Exp Brain Res (1994) 100:85–92

ORIGINAL PAPER

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Spontaneous recognition of object configurations in rats: effects of fornix lesions

Received: 23 June 1993 / Accepted: 5 April 1994

Abstract The effects of fornix lesions were examined in an object recognition memory test based on spontaneous exploration. In the standard condition an object (A) was presented in the sample phase and then presented again in the test phase alongside a new object (B). Both fornix-transected (Fx) and control (Co) rats spent more time exploring the new object than the familiar object after retention delays of 1 min and 15 min. In two configural conditions designed to test sensitivity to reconfigured stimuli, the original sample (A) was now either re-presented alongside its rearranged version (∀), or the re-arranged version itself (∀) was presented with a new object (B). In the first configural condition, both the Co and Fx rats spent more time exploring the reconfigured sample (∀) than the original version of the sample (A) following a delay of 1 min, but not 15 min. In the second configural condition, both Co and Fx rats spent more time exploring the new object (B) than the reconfigured version of the sample (∀) following a delay of 15 min but not 1 min. These present results do not support Sutherland and Rudy's hypothesis on hippocampal function; however, they demonstrate that memory of objects as well as memory of reconfigured objects could easily be examined in a test based on spontaneous exploratory behaviour.

Key words Object recognition
Configural discrimination · Memory · Fornix · Rat

Introduction

Sutherland and Rudy (1989) have proposed that the hippocampal formation is involved in the creation of configural associations. According to these authors, there is a simple associative process that permits bonding between elementary stimulus events, and there is a configural associative process which combines the representations of the elementary stimulus events to construct unique representations. The hippocampus is thought to permit an event to be processed as a configured unit composed of its various constituents or attributes. In this way, the hippocampus is necessary for normal memory when behaviour is guided by the relationship between two or more discriminative stimuli. Interest in this hypothesis has been heightened by the failure of certain other descriptions of hippocampal function such as working memory (Olton et al. 1979) or temporary storage memory (Rawlins 1985) to fulfil their predictions (Aggleton et al. 1986; Rasmussen et al. 1989; Ennaceur and Meliani 1992; Mumby et al. 1992). While many of the deficits seen after hippocampal damage can be accorded within the 'cognitive map' hypothesis (O'Keefe and Nadel 1978; Rasmussen et al. 1989), the impact of hippocampal system damage appears to extend beyond the spatial domain and, hence, has led to the quest for a more general description of hippocampal function.

In an attempt to develop such a description Sutherland and Rudy (1989) proposed their 'configural hypothesis'. The hypothesis has typically been tested with complicated experimental procedures that rely on some ambiguity between stimuli, their elements and the kind of association they have with reinforcement (Pearce and Wilson 1990; Alvarado and Rudy 1992; Wilson and Pearce 1992). An examination of such procedures (e.g. the biconditional discrimination task, negative patterning and the transverse patterning problem) shows that they frequently involve high levels of interference and a reduction of the saliency of the stimuli; conditions that may, themselves, contribute to an impairment (Davidson et al. 1993; Pearce and Wilson 1990).

The purpose of the present experiment was to test a more direct measure of configural memory using a modified version of the object recognition task devised by Ennaceur and Delacour (1988). An important feature of

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this task is that the measured behaviour is spontaneous, and hence does not rely on learnt associations. For this reason, it can be used to assess the ability to discriminate configured stimuli directly. In the standard version, rats are exposed to two identical objects in the sample phase and, in a subsequent choice phase, to two further objects: one identical to those in the sample phase, the other novel. Recognition memory is measured by the differential exploration of the familiar and novel objects. It has consistently been found that normal rats spend more time exploring the novel object, even after delays as long as 60 min. After a 24 h delay, however, the exploration of each object becomes indistinguishable (Ennaceur and Delacour 1988; Ennaceur and Meliani 1992). This task can then be modified to assess memory for stimuli that only differ configurally. In this 'configural condition', the sample object is re-presented in the choice phase, but now one or more of the elements that constitute this object are re-arranged spatially.

Materials and methods

Subjects

Twenty-one rats of a pigmented strain (DA) supplied by Bantin and Kingman (Hull, UK) were used. Their weights at the time of surgery were between 230 and 245 g.

Surgery

Each rat was anaesthetised with an intraperitoneal injection (4 ml/kg) of a solution containing 42 mg/kg of chloral hydrate and 9.7 mg/ml pentobarbitone sodium (equithesin). The animal was then placed in a stereotaxic frame (David Kopf Instruments, Tujunga). The scalp was cut and reflected to expose the skull, part of which was then removed using a dental drill to expose the dura above the sagital sinus. Eight rats received bilateral radiofrequency fornix (Fx) lesions, while 13 were sham-operated (Co). For the fornix lesions, a radionics TCZ electrode (0.3 mm tip length and 0.25 mm diameter) was lowered vertically into the fornix, and the tip temperature raised to 70°C for 60 s using an RFG4-A lesion maker (Radionics Inc. Burlington). Two lesions were made in each hemisphere. The stereotaxic coordinates of the lesion relative to ear-bar zero were: AP 5.3, HT 7.1, LAT $\pm$0.7 and AP 5.3, HT 7.1, LAT $\pm$ 1.6. For the control animals, the procedure was the same, except that the electrode was lowered to a height of 8.6, and no lesion was made. One month after recovery, all animals were submitted to the standard object recognition test.

