayed matching to sample task. The sequence of events was as follows. First a 500 ms tone (400 Hz) was sounded, followed immediately by the sample stimulus for 1.0 s. Following this there was a delay of between 2.0 and 5.0 s, followed by another tone, and the test stimulus. If the test stimulus was the same as the sample the monkey could lick from a lick tube to obtain fruit juice reward. If the monkey licked on non-match trials, he obtained aversive hypertonic saline. The stimuli used in this task were simple geometric shapes which differed along the dimension of shape or color. At any one time a set of only four stimuli was constantly recycled, that is the testing was with non trial-unique stimuli.

2. Serial recognition task. This was based on the serial recognition task of Gaffan (1974) and Rolls et al. (1982), and was in brief as follows. The first time a visual stimulus (either a video image or "junk object" – see above) was presented – "novel" – the monkey had to withold a lick to avoid obtaining saline. The second time a given stimulus was presented – "familiar" – the monkey could lick to obtain fruit juice reward. Between the first and second presentations of a stimulus 0–10 other stimuli could intervene. Thus the monkey had to remember stimuli across a variable number of intervening trials. Any stimulus was shown only twice in any given day on this task. The large number of stimuli meant that the set took four to six weeks to recycle.

3. Visual discrimination task. A visual discrimination task was run in order to control for the possibility that neurons which responded differently to novel and familiar stimuli in the short term memory tasks might have responses related to the reward which was given to familiar stimuli and saline which was given if the monkey licked to novel stimuli. In the visual discrimination task, one stimulus was associated with reward, and a different stimulus with saline if the monkey licked, but the two stimuli were both very familiar. As in previous studies, the reward or punishment association of visual stimuli was not found to influence the responses of inferior temporal cortex neurons (see Rolls et al. 1977; Rolls 1986). The task was performed either with three-dimensional or video image discriminanda. For example, the monkey could lick to obtain fruit juice if a circle appeared on the video monitor, but had to withold a lick if a square appeared. The reward value of each pair of discriminanda could be reversed, and the monkey was trained to accept such reversals.

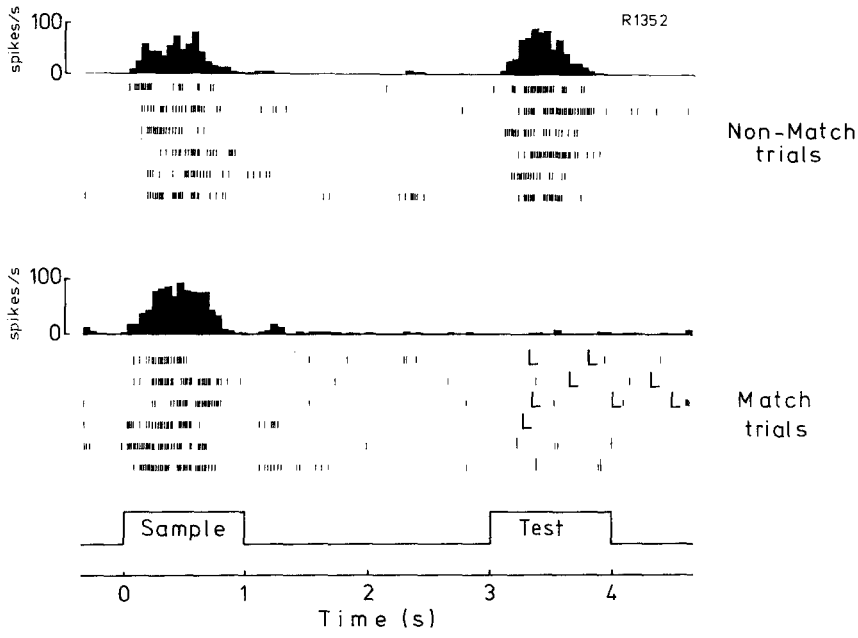

Fig. 1. Rastergram showing the responses of neuron R1352 in the delayed match to sample task. It can be seen that this neuron responds vigorously to all sample stimuli and to test stimuli only if these were non-matching to the previous sample. Match and non-match trials were originally presented in pseudorandom order

Procedure

Monkeys were trained on the visual discrimination, serial recognition, and delayed match to sample tasks to a criterion of 95% correct before recording commenced. On occasion the monkeys dropped below this performance level, in which case data were discarded from this study.

