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Responses of single neurons in the hippocampus of the macaque related to recognition memory

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Abstract. In order to analyse how hippocampal activity is related to memory, the activity of single hippocampal neurons was recorded while macaques performed a recognition memory task. In the task, the first time a stimulus was shown, no reward could be obtained, and the second time a visual stimulus was shown, the monkeys could lick to obtain fruit juice. Many other stimuli could intervene between the novel and familiar presentations of each stimulus. Of 660 neurons analysed, 15 (2.3%) responded differently to novel and to familiar stimuli, with the majority of these responding more to novel than to familiar stimuli. The latencies of the differential responses of the neurons were typically in the range 140–260 ms. The responses of these neurons reflected whether a visual stimulus had been seen recently, in that the neurons responded differently to novel and familiar presentations of a stimulus when a median of 21 other stimuli intervened between the novel and familiar presentations. The responses of these neurons were shown to be related to whether the stimuli had been seen before, not to the reinforcement or the lick responses made, in that the neurons did not have comparable responses in a visual discrimination task in which licks were made to a rewarding stimulus but not to another stimulus. It is concluded that the activity of a small but significant proportion of hippocampal neurons is related to whether a stimulus has been seen before recently, and that this processing is likely to be involved in memory.

Key words: Hippocampus – Memory – Recognition – Temporal lobe – Monkey

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Introduction

Bilateral damage to the temporal lobe in humans can cause anterograde amnesia (Scoville and Milner 1957; Milner 1972; Squire et al. 1989; Zola-Morgan et al. 1986). A number of structures are damaged, and these include the hippocampus. Because of the potential importance of the hippocampus in memory and of damage to the hippocampus in producing amnesia, experimental investigations have been performed to determine which brain structures are crucial in producing the amnesia, and to analyse the neural bases of the different types of amnesia (see Squire 1992). In analyses of the way in which the hippocampus could contribute to a memory deficit in primates (see Rolls 1990, 1991), it has been shown that memory tasks which are particularly affected by damage to the hippocampus or fornix in the primate include non-spatial tasks, such as recognition memory (Gaffan 1974, 1977; Gaffan and Weiskrantz 1980; Owen and Butler 1981; Gaffan et al. 1984b; Zola-Morgan and Squire 1985). The deficit produced by hippocampal damage can be seen in a simple form of recognition memory task, the delayed match to sample task (see Squire 1992). Non-spatial memory deficits can also be produced by damage to the perirhinal and entorhinal cortex which overlies and sends afferents to the hippocampus (Murray et al. 1989; Zola-Morgan et al. 1989b). The spatial memory tasks which are particularly affected by damage to the hippocampus or fornix in the primate include (1) memory of where in space an object has been seen before (Smith and Milner 1981; Gaffan and Saunders 1985; Parkinson et al. 1988), (2) utilisation of spatial cues to determine which object to select (Gaffan and Harrison 1989) and (3) learning where to make a spatial response (in, for example, a conditional spatial response task: Gaffan et al. 1984a; Petrides 1985; Rupniak and Gaffan 1987).

To analyse neurophysiologically how the hippocampus is involved in the spatial memory tasks noted above, we have recorded from single hippocampal neurons in macaques performing object and place memory tasks (Rolls et al. 1989; Feigenbaum and Rolls 1991), delayed

spatial response tasks (Cahusac et al. 1989), and conditional spatial response tasks (Miyashita et al. 1989). In this paper we describe an analysis of hippocampal neuronal activity in macaques performing a non-spatial memory task: recognition memory for pictures. The recognition task used was running recognition of stimuli which were shown only twice daily – once as novel and once as familiar – and in which a variable number of other stimuli intervened between the novel and familiar presentations of a stimulus. This task was used because it is known to be impaired by damage to structures in the medial temporal lobe (such as the hippocampus and overlying structures such as the entorhinal and perirhinal cortex which provide routes for information to reach the hippocampus), and because this task enabled estimation of the number of intervening stimuli over which the memory of hippocampal neurons was retained.