Apparatus

The apparatus used was an open box (100 × 100 × 50 cm) made of aluminium with the inside painted grey. The floor was covered with sawdust. The objects to be discriminated were in triplicate and made of glass, plastic or metal. The weight of the objects ensured that they could not be displaced by the rats.

Behavioural testing

All rats were given five habituation sessions in which they were allowed 3 min to explore the apparatus. Forty-eight hours later, testing began. Rats were first tested on the standard condition (Fig. 2a) with retention delays of 1 min, 15 min and 240 min (experiment 1). After that they were tested under the 'configural conditions' (Fig. 2b,c) using retention delays of either 1 or 15 min (experiment 2). Each rat was tested once under each condition, and the interval between each testing condition was 48 h. A testing condition consisted of one session made up of a sample phase (A1 vs A2) and a choice phase (A vs B, A vs ∀ or ∀ vs B). The duration of each phase was 3 min.

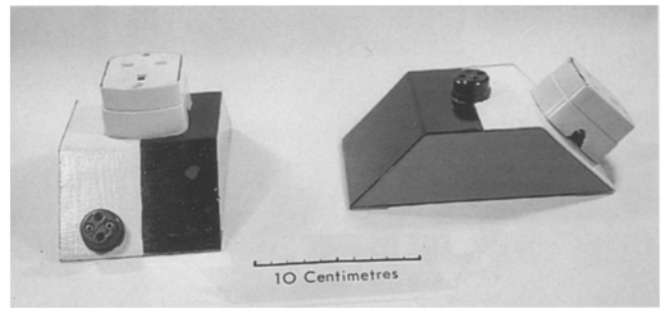


Fig. 1 Example of an object and its reconfiguration as used in the present experiment

The configural testing conditions were based on reconfigurations of the sample objects (represented as ∀). A reconfiguration consisted of a different spatial arrangement of the elements of the original sample (A). This meant that although each constituent part of the reconfigured sample was familiar, the overall appearance was novel. Care was taken not to introduce any hidden aspect of the sample object (e.g. the base) when it was re-arranged as a reconfigured object (Fig. 1).

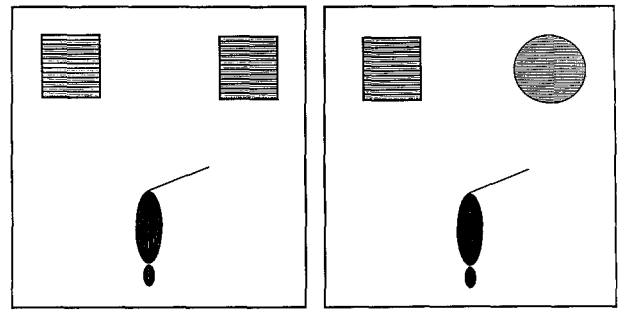
Two different 'configural' tests were employed. In the first condition (Fig. 2b), the sample (A) was presented in the choice phase with its reconfigured version (∀). In the second condition (Fig. 2c), the sample (A) was presented in its reconfigured version (∀) in the choice phase with a new object (B). New sample stimuli were used for every session.

The objects were always presented in the back corner of the box 10 cm from the side wall. In most of the test conditions, three identical copies of each sample object were used. Two identical copies were used in the sample phase (A1 and A2) and a third copy was used in the choice phase (A3) as the familiar object to be compared with either a new object (B) or a reconfigured object (∀). From rat to rat, the role as well as the locations of the two objects (sample, reconfigured or new) were counterbalanced and randomly assorted. It should be noted that the objects were not known to have any natural significance for the rats, and they had never been associated with a reinforcer.

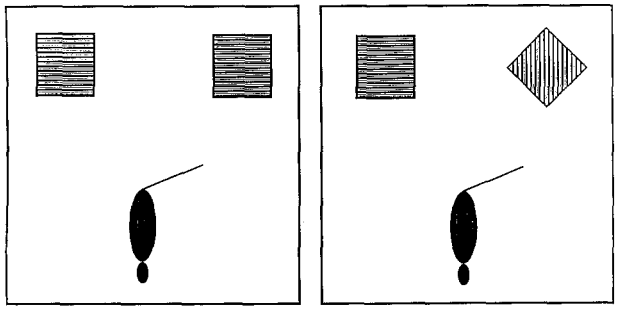
Measurements and statistical treatments

The basic measure was the time spent by the rats in exploring objects during the sample phase and during the choice phase. Exploration of an object was defined as follows: directing the nose to the object at a distance $\leq$2 cm and/or touching it with the nose; turning around or sitting on the object was not considered as exploratory behaviour.