Over 600 neurons were isolated and studied in the cortex of the inferior temporal cortex and cortex in the anterior part of the superior temporal sulcus of two rhesus monkeys. Testing was first carried out to determine whether a neuron showed visual responses according to the criteria described previously (Rolls et al. 1977; Sanghera et al. 1979). The activity of all neurons showing visual responses was investigated in both the serial recognition task and the delayed matching to sample task. Any neuron showing selective responses in either task was also tested in the visual discrimination task to ascertain whether such selectivity could be based on the reward value of a stimulus.

Results

A total of 264 visual neurons were identified and tested on one or both of the memory tasks. Figure 1 shows the activity of one neuron (R1352) in the delayed match to sample (DMS) task. It can be seen that during presentation of the "match" stimulus this neuron showed a vigorous response only on trials in which this was different from the preceding sample stimulus. On all trials this neuron responded to the sample stimulus. It should be noted that the design of the task was such that the sample stimulus on a given trial was always different from the match stimulus of the preceding trial. Thus all "sample" stimuli were in many senses equivalent to a non-match.

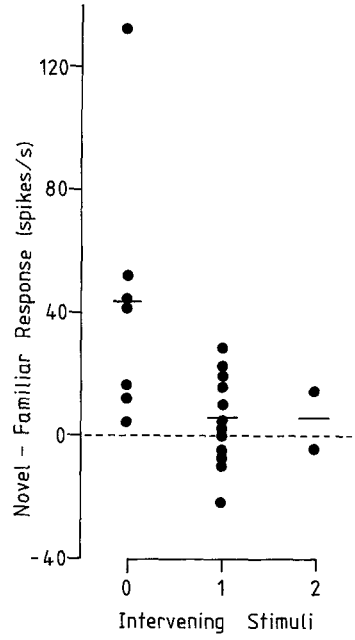

Fig. 2. Values of the difference in response of neuron R1352 to stimuli when shown as novel from that when the same stimulus was presented as familiar. These values were calculated for different numbers of stimuli intervening between the first and second presentation of a stimulus. The horizontal lines represent the mean difference in response at a given number of intervening stimuli

The responses of this neuron were also tested in the serial recognition task. Because for some neurons the degree of selectivity between stimuli was very great (see below), the effect of "novelty" or "familiarity" on the response was calculated as the difference in response to a given stimulus shown as "novel"

Table 1

	Number of cells		
	N = F	N > F	N < F
Broadly tuned	108	27	6
Visually selective	92	23	8

Abbreviations: N = F: no difference in the response to the first and second presentations of a stimulus; N > F: a significantly greater response to the first presentation of a stimulus; N < F: a greater response to the second presentation of a stimulus

and "familiar". For this neuron (R1352) the values of this difference (response to novel – response to familiar) for different numbers of stimuli intervening between the first and second presentation are shown in Fig. 2. It can be seen that when no stimuli intervened between the first and second presentations a significant difference in response was found (as shown by ANOVA). However when even one intervening stimulus was introduced there was no difference between the neuronal responses to novel and familiar presentations.

The responses of another less common (see Table 1) type of neuron are shown in Fig. 3. This figure shows the responses of a neuron (R1253) in the delayed matching to sample task. It can be seen that this neuron showed a strong response to match stimuli only on match trials, that is a strong response occurred only when a stimulus was the same as the preceding one. It can also be seen that this cell never showed any response to the sample stimulus. (As noted above the sample stimulus was never the same as the match stimulus from the preceding trial). The responses of this neuron in the serial recognition task were also tested. Since responses to "familiar" stimuli were generally greater than to "novel" stimuli the difference of response (familiar – novel) was calculated for this neuron. Figure 4 shows the effect of intervening stimuli on this measure, in a form analogous to Fig. 2. Again it can be seen that introducing intervening stimuli leads to the disappearence of the difference of the neuronal response to novel and familiar stimuli. That is, with two or more intervening stimuli, the neuron treated a familiar stimulus as novel.