Materials and methods

The serial recognition task

The monkeys were trained to perform a serial recognition task which was an automated version of one used previously (cf. Gaffan 1977; Rolls et al. 1982). Each stimulus was presented twice daily, once as novel and once as familiar. When a stimulus was novel, the monkey had to refrain from licking in order to avoid the taste of saline. When a stimulus was familiar, the monkey could obtain fruit juice by licking the tube in front of his mouth. Up to 17 other stimuli intervened between the novel and familiar presentations of a given stimulus, and not more than three novel or familiar stimuli occurred consecutively. Many of the stimuli were completely novel and others had been seen before, but only a number of days previously. The time interval between stimuli was 6 s. The stimuli were displayed 30 cm from the monkey on a colour video monitor which subtended 12 deg at the retina. The stimuli were either pseudo-coloured stimuli digitised with a frame-grabber from the television, or were simple geometric shapes such as boundary curvature descriptors (Schwartz et al. 1983). The resolution of these images was 256 pixels wide by 256 pixels high with 256 gray levels or colors. The stimuli were stored on a PDP11 or Microvax II computer disk ready for random access loading into an AED512 video framestore. A 0.5 s signal tone (400 Hz) preceded the presentation of the stimulus and if the monkey was looking correctly at the monitor screen before the stimulus appeared, he had sufficient time to perform the discrimination and obtain multiple licks of the fruit juice tube in the short (1.0 s) period in which the stimulus was on. This procedure was designed to ensure fixation of the stimuli (Rolls et al. 1979). Recordings of the electro-oculogram (EOG) confirmed that this procedure resulted in consistent fixation of the stimuli. The task was completely computer-controlled to ensure that no influence of the experimenters on the monkey's behaviour or on the neuronal activity was possible. The computer switched the stimuli on and off for each trial and synchronized its data collection so that the stimulus was turned on at the start of the 21st bin of a peristimulus time histogram. (Each bin of the 100-bin histogram was normally 20 ms in duration.)

Control visual discrimination task

The monkeys were also trained to perform a visual discrimination task which was run as a control to ensure that any results obtained were not due to obtaining reinforcement (fruit juice), movements associated with licking for the fruit juice, or other extraneous factors. If a circle (the positive discriminative stimulus (S+)) appeared on the monitor, 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.

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 three male macaque monkeys (*Macaca mulatta*) (weight 3.0–4.5 kg) seated in a primate chair using techniques which have been previously described (Rolls et al. 1976, 1982). The monkeys had been implanted under thiopentone sodium anaesthesia (5%, initial dose 1 ml i.v., preceded by tranquillization with ketamine at 10 mg/kg i.m.) with stainless-steel holders on which an adaptor could be fitted for the later daily recording sessions. 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 or Microvax II computer. The computer collected peristimulus rastergrams of neuronal activity for each trial and displayed, printed and stored each trial, as well as computing the peristimulus time histogram by summing trials of a given type. To facilitate latency measurements, the cumulative sum distribution was calculated from the sum peristimulus time histogram. For each trial, the number of action potentials occurring in a 500 ms period (and a 250 ms period) starting 100 ms after the stimulus onset was printed. This period of 500 ms was chosen because the neurons studied responded to visual stimuli with latencies which were typically 100 ms or more, and the monkeys consistently fixated the stimuli for more than 500 ms. Fixation of the stimuli was confirmed using permanently implanted silver/silver chloride electrodes for EOG recording. The EOG recordings indicated eye position with an accuracy of 1–2 deg and were sampled by the computer every 10 ms and saved with the action potentials for each trial.

X-radiographs taken in the coronal and parasagittal planes were used to locate the position of the microelectrode in each recording track relative to permanently implanted reference electrodes and bony landmarks such as the posterior tip of the sphenoid bone (Aggleton and Passingham 1981). At the time of histology, the animals were tranquillised with ketamine (10 mg/kg i.m.), deeply anaesthetized with intravenous pentobarbitone sodium (30 mg/kg initially), and perfused with normal saline followed by 10% formal saline. Sharpened hollow tubes (diameter 1.5 mm) were passed stereotaxically through the brain parallel to the intra-aural/inferior orbital plane to provide a dorso-ventral reference point between sections. The position of cells was reconstructed from the X-ray co-ordinates taken together with serial, 50-μm histological sections in the coronal plane, stained with cresyl violet (which showed the reference electrodes), and microlesions made at the end of some of the microelectrode tracks. Drawings were made in coronal planes 0.5 mm apart from the X-radiographs, showing the position of the electrode at the end of each track with a $\times 10$ scale. (The X-radiographs were corrected for the 10% magnification). The position of each unit recorded was marked on these drawings. Towards the end of each experiment (in the last 2-3 weeks), small electrolytic lesions (40–80 μA for 50–60 s) were made at the end of each recording session, usually at the site of a responsive neuron. X-rays were again taken. This allowed the relationship between positions measured from radiographs and the position in the brain when the microlesions were identified histologically to be calculated. A linear regression was then performed in each of the three dimensions between measurements in the brain and measurements on the radiographs. The accuracy of reconstruction according to this method was better than 0.5 mm.

Analysis

For each cell, measures of responses were calculated from the total number of action potentials occurring during each trial in the peri-

od 100–600 ms following stimulus onset. This period was chosen for the reasons given above.