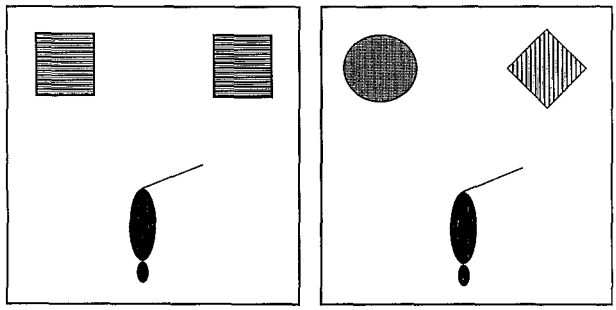
As shown in Table 1, the times spent exploring the two identical objects in the sample phase are represented by A1 and A2. The time spent in exploring the two different objects in the choice phase are represented by A and B, A and ∀, or ∀ and B. Analyses of variance were performed on the following measures: (1) e1, which is the total time spent in exploring the two identical objects in the sample phase; (2) e2, which is the total time spent exploring the two objects in the choice phase; (3) d1, the discrimination index, which is the difference in time spent exploring the two objects in the choice phase (e.g. B-A in the standard condition, ∀-A or B-∀ in the configural conditions); (4) d2, the discrimination ratio, which is the difference of exploration time divided by the



a Object recognition test: standard condition



b Object recognition test: Configural condition 1



c Object recognition test: Configural condition 2

Fig. 2a–c The different testing conditions in the object recognition test. *Left* (sample phase): in all testing conditions, rats are exposed to two identical objects. *Right* (choice phase): **a** in the standard condition (A vs B), rats are exposed to two different objects, the previously object sample explored in the sample phase which is now familiar (A) and a new object (B), never seen before; **b** in the first configural condition (A vs ∀), rats are exposed to two different objects, the sample object previously explored in the sample phase which is now familiar (A) and a reconfiguration of the sample object (∀); **c** in the second configural condition (∀ vs B), rats are exposed to two different objects, the reconfiguration of the sample object (∀) and a new object (B), never seen before

total time spent exploring the two objects in the choice phase e.g. $\frac{B-A}{B+A}$ in the standard condition, $\frac{\forall-A}{\forall+A}$ or $\frac{B-\forall}{B+\forall}$ in the configural conditions).

In addition, paired Student *t*-tests (one-tailed) were used to compare the time spent exploring each of the objects in the choice phase of the various conditions, for each of the separate groups. The threshold level for significance was $P \leq 0.05$.

Table 1 Index of the different measures involved in the object recognition test: e1 is the measure of the time spent exploring the two objects A1 and A2 in the sample phase, whereas e2 is the measure of the time spent exploring both objects B and A, A and ∀, or ∀ and B in the choice phase. A is the copy of the sample which is now familiar, ∀ is the reconfiguration of the sample, and B is the new object. d1 is the discrimination index (difference in time spent exploring the two objects in the choice phase) and d2 is the discrimination ratio (difference of exploration time divided by the total time spent exploring the two objects in the choice phase)

Variables	e1	e2	d1	d2
Condition 1	A1 + A2	A + B	B - A	B - A/B + A
Condition 2	A1 + A2	A + ∀	∀ - A	∀ - A/B + A
Condition 3	A1 + A2	∀ + B	B - ∀	B - ∀/B + A

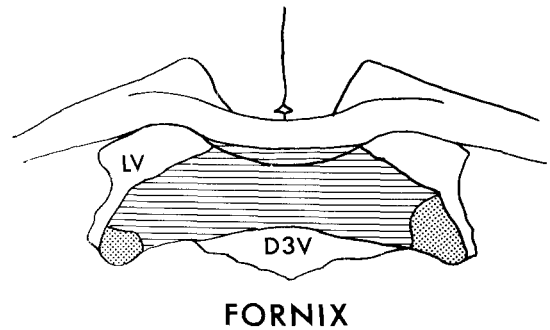


Fig. 3 Coronal section illustrating the extent of the largest (*stippled plus horizontal lines*) and smallest (*horizontal lines*) fornix lesions. (*D3V* dorsal portion of third ventricle, *LV* lateral ventricle)

Results

Histological examination showed that all Fx rats (except one which was discarded) sustained extensive lesions of the fimbria-fornix, the only sparing occurring in the most lateral tips of the fimbria. This is depicted in Fig. 3, which shows the largest and the smallest of the lesions. In some cases the lesion also affected the adjacent ventral parts of the corpus callosum. Slight damage was sometimes observed in the extreme dorsal portion of the anterior ventral nucleus of the thalamus.