The number of stimuli which can intervene between the first and second presentation of a stimulus and still allow a difference in response was calculated for 53 neurons. The results are summarised in Fig. 5. The great majority of neurons could accept no intervening stimuli, and only two could accept more than a single stimulus. It can be seen that the pattern of results for the two monkeys was very similar.

Typically it was found that these neurons did not continue to respond in the delay between the sample and match stimuli. Indeed, only 6/94 neurons with visual responses in the DMS task had firing in the delay period greater than the spontaneous rate, and for only two of these neurons did this firing in the delay depend on which stimulus had been shown as the sample, so that maintained firing of inferior temporal cortex neurons does not appear to be an important factor in instantiating short term visual memories. (An additional 21 neurons did not respond to the sample or match stimuli, but did show a small elevation of firing rate, i.q. range 7–13 spikes/s,

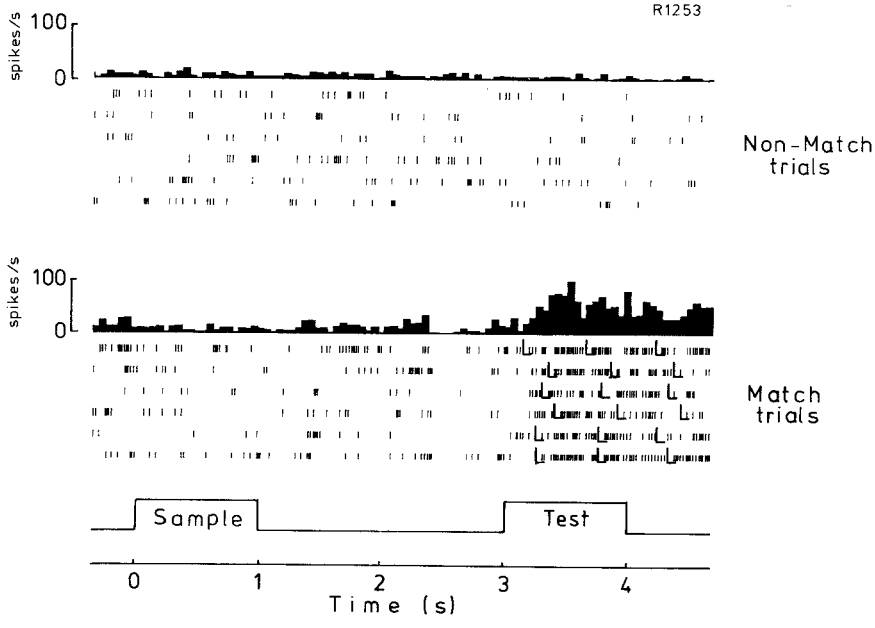

Fig. 3. Rastergram showing the responses of a neuron (R1253) in the delayed match to sample task. It can be seen that this neuron responds vigorously to test stimuli only on match trials and to none of the sample stimuli. Match and non-match trials were originally presented in pseudorandom order

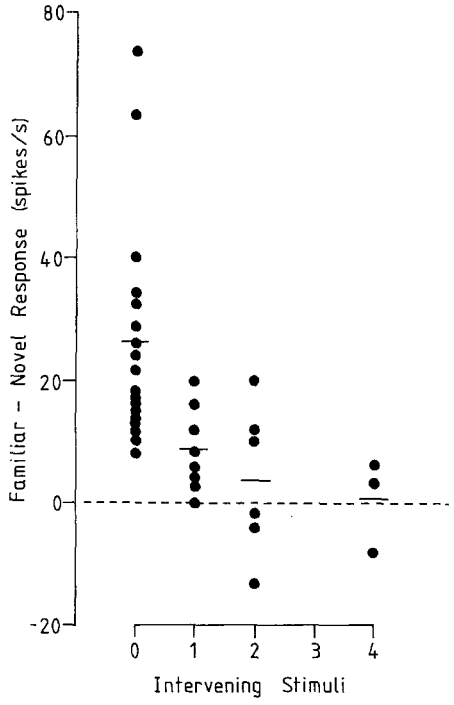

Fig. 4. Values of the difference in response of neuron R1352 to stimuli when shown as familiar from that when the same stimulus was presented as novel. These values were calculated for different numbers of stimuli intervening between the first and second presentation of a stimulus. The horizontal lines represent the mean difference in response at a given number of intervening stimuli