A Student's t-test was performed for the differences between the responses of each cell to novel and familiar stimuli. If a significant difference between the responses was found then a regression analysis was performed on the neuronal response as a function of the number of other stimuli that intervened between the novel and the familiar presentations of a given stimulus. The point where this regression line reached the level of response produced to novel stimuli gave an indication of the number of intervening stimuli for which the neuron responded differently to novel and familiar stimuli and was taken as the 'memory span'. The responses of each neuron to the S+ and S– stimuli were also compared with a Student's t-test in the visual discrimination task, to check that the responses in the recognition tasks were not simply due to the fact that the monkey responded to novel stimuli as indicating that no behavioural response should be made, and to familiar stimuli as indicating that a lick response should be made to obtain fruit juice. Cells were classified as showing differential responses to novel and familiar stimuli if the t-test was significant beyond the $P<0.05$ level, but for most of the cells described here with differential responses, the differences were significant at beyond the $P<0.01$ level. To test whether more cells had significant results than would be expected by chance, the number of cells with significant results at each level (e.g. $P<0.05$, $P<0.01$ and $P<0.001$) found in an analysis of variance was compared using a goodness of fit Chi-square test with the number that would be predicted by chance.

The latency of neuronal responses, or the differential latency of the neuronal response, i.e. the latency at which the neuron fired significantly differently in two conditions, such as two different stimulus positions, was determined using cumulative sum, and running mean, statistics. The cumulative sum (Woodward and Goldsmith 1964) was calculated on line, using 18 prestimulus bins as the reference. The point at which the slope of the cusum changed was taken as the latency. Running mean t-tests, which compared the mean number of neuronal spikes in 18 prestimulus bins with the mean number of spikes in two, three, four or five poststimulus bins, were performed over the sums of trials in any one condition, for the difference of the sums of trials for two conditions, or for the cumulative sums of these arrays of values.

Results

The activity of 660 neurons in the hippocampus or parahippocampal gyrus was analysed in three monkeys during the performance of the serial recognition task.

Peristimulus time histograms and rastergrams of the activity of one hippocampal neuron recorded in the serial