Experiment 1 ('Standard version')

Overall levels of exploration

Comparisons of the total time spent exploring the test objects were not significant in the sample phase (e1, $F_{1,18}=4.26$, $P=0.054$), but there was clear evidence of a group effect in the choice phase (e2, $F_{1,18}=13.09$, $P \leq 0.002$). These group effects reflected the overall higher levels of exploration by the Fx group during the test phase (e2) for the delays of 1 min ($F_{1,18}=5.85$,

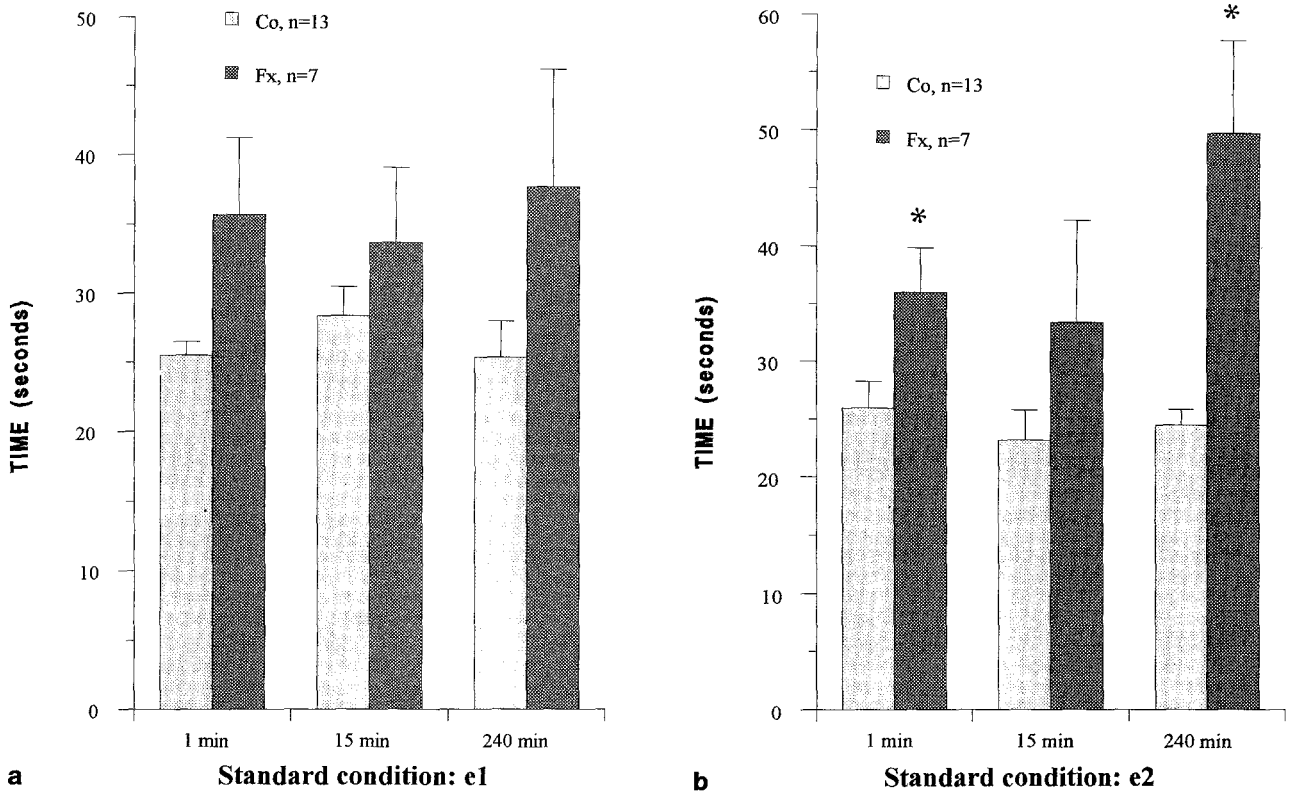


Fig. 4a,b Mean value (±SEM) of the total exploration time spent by rats exploring objects in the sample phase (**a**) and the choice phase (**b**) of each delay condition. There is an overall significant group effect in the choice phase ($F_{1,18}=13.09$, $P\leq 0.002$). The post-hoc comparisons show that Fx group spent more time exploring the two objects during the test phase for the delays of 1 min ($F_{1,18}=5.85$, $P\leq 0.03$) and 240 min ($F_{1,18}=17.49$, $P\leq 0.001$) compared to Co

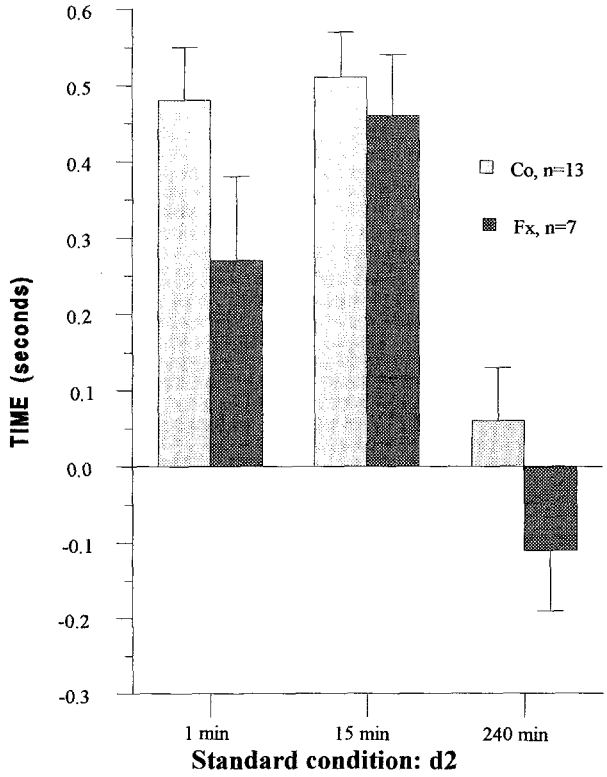


Fig. 5 Mean value (±SEM) of the discrimination ratio d2 in each delay of the standard test condition. There are no differences between groups ($F_{1,18}=4.23$, $P>0.05$)

$P\leq 0.03$) and 240 min ($F_{1,18}=17.49$, $P\leq 0.001$). There was, however, no delay effect and no group × delay interaction (Fig. 4a,b).