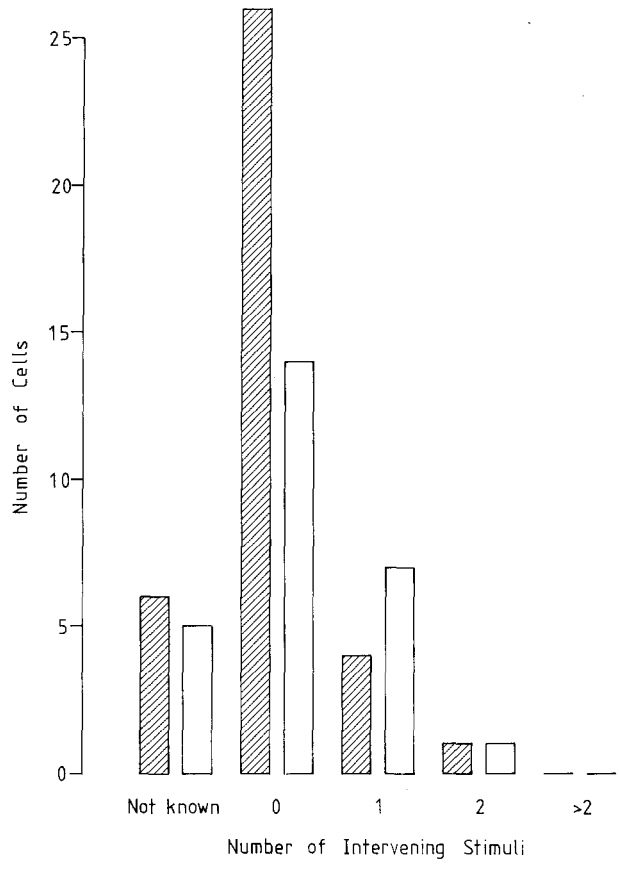

Fig. 5. Histograms showing the number of intervening stimuli which could be accepted between the first and second presentations of a stimulus and still allow a significant difference between the response to novel and familiar presentations. Values for monkey R are shown clear for monkey Z shaded to allow within monkey comparison

during the delay period. This firing did not depend on the sample stimulus shown, and thus could not instantiate a short term memory for the visual stimuli.) Further, it was noted that the offset latencies of these neuronal responses (the time taken for the neurons to cease responding to the stimuli when they were turned off) were typically 100–150 ms. These values are quite short, and compare to onset latencies for neurons in these regions of typically 80–160 ms (Baylis et al. 1986).

For only 5 neurons was a significant response to the stimuli in the visual discrimination task seen, and in only 2 cases was a significantly different response to the go and no-go stimuli seen. Neither of these latter neurons showed reversal of their response during visual discrimination reversal performed successfully by the monkey. This result indicates that in the visual discrimination task the difference in response of these two neurons to the two discriminanda was based on their physical properties rather than their association with reward. Overall the results in the visual discrimination task showed that for none of the neurons described here which responded differently to novel and familiar stimuli could the difference of response be ascribed to the reward or punishment association of the stimuli.

A large number of neurons showed a high degree of selectivity for visual stimuli. It was found that the dimensions of selectivity and novel-familiar differences were orthogonal, as can be seen from Table 1. The great majority of differential responses were such that the response to the novel stimulus was greater than that to the familiar (see Table 1). It is of interest to consider whether there is a qualitative difference between such greater responses to novel than to familiar presentations, and habituation of a response. At the extreme a neuron encoding novelty might show a difference in response between the first and second repetition of a stimulus, and no further reduction with further repetition, whereas habituation might be expected to show an exponential decline with further repetition. Figure 6 shows the responses of a neuron in the inferior temporal cortex with selective visual responses, which habituated