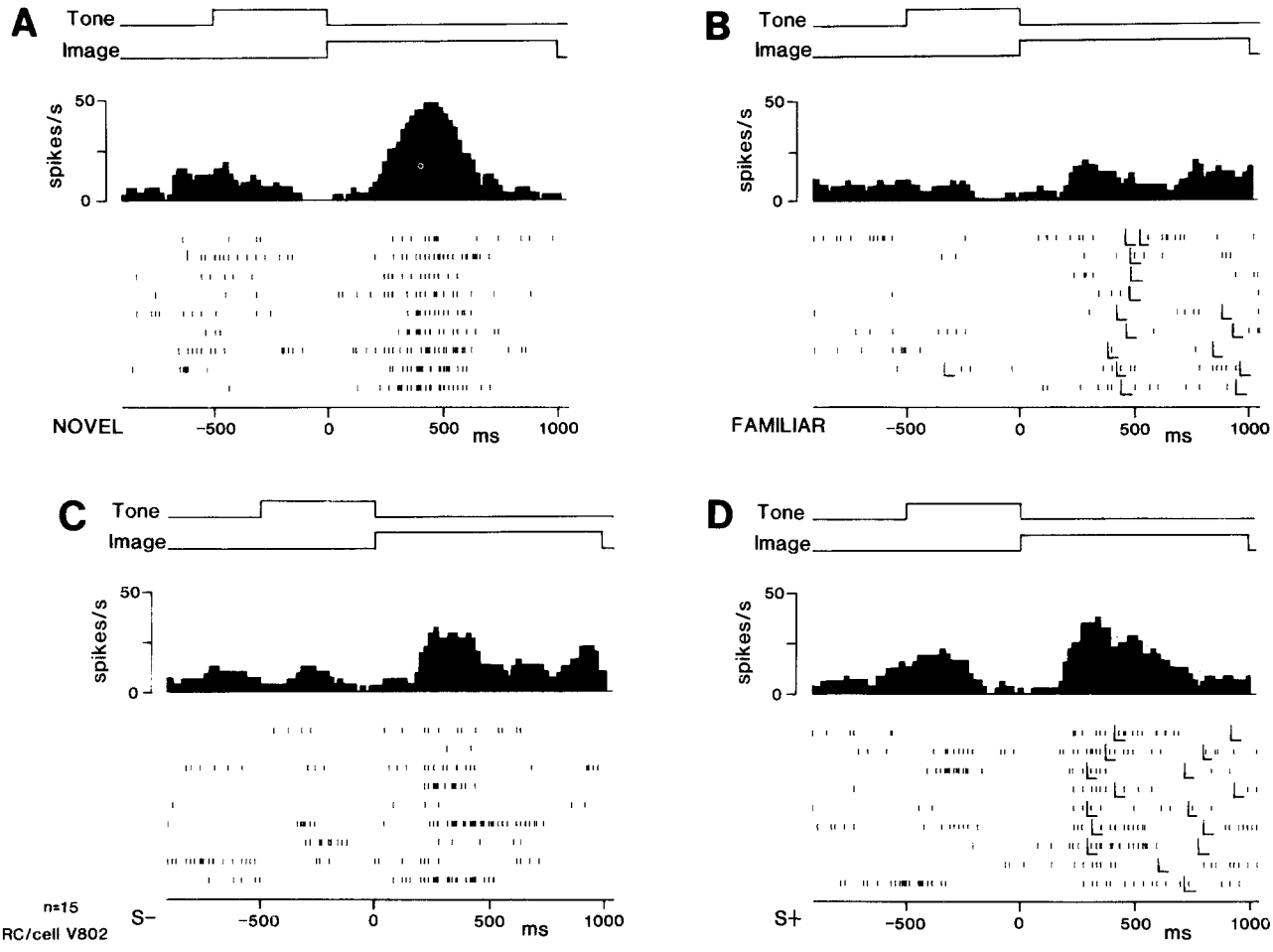

Fig. 1A–D. Peristimulus time histograms and rastergrams of the activity of a hippocampal neuron recorded in the serial recognition task. **A** Novel stimulus; **B** familiar stimulus; **C** S– stimulus; **D** S+ stimulus. In the rastergrams, each vertical line represents one action potential from the neuron, and each row shows data for one trial. The visual stimulus appeared at time 0. Lick responses made by the monkey to obtain fruit juice are shown by *L*. The neuron responded by increasing its firing rate to novel stimuli, but not to the same stimuli when they were familiar. Small responses were found on some S+ and S– trials, when these stimuli had not been seen for several intervening trials

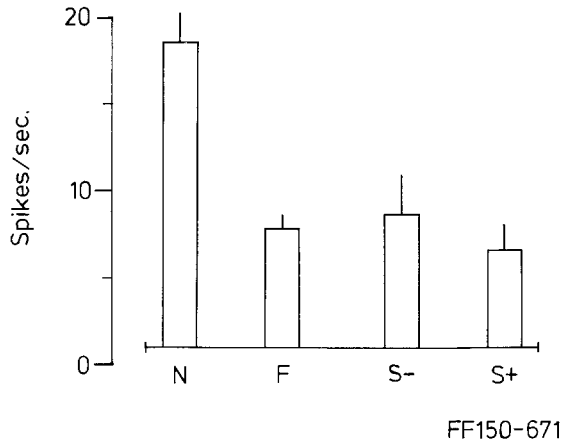

Fig. 2. The responses of a hippocampal neuron in the recognition and association memory tasks. The neuron responded to novel stimuli (*N*) by increasing its firing rate, and did not respond to familiar stimuli (*F*) in the recognition memory task. In the association memory task, the neuron did not respond to aversive (*S*–) nor to rewarding (*S*+) stimuli. The histograms show the mean and the standard error of the response, and the spontaneous firing rate is also shown as the baseline rate

recognition task are shown in Fig. 1A, B. It is shown in Fig. 1B that the neuron did not respond to the stimuli when they were familiar. The licks made to the familiar stimuli are indicated by the L symbols. Figure 1A indicates that, in contrast, the neuron did respond to the same stimuli when they were novel. This difference, over all the data collected, was significant at the $P < 0.001$ level, and the latency of the differential response, again determined over many more trials than those illustrated, was 160 ms.

The responses of another hippocampal neuron in the recognition and association memory (i.e. visual discrimination) tasks are compared in Fig. 2. The neuron responded to novel stimuli by increasing its firing rate and did not respond to familiar stimuli in the recognition memory task. In the association memory task (i.e. the visual discrimination task), the neuron did not respond to the S– or to the S+ stimuli, so that the differential neuronal responses in the recognition memory task were not due to different associations with reinforcement or to different lick responses made. It was a criterion for a neuron to be classified as responding in relation to recognition that its responses could not be accounted for by an association with reinforcement or by lick responses, as controlled by comparing the activity of each neuron in the recognition and association memory tasks.