Discrimination performance

In the standard condition (Fig. 5), both Fx and Co rats spent significantly more time exploring the new object than the familiar one, after delays of either 1 min or 15 min (All $P\leq 0.01$). The failure of both the Co and Fx rats to discriminate between the objects after a delay of 240 min is consistent with the notion that the differential levels of exploration seen after 1 and 15 min reflected the ability to remember the novel object. An analysis of variance using the discrimination ratio (d2) confirmed that there were delay effects ($F_{2,36}=26.81$, $P\leq 0.0001$), but no group effects ($F_{1,18}=4.23$, $P>0.05$) and no group × delay interaction ($F_{2,36}=0.57$, $P>0.10$). The discrimination performance of the rats in each group was significantly higher after both 1 min and 15 min than after 240 min (maximum $P\leq 0.02$).

Experiment 2 ('Configural conditions')

Overall levels of exploration

As in the standard condition, there was evidence that levels of exploration were affected by the Fx lesions in

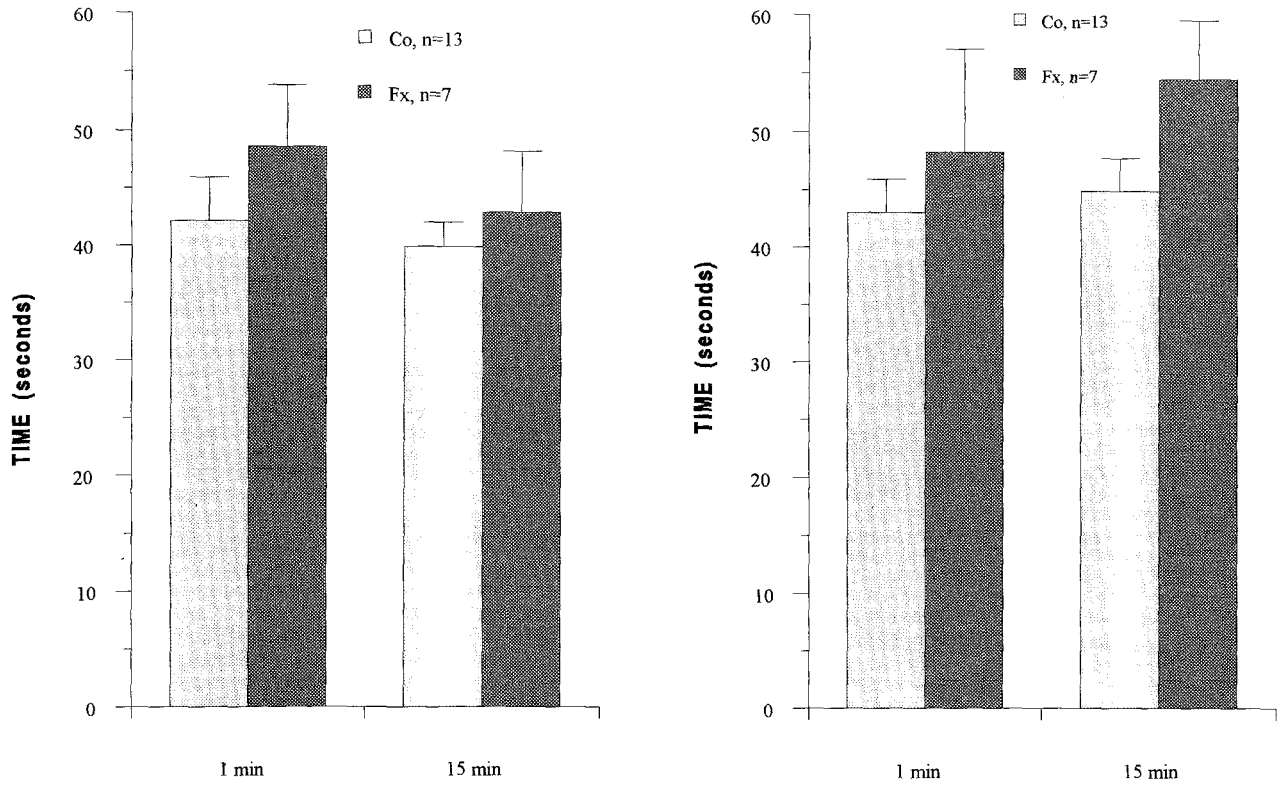


Fig. 6a,b Mean value (±SEM) of the total exploration time spent by rats exploring objects in the sample phase of the first (A vs. ∀, **a**) and the second (∀ vs B, **b**) configural conditions. There is no overall significant group effect (respectively, $F_{1,18}=0.89$ and $F_{1,18}=1.77$, $P>0.10$)