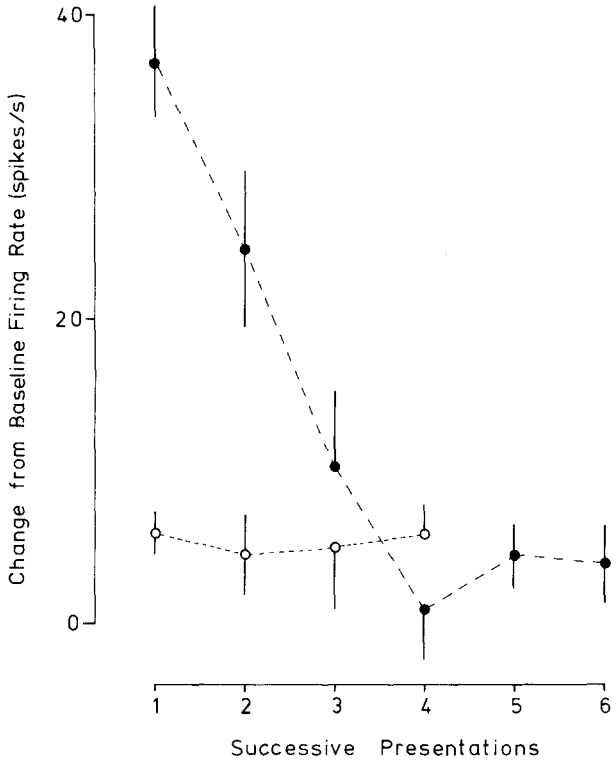

Fig. 6. Responses of a neuron showing visual selectivity which habituates. The mean and standard errors are shown. Closed circles: neuronal response to elongated edge stimuli. Open circles: responses to other (ineffective) stimuli

over four presentations of the stimulus. This neuron also fulfilled the criterion of a significant decline between the first and second presentations of a stimulus, and was included in the analysis above. (A single intervening stimulus dishabituated this neuron). One method of assessing this continuum between habituation and "novelty" is to calculate, by linear interpolation, the number of repetitions of a stimulus before the response is reduced to one half that to novel stimuli. For the neuron shown in Fig. 6, this measure has a value of 1.4. For a neuron which responded *only* to novel stimuli, this would be 0.5. The distribution of values of this measure is shown in Fig. 7. It can be seen that a large proportion (9/23 or 39%) show a reduction of the response to a half between the first and second presentations of a stimulus, although a number continued to show a decline with further presentations. All neurons had reached a response which was half that to a novel stimulus after 4 presentations (= 3 repetitions).

The sites at which these neurons were recorded are shown in Fig. 8. It can be seen that these are distributed throughout the inferior temporal cortex, and cortex of the superior temporal sulcus. A majority were located in areas TPO, TEa, TEm and TE3

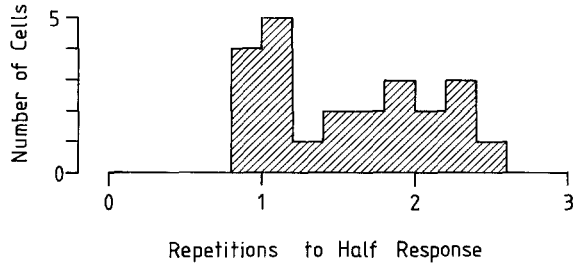

Fig. 7. The number of repetitions of a stimulus until the response declined to one half that to novel stimuli. This was calculated by linear interpolation on curves such as shown in Fig. 6

(Seltzer and Pandya 1978). No difference in distribution of this population of neurons with memory-related activity, and visual neurons in general (see Baylis et al. 1986; Desimone and Gross 1979) was noted.

Discussion

The responses of a population of neurons in the inferior temporal cortex in a short term (DMS) and serial recognition task were described. Many neurons were found to have a different response to the first and second presentations of a stimulus, and in many cases further repetitions led to a further decrement of response. This property appears to be distributed across all visual areas of this part of the temporal lobe visual neocortex (see Baylis et al. 1986), and appears to be orthogonal to other characteristics such as visual selectivity. The finding that a large number of neurons show a difference in response to the first and second presentations of a visual stimulus suggests that this area of cortex may have a role in sensory storage across short time periods.