Peristimulus time histograms and rastergrams of the activity of a hippocampal neuron as a function of the number of other stimuli which intervened between the novel and familiar presentations of a given stimulus are shown in Fig. 3. The neuronal response to the stimuli when novel is shown in Fig. 3A and the lack of neuronal response when the stimulus is presented again with no intervening stimuli is shown in Fig. 3B. However, if two stimuli intervened between the novel and familiar presentations of a stimulus then a small neuronal response occurred (Fig. 3C), and as the number of intervening stimuli became larger (i.e. as the repeated stimuli became less familiar), the neuronal response became larger and more like that to novel stimuli (Fig. 3D,E). Such data also

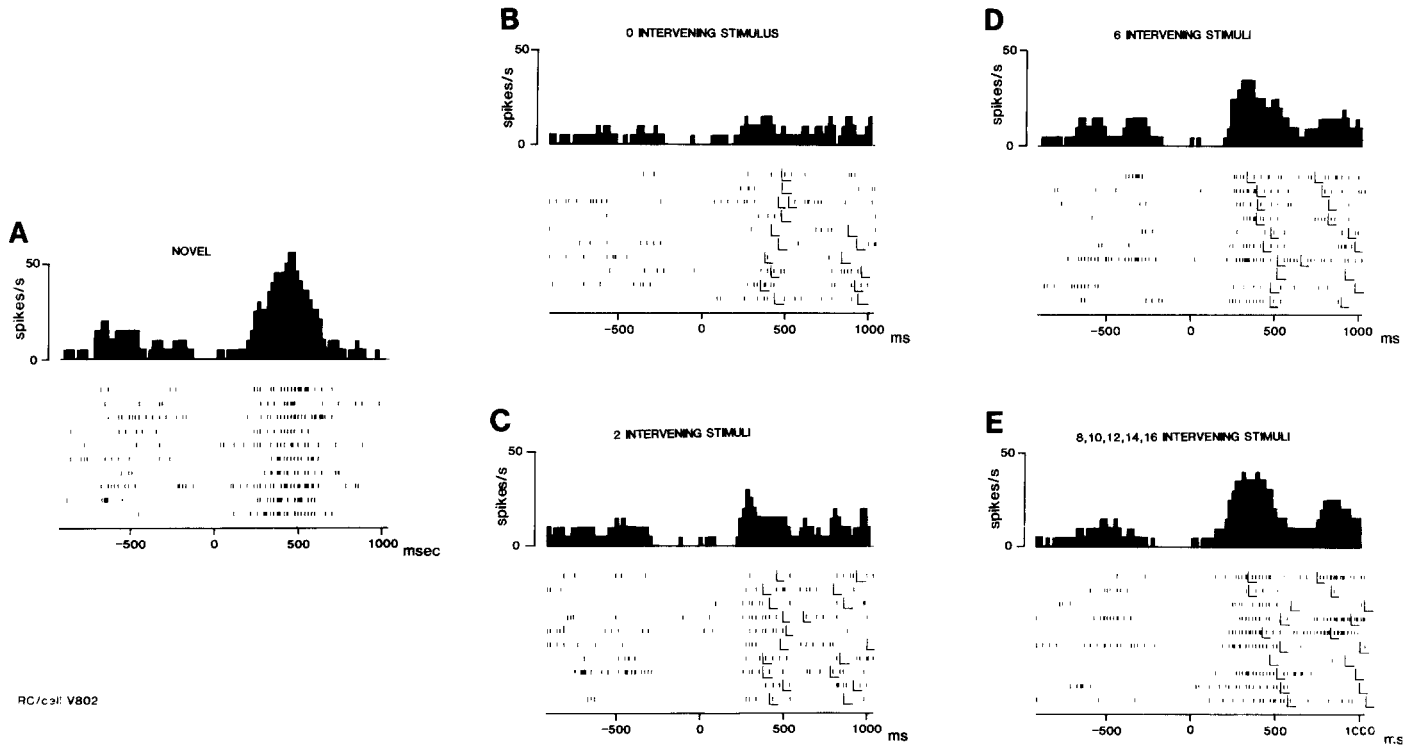

Fig. 3A–E. Peristimulus time histograms and rastergrams of the activity of a hippocampal neuron as a function of the number of other stimuli that intervened between the novel (**A**) and familiar (**B–E**) presentations of a given stimulus. Conventions as in Fig. 1

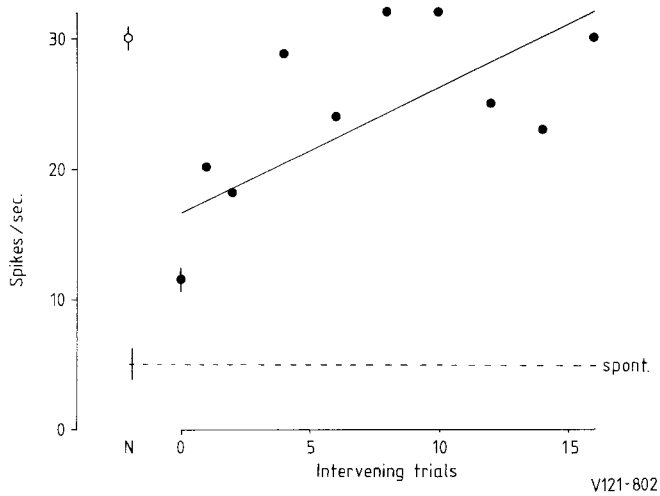

Fig. 4. The responses of a hippocampal neuron as a function of the number of intervening stimuli. The regression line through the responses to different numbers of intervening stimuli is shown. The mean response is shown. The *vertical lines* show the standard errors. *N*, Response to novel stimuli