the choice phase. An overall significant group effect was found for the total amount of exploration (e2) during the choice phase in the second configural conditions (Fig. 7b; $F_{1,18}=6.73$, $P\leq 0.02$). However, post-hoc comparisons between groups were not significant for either 1 min ($F_{1,18}=1.66$, $P>0.10$) or 15 min ($F_{1,18}=3.39$, $P=0.08$) delays. There was no overall significant group effect in the first configural condition (*F*ig. 7a; $F_{1,18}=3.06$, $P=0.10$). The levels of exploration in the sample phase (e1) did not, however, differ between the groups in both configural conditions, respectively $F_{1,18}=0.89$ (Fig. 6a) and $F_{1,18}=1.77$, $P>0.10$ (Fig. 6b).

Discrimination performance

In the first condition (A vs ∀), both the Co and Fx rats spent more time in exploring the configured sample (∀) compared to the time spent with the original sample (A) after the 1 min delay. This effect on d1 was, however, significant only for the Co (Co, $t_{12}=4.28$, $P\leq 0.001$ and Fx, $t_6=1.87$, $P=0.055$,). Neither group showed clear evidence of discrimination after the 15 min delay (Co, $t_{12}=1.62$, $P=0.066$ and Fx, $t_6=1.19$, $P>0.10$). In the second condition (∀ vs B), both the Fx and Co rats spent similar amounts of time exploring the new (B) and the configured (∀) object after a 1 min delay (Co, $t_{12}=1.14$, $P>0.10$ and Fx, $t_6=1.11$, $P>0.10$) i.e. they did not appear to discriminate between the objects on the basis of familiarity. But, after a 15 min delay, the Co and Fx rats spent significantly more time exploring the new (B) rather than the configured (∀) object (Co, $t_{12}=1.91$, $P\leq 0.04$ and Fx, $t_6=2.64$, $P\leq 0.02$).

An analysis of variance using the discrimination ratio (d2) showed only an overall significant delay effect from the first configured condition (Fig. 8a; A vs ∀, $F_{1,18}=10.31$, $P\leq 0.005$) and the second configural condition (Fig. 8b; ∀ vs B, $F_{1,18}=5.31$, $P=0.03$). It can be senn in Fig. 8a and 8b that the discrimination ratio (d2) was higher after 1 min than 15 min in the first configural condition, but that this was reversed in the second configural condition. For neither condition was there a significant group effect (A vs ∀, $F_{1,18}=0.05$, $P>0.10$; ∀ vs B, $F_{1,18}=4.04$, $P=0.06$), or a group × delay interaction (A vs ∀, $F_{1,18}=0.001$, $P>0.10$; ∀ vs B, $F_{1,18}=0.21$, $P>0.10$).

Discussion

The results of the present experiments show that rats with fimbria-fornix lesions are unimpaired on the standard version of an object recognition test. This finding is not only consistent with a similar study looking at the