The serial recognition task with no stimuli intervening between the novel and familiar presentations of a stimulus is analogous to match trials of the delayed match to sample task, with the exception that the stimuli were trial unique in the serial recognition task. Similarly, a familiar trial followed by a novel, is analogous to a non-match trial in the delayed match to sample task. Neurons showing a difference is response on match and non-match trials were tested on the serial recognition task to determine whether this difference in response could be maintained across intervening stimuli. For all neurons showing a difference in response to stimuli depending on whether they were seen on match or non-match trials in the DMS task, a difference was seen in the serial recognition task with no intervening stimuli. However, not all neurons shown to be selective between novel and familiar trials in the

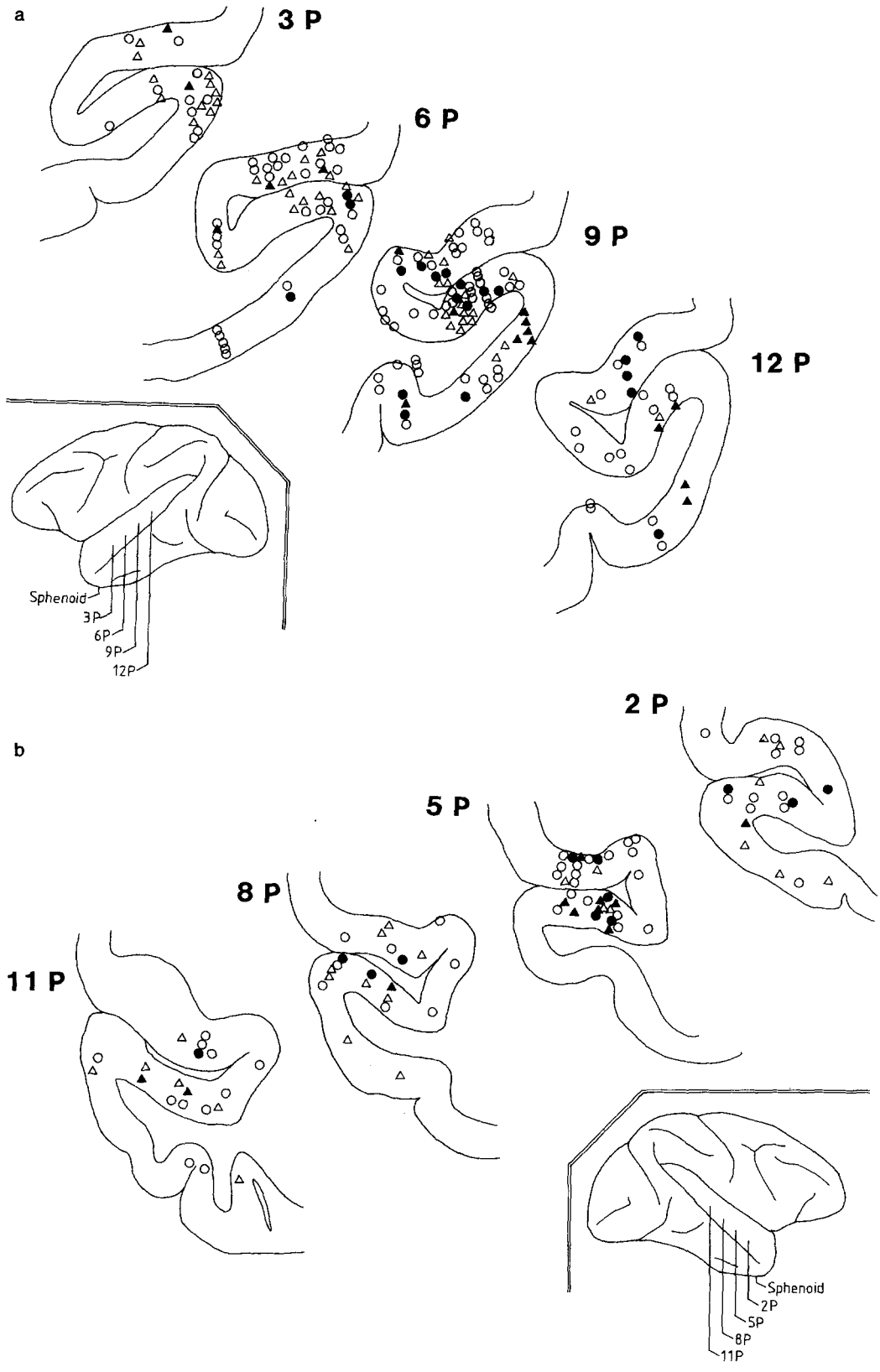

Fig. 8a, b. Coronal sections through the temporal lobe showing the recording sites of the neurons described in this study (**a**) Monkey R; (**b**) Monkey Z; inserts show the positions of these sections on a lateral view of the cortex. Numbers refer to mm. posterior to sphenoid (Aggleton and Passingham 1980). Filled symbols – neurons showing a difference in response between the first and second presentation of a stimulus; open symbols – neurons showing no such difference; circles – broadly tuned visual responses; triangles – selective visual responses

serial recognition task had significant visual responses in the DMS task. This was due to the simple stimuli of the DMS task being incompatible with the stimulus requirements of the neuron.

In no cases did neurons show a difference between novel and familiar presentations of a stimulus with more than two intervening stimuli, and in most cases a single stimulus prevented such a difference. These results suggest that the responses of neurons in the inferior temporal cortex do not reflect the computation of recency of the type required for serial recognition tasks with two or more intervening stimuli. However, neurons in the inferior temporal cortex can code information about objects invariant across low-level transforms such as retinal position, size, orientation etc. (Sato et al. 1982; Schwartz et al. 1983; Rolls and Baylis 1986). This highly processed visual information would be necessary (or at least useful, especially in the acquisition phase – see Gaffan and Weiskrantz 1980; Gaffan et al. 1986a, b) to structures to which the inferior temporal cortex projects which may be involved in the performance of other, longer term, memory tasks. These structures include the hippocampus and amygdala, combined damage to which is known to impair the performance of serial visual recognition memory tasks, particularly with long delays (Mishkin 1978, 1982; Rolls 1986).