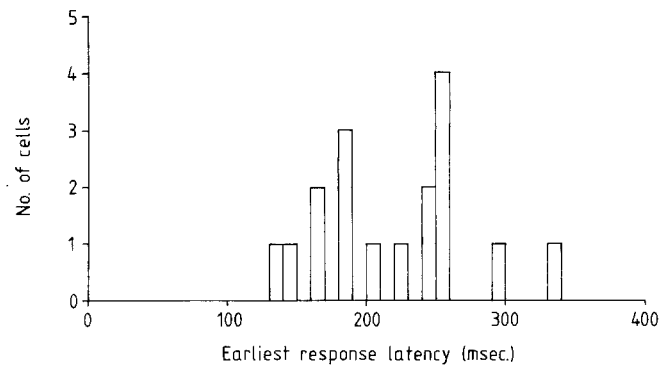

Fig. 5. The latencies of the differential responses of the neurons to novel and familiar stimuli of the population of neurons

provide clear evidence that the neuronal response is not related to the behavioural responses being made in the task, which for all values of the number of intervening stimuli consisted of lick responses. (A period of reduction in the spontaneous firing rate of the neuron during the tone period, during which the monkey prepared to perform the novelty/familiarity discrimination, is evident in Fig. 3, and in Fig. 1, and was common in the neurons described here. We note that this effect enabled the neurons to discriminate with a maximal difference of firing rate between novel and familiar stimuli.)

The responses of a hippocampal neuron as a function of the number of intervening stimuli are shown in Fig. 4. The regression line through the responses to different numbers of intervening stimuli is shown. The regression line in this case showed that the response to familiar stimuli became equal to that to novel stimuli with 14 intervening stimuli, thus defining a 'memory span' for this neuron of 14 intervening stimuli. (In an earlier investigation by Rolls et al. (1982), the possibility of fitting the data to an exponential regression as compared to a linear regression was considered. In this paper a linear regression was used, partly to facilitate direct comparisons with the memory spans of neurons recorded in the inferior temporal visual cortex (Baylis and Rolls 1987) and amygdala (Wilson and Rolls 1993).

Of the 660 neurons analysed in the hippocampus and parahippocampal gyrus in the serial recognition tasks, 15 (2.3%) responded differentially to novel and familiar stimuli and did not have differential neuronal activity in the discrimination task which could have accounted for their responses in the recognition task. (In the visual discrimination task, these neurons typically had no statistically significant responses relative to the prestimulus firing rate or only small responses to the reward-associated (S+) and saline-associated (S–), visual stimuli. Data from a neuron that had a small response to the S+ and S–, but a much larger response to novel stimuli, is illustrated in Fig. 2. Some of the neurons that responded to novel stimuli responded in the discrimination task to the discriminanda as novel if the discriminanda had not been seen for many trials, i.e. even in the visual discrimination task: these neurons could not respond on the basis of reinforcement, but on the basis of familiarity.) Of these 15 neurons, 14 responded to novel stimuli (12 by an increase in rate and 2 by a decrease), and 1 to familiar stimuli (by an increase in rate). The responses of this population of neurons occurred to all the novel stimuli used; their responses were not pattern specific. This population of neurons did not have statistically significantly different responses to novel and familiar stimuli just because many statistical tests were performed and some significant results would be expected, in that nine of these cells had effects significant at $P<0.001$, one such result would be expected by chance, and the probability of this unlikely outcome, as evaluated with a binomial test, was $P<3\times10^{-9}$.

The memory spans of the population of 15 neurons in the hippocampus and parahippocampal gyrus that responded differently to novel and familiar stimuli had a median of 21 intervening stimuli and an interquartile range of 14–62 intervening stimuli. It should be noted that the neurons were tested with only up to 17 intervening stimuli so that some of these values are based on linear extrapolation. Nevertheless, the point made by these memory span analyses is that the neurons reflect a memory which is much longer than that for the past one or two stimuli.

The latencies at which these neurons responded differently to novel and familiar stimuli are shown for this population of 15 neurons in Fig. 5. The differential response latencies were typically in the range 140–260 ms.

The sites at which these neurons were recorded in the hippocampus are shown in Fig. 6. The neurons were found not only in the dentate gyrus but also in the CA3 and CA1 pyramidal cell regions.