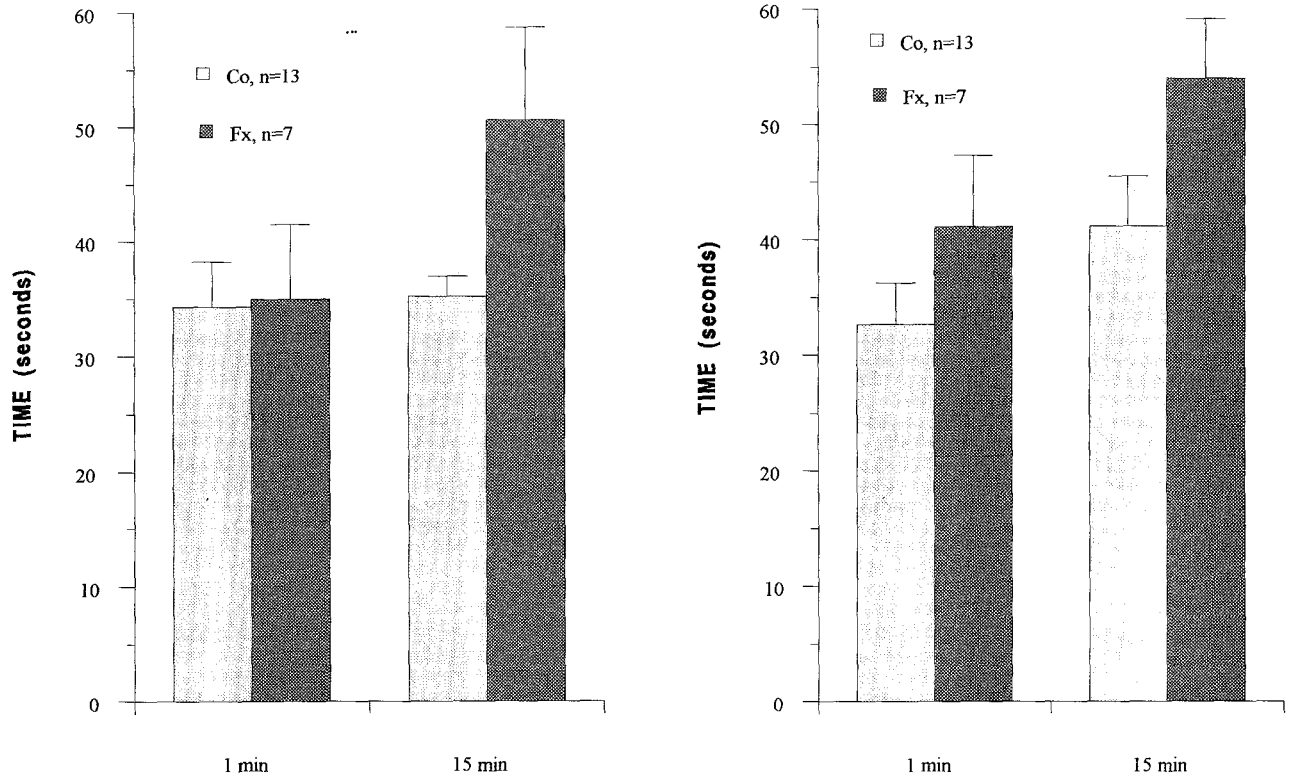


Fig. 7a,b Mean value (±SEM) of the total exploration time spent by rats exploring objects in the choice phase of the first (A vs. ∀, **a**) and the second (∀ vs B, **b**) configural conditions. There is an overall significant group effect in the second configural condition ($F_{1,18}=6.67$, $P\leq 0.02$). However, post-hoc comparisons between groups is not significant in either 1 min ($F_{1,18}=1.66$, $P>0.10$) or 15 min delay ($F_{1,18}=3.39$, $P=0.08$)

effects of medial septal lesions (Ennaceur and Meliani 1992), it also accords with a number of other tests of object recognition following hippocampal or fornix damage in rats (Aggleton et al. 1986; Mumby et al. 1992; Shaw and Aggleton 1993; Rothblat et al. 1993). In addition, the first experiment confirmed that the spontaneous preference design could be used with a variety of rat strains, previous studies being confined to the Wistar strain (Ennaceur and Delacour 1988; Ennaceur and Meliani 1992). The second experiment also showed that the configural hypothesis could be examined in a test based on spontaneous exploratory behaviour. Evidence that the performance of rats is delay dependent in the standard and the configural conditions helps to show that these are tests of memory.

In the first configural condition, both the Co and Fx rats spent less time exploring the sample stimulus (A) and more time exploring its reconfigured version (∀) following a delay of 1 min. While they were able to distinguish the sample stimulus from its reconfigured version at this short delay, they could not after a longer retention delay of 15 min. In this experiment, fornix lesions did not demonstrate a clear-cut significant discrimination between objects when the delay is 1 min ($P<0.06$, one tailed), but according to the index of discrimination measure they did not differ from the control animals. In a replication experiment (not reported), however, fornix rats were found to demonstrate a significant spontaneous preference for the reconfigured objects against the familiar one after a delay of 1 min.

In the second configural condition of the task, both Co and Fx rats failed to discriminate between the completely novel (B) object and the reconfigured version of the sample (∀) after a retention delay of 1 min i.e. both stimuli were treated like novel objects. After a delay of 15 min, however, they spent significantly more time exploring the novel object (B) than the reconfigured familiar objects (∀). In this way they appeared to be treating the reconfigured stimulus (∀) as though it was familiar and hence were insensitive to the configural shift (Fig. 8b).

Throughout the experiment it was observed that the Fx rats tended to spend more time overall exploring the test objects in the choice phase. There was a significant difference between the two groups ($P<0.03$) in 1 min and 240 min delay conditions of the standard test (Figs. 4b), there was no clear difference in the sample phases. In spite of this difference in behaviour, the results using d1 and d2 were qualitatively the same. Thus the exploratory activity levels of the fornix lesioned rats were not reponsible for the lack of lesion effects.