It was a possibility that the differential responses to novel and familiar stimuli was related in some way to the training of the monkey on the serial recognition and DMS tasks. To investigate this, in a third monkey, which was not trained in either task, responses to the first and second successive presentations of a stimulus were tested. A total of 43 visually responsive neurons was tested in this way, of which 31 showed no difference in response to the novel and familiar presentations, 11 showed a greater response to the novel, and 1 showed a greater response to the familiar. These proportions are very similar to those reported in the trained monkeys. This indicates that training was not important to the existence of such a population of neurons.

The fact that neurons in this area of cortex show a high degree of visual selectivity could reflect the function of this part of the brain in a long term memory for visual stimuli, if this selectivity were set up as a result of experience. Indeed, we think it likely that their responses do become tuned by experience so that an ensemble of such neurons provides a long term representation of visual stimuli (Baylis et al. 1985; Rolls 1986). The finding described here that at least some of these neurons respond differently to a repeated visual stimulus if there are no intervening stimuli suggests that once these neurons are activated, they are in a state which reflects their very recent activation. This representation is disrupted by intervening visual information. Thus the inferior temporal cortex may hold in terms of its neuronal response selectivity a long term memory representation of the visual world, and activation of these neurons provides a short term holding store of the visual scene as just seen. Memory for visual stimuli seen recently, in perhaps the preceeding 3–20 trials, appears not to be reflected in the response properties of inferior temporal cortex neurons, and may be provided by structures which receive inputs from the inferior temporal visual cortex such as the amygdala, hippocampus, and frontal cortex.

It is of interest that the activity of inferior temporal cortex neurons is not generally maintained in a delay period in which a visual scene is being remembered, and indeed that the offset latencies of inferior temporal cortex neurons are typically 100–150 ms. This interestingly parallels visual experience, in that the details of the visual scene disappear quickly when the eyes are closed. It may be that inferior temporal cortex neurons, with their large receptive fields, are useful in building up and maintaining a stable representation of the visual scene which can even make use of changes in fixation and is not disrupted by eye blinks, but do not hold a visual memory as a pattern of firing in a delay period of even as little as 1 s. Instead, they may contribute to such short term visual memories, by showing altered responsiveness to visual stimuli which occur again soon, provided that there have been either no, or for a few neurons up to one, other intervening visual stimuli.

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