Discussion

First, this study shows that there are some neurons in the hippocampus of the primate with responses that differen-

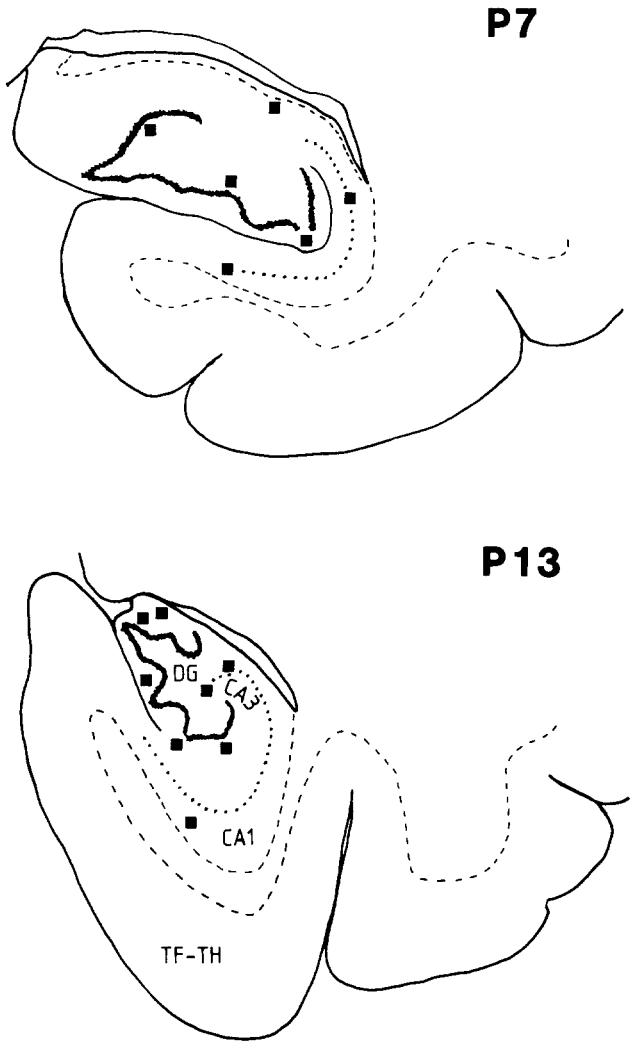

Fig. 6. The sites (shown by *squares*) in the hippocampus at which the neurons with differential responses to novel and familiar stimuli were recorded. The coronal sections are 7 and 13 mm posterior to the sphenoid (see Aggleton and Passingham, 1981). *CA3* and *CA1*, hippocampal pyramidal cell regions; *DG*, dentate gyrus; *TF-TH*, parahippocampal gyrus

tiate between novel and familiar stimuli in a recognition task. The memory spans of these neurons are sufficiently long (with a median of 21 and an interquartile range of 14–62 intervening stimuli) for them to play a role in solving the recognition memory tasks for which the hippocampus has been shown to be necessary. In these lesion studies, the memory spans tested were typically in the range 0–12 (Gaffan 1974, 1977; Gaffan and Weiskrantz 1980; Owen and Butler 1981; Gaffan et al. 1984b; Zola-Morgan and Squire 1985). The information required to solve the recognition memory task is present in the responses of the neurons described here; and the correct behavioural responses in the recognition memory task being performed, with spans of up to 17 intervening stimuli, could be based on the responses of these neurons.

Second, the proportion of hippocampal neurons that responded in relation to recognition was low – 2.3% in this study. This means that these neurons could easily be missed if a sample of neurons of less than several hundred were recorded from. We make this point because in a study of the responses of human hippocampus, neurons are being investigated during recognition memory tasks (Heit et al. 1988), but it is likely, based on our findings, that neurons which respond differently to novel and familiar stimuli will only be found if a rather large sample of neurons is studied. The low proportion of recognition-related neurons in the hippocampus may also account for the fact that Riches et al. (1991) did not report finding such neurons in their sample of hippocampal neurons, which was smaller than the one analysed here.

Third, it is of interest that the majority of these neurons had activity related to recent memory, rather than to memory of whether a stimulus had ever been seen before. The memory spans of the neurons were usually found to be, or were estimated to be, of finite length (with a median of 21 and an interquartile range of 14–62 intervening stimuli). Also, although the stimuli had been seen in some cases during testing on previous days, nevertheless the neurons described here responded to these stimuli as novel. It is of course possible that with further sampling in the hippocampus using completely novel stimuli, neurons will be found that respond only to stimuli which have never been seen before, and which could therefore be related to absolute recognition. In addition to responding to completely novel stimuli, the neurons described here responded as much to stimuli that had been seen a number of trials earlier in that day (as shown by their memory spans), and it is from this evidence that we relate their function to recent memory.