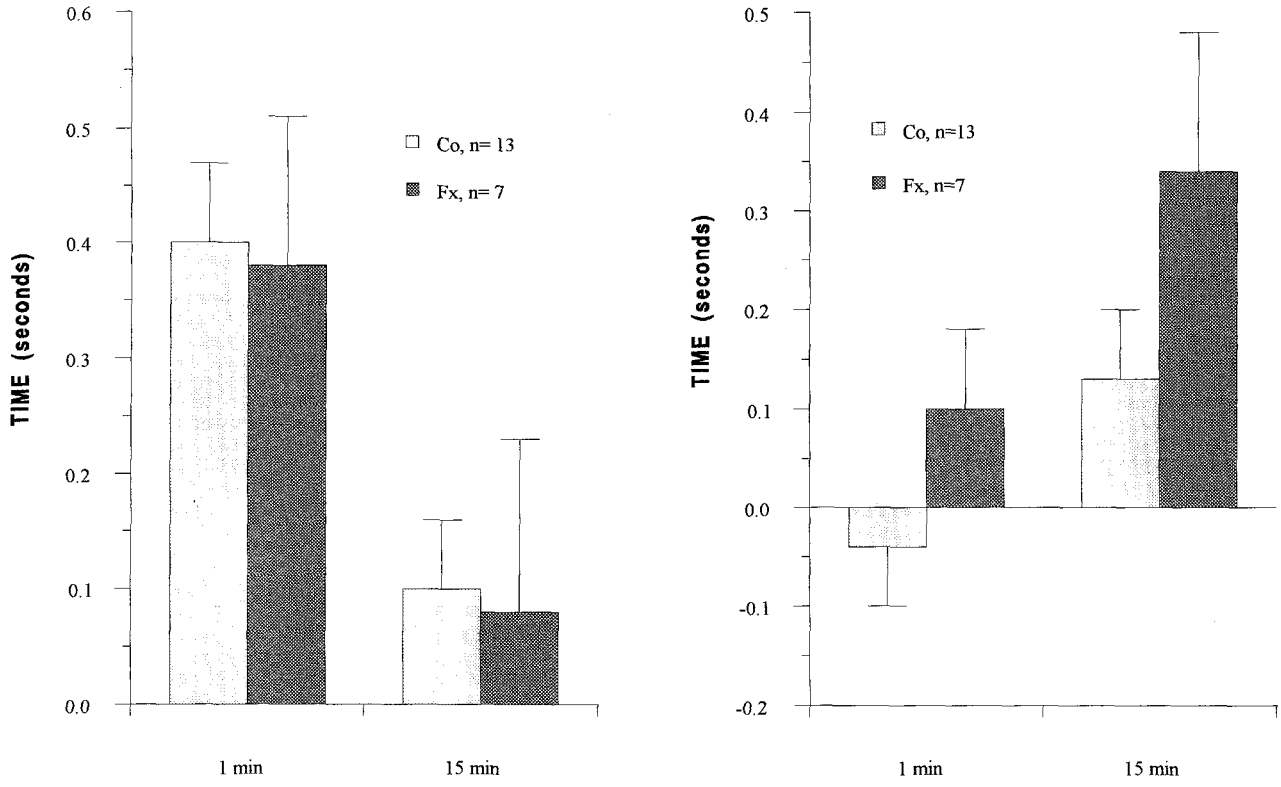


Fig. 8a,b Mean value (±SEM) of the discrimination ratio d2 in each configural and delay condition. There is no significant group effect in either of the two configural conditions (**a** A vs ∀: $F_{1,18}=0.05$, $P>0.10$; **b** ∀ vs B: $F_{1,18}=4.04$, $P=0.06$)

From the above results, it would appear that the rates of forgetting of the various attibutes of the stimuli are different. The memory of the attributes of the sample is unaffected in presence of a new object but it is altered in presence of the reconfigured sample. Taking the example of the second configural condition, it was found that after just 1 min the rats treated both the novel stimulus and the reconfigured stimulus as though they were both unfamiliar; however, after a delay of 15 min, the rats spend relatively less time exploring the reconfigured stimulus. The most obvious explanation of this is that during the 15 min delay the rats had forgotten the spatial attributes of the sample stimulus, but were still able to recognise the individual features as familiar. This explanation is consistent with the ability of the rats to discriminate the sample stimulus from its reconfigured version after a delay of 1 min, but not 15 min.

It has already been demonstrated that the attributes of stimuli play a crucial role in memory performance (Reynolds 1961; Riccio et al. 1992). For instance, changing an attribute should impair performance if the subject has encoded information about that attribute during acquisition. It is therefore possible that the degree of similarity or dissimilarity of some particular attributes of the sample and its reconfiguration may account for the conflicting results on the effects of hippocampal damage (Sutherland and Rudy 1989; Sutherland et al. 1989a; Sutherland et al. 1989b; Whishaw and Tomie 1991; Gallagher and Holland 1992; Whishaw et al. 1992; Davidson et al. 1993). Thus, hippocampal lesions may only be sensitive to subtle modification of the attributes of the sample, while in our configural conditions, the alteration of the spatial attributes of the stimuli were highly salient and so affected the memory of both control and fornix lesioned rats. It is also possible, according to the spatial memory theory, that alteration of the non-spatial attributes of a stimulus may not be sensitive to the effect of hippocampal lesions. Further experiments are needed to clarify these points.

While the present findings appear to be inconsistent with the configural theory of Sutherland and Rudy (1989), a number of important issues are raised. First, there is the need to set out independent criteria that help define those stimuli that recruit the putative 'configural association system' (Nadel 1991, 1992). This is necessary in order to avoid a circular definition that relies on sensitivity to hippocampal dysfunction. A particular strength of the present study is the use of a task that relies on spontaneous behaviour, so making it both easy to administer and insensitive to acquisition deficits. As a consequence, it offers a ready means of exploring sensitivity to certain classes of configural associations, and so might be used to address the problem of independent

criteria. A second issue concerns those studies using configural tasks that have reported normal or near-normal behaviour in rats with hippocampal lesions (Whishaw and Tomie 1991; Gallagher and Holland 1992; Whishaw et al. 1992; Davidson et al. 1993). Such studies raise the possibility that other brain regions can solve configural problems. This possibility is currently being explored.

Acknowledgements This work was supported by the Wellcome Trust, grant number M/90/3028.

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