Fourth, the low proportion of hippocampal neurons which respond in the way described in the recognition memory task should not be unexpected if the hippocampus is involved in storing information. For neuronal networks which consist of interconnected neurons with Hebb-like synaptic modifiability, it is important that the proportion of neurons active in relation to any one memory or memory task is low, to maximise the number of memories which can be stored in the network (see Rolls 1987, 1989a,b, 1990; Rolls and Treves 1990; Treves and Rolls 1991). The finding that the neurons described here responded to all the novel stimuli (or, in one case, to all the familiar stimuli) suggests that these neurons do not themselves represent the information which is stored, for, if this were the case, the neurons should respond differently to the different visual stimuli. Rather, these neurons may reflect a read out from a memory store, and may be part of a system for interfacing the memory to the output.

Fifth, the question is raised of how the hippocampus is involved in recognition memory. In lesion studies, in which the fornix was sectioned, it has been found that the impairment in recognition memory tasks as usually implemented (e.g. "choose or respond to objects seen before", i.e. delayed match-to-sample, perhaps with intervening stimuli) is much less clear if delayed non-match-to-sample is used ("choose the novel stimulus") and if the monkeys are trained initially with the long (and therefore difficult) intervals between stimuli with which they are later tested (Gaffan et al. 1984b). The implication of this is that the deficit produced by the fornix section is due

not simply to an inability to distinguish novel from familiar stimuli, but perhaps just as much to a difficulty these lesioned animals have in altering their instrumental response strategies to make them suitable in a particular context. For example, the natural tendency of monkeys is to respond to novel stimuli, yet, in the context of the recognition memory task, they must respond to familiar stimuli. Further, the monkeys are typically pretrained to respond with short memory intervals, and part of their difficulty may arise when in the changing context of further training, they must learn to perform with long memory intervals (see Gaffan et al. 1984b). Further evidence for an impairment which may be related to difficulty with interfacing memory to certain types of behavioural response comes from the impairment produced by fornix section in monkeys learning the unnatural instrumental response rule "Choose the object not previously paired with reward" (Gaffan et al. 1984a). (Fornix section did not impair use of the natural instrumental rule "Choose the object previously associated with reward", Gaffan et al. 1984a). It is possible that the hippocampus, by storing situation-specific or context-specific episodic information, allows particular behavioural responses (such as responding only to familiar visual stimuli) to be performed only in specific situations (e.g. a running recognition task) (see Rolls 1990, 1991). The neurophysiological findings described here show that the activity of these hippocampal neurons is not just related to behavioural responses being made, in that the neurons indicate how recently a stimulus has been shown, even though the same behavioural responses are being made to all the familiar stimuli (e.g. Fig. 3). Our conclusion from the neurophysiological findings we describe is that information about the recency with which a stimulus has been seen is present in the hippocampus and could be used in memory tasks in which recent memory is a component, as in a running recognition memory task. The ways in which the hippocampus could operate to link together the attributes or components of an episodic memory which would enable identification of a particular stimulus or episode are considered elsewhere (Rolls, 1987, 1989a,b, 1990, 1991).

Sixth, although neurons with responses related to visual recognition memory are found in the primate hippocampus, it is of interest to consider whether this is the first part of a memory system in which neuronal responses which reflect the memory for visual stimuli seen (even when other stimuli intervene) are found. In the inferior temporal visual cortex, neurons have been analysed in the performance of serial recognition memory tasks, and it has been found that although for some neurons there is a larger response to a novel and an immediately re-presented stimulus, this effect reflects a short term visual memory, which does not persist over more than one, or in a few cases two, intervening stimuli (Baylis and Rolls 1987). In the more ventral temporal lobe cortex, neurons have been found which mediate the memory for a stimulus in that they fire in the delay period of a delayed match-to-sample task to some stimuli (Fuster and Jervey 1982; Miyashita and Chang 1988), or fire more to novel than to familiar stimuli in a delayed match to sample task (Riches et al. 1991). This task requires only a very short term visual memory, which need not span the intervening stimuli, and it is not clear whether such neurons have activity related to the longer-term recent memory studied here, in a running recognition memory task, and for which the hippocampus is needed. It would be of interest in future investigations to test whether or not the responses of neurons in this ventral temporal lobe cortex have recent memory spans as long as those of the hippocampal neurons described here, to provide evidence on whether hippocampal or earlier neurons implement recent memory for visual stimuli. One view is that, although the inferior temporal visual cortex and the more ventral cortical areas have some capacity for recent memory which spans across intervening stimuli, the number of intervening stimuli over which the neurons show evidence of memory is relatively low (Baylis and Rolls 1987; Miyashita and Chang 1988; Riches et al. 1991). Further, when the task is made more difficult by increasing the number of intervening stimuli, or requiring associations of the object with other attributes such as spatial location, then the extra computational capacity provided by the autoassociation processed in the hippocampus becomes relatively more important in implementing the memory (see Rolls 1989a,b, 1990, 1991; Rolls and O'Mara 1993).

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