Revisiting places passed: Sensitization of exploratory activity in rats with hippocampal lesions

Online Publication Date: 01 May 2007
To link to this article: DOI: 10.1080/17470210601155252
URL: http://dx.doi.org/10.1080/17470210601155252

The Quarterly Journal of Experimental Psychology

Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t716100704

Full terms and conditions of use: http://www.informaworld.com/terms-and-conditions-of-access.pdf

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

© Taylor and Francis 2007
We examined the involvement of the hippocampus in short-term changes in exploratory behaviour in an open field (Experiment 1) and experimental contexts (Experiment 2). In Experiment 1, rats with excitotoxic lesions of the hippocampus were more likely to revisit recently visited zones within the open field than were control rats. Similarly, in Experiment 2 rats with hippocampal lesions showed greater exploration of a context that they had recently explored than a context that they had less recently explored. This short-term sensitization effect was not evident in control rats. These findings are consistent with the suggestion that the recent presentation of a stimulus has two opposing effects on behaviour, sensitization, and habituation, and that hippocampal lesions disrupt the short-term process responsible for habituation, but not that responsible for sensitization.

It is well established that the tendency of a stimulus to provoke responding can be modulated by whether or not that stimulus has been recently encountered. For example, depending on parameters, the first presentation of a stimulus can affect a reduction in responding to the second presentation (i.e., produce short-term habituation) or an increase in responding (i.e., produce short-term sensitization), or indeed result in no effect: The behavioural sequelae associated with repeated stimulus presentation are surprisingly complex (see Groves & Thomson, 1970; Hawkins & Kandel, 1984; Horn & Hill, 1964; Wagner, 1981). The neural mechanisms that contribute to short-term changes in behaviour have not been established, but the hippocampus has often been linked to the process of habituation (Gray, 1982; Sokolov, 1963; Vinogradova, 1975) and, more generally, to short-term mnemonic processes (e.g., Olton, Becker, & Handelmann, 1979; Rawlins, 1985).

The finding that rats with selective lesions of the hippocampus show higher levels of exploratory activity than do control rats, when given a brief period of exposure to a context, provides indirect support for the view that repeatedly sampling aspects of a context has a different effect on the behaviour of hippocampal than control rats
In particular, this finding suggests that hippocampal damage reduces the likelihood of observing short-term habituation (or increases the likelihood of observing sensitization). This indirect evidence is complemented by the results of other studies where rats with hippocampal lesions have been reported to show atypical exploratory behaviour (e.g., see Save, Buhot, Foreman, & Thinus-Blanc, 1992; Save, Poucet, Foreman, & Buhot, 1992b).

Direct evidence that the hippocampus is involved in the processes that underlie habituation and sensitization comes from recent studies of the orienting response (OR) that rats show to localized visual stimuli. These studies have demonstrated that selective hippocampal damage increases the likelihood of observing short-term (and stimulus-specific) sensitization of the OR and reduces the likelihood of observing habituation of the OR (Marshall, McGregor, Good, & Honey, 2004; see also, Honey & Good, 2000a, 2000b; Honey, Watt, & Good, 1998). Here, we examine whether this effect of hippocampal lesions is also apparent in rats' exploratory behaviour in complex environments of two types. In Experiment 1, the pattern of exploration that control and hippocampal rats show when allowed to explore a novel environment (a 1-m square open field) was assessed. In particular, we monitored rats' tendency to revisit recently entered zones within the open field. In Experiment 2, we directly manipulated the relative recency with which rats sampled two contexts (A and B) and examined whether rats' subsequent exploratory behaviour in A and B was influenced by this manipulation. Thus, rats received training trials in which they were placed in Context A (e.g., an operant chamber with spotted wallpaper) for a brief period and 1 hour later were placed in a second context (B: e.g., an operant chamber with checked wallpaper) for a brief period. One minute after exposure to Context B, rats received test trials in which they were re-placed in either B (the recently sampled context) or A (the remotely sampled context). Our primary interest was in whether rats with hippocampal lesions would be more likely than control rats to show short-term sensitization (i.e., show preferential exploration of Context B; cf. Marshall et al., 2004).

Method

Subjects and surgery

Of the 55 Lister hooded rats (Rattus norvegicus; supplied by Harlan Olac Ltd., UK) that served in Experiment 1 (conducted in 2 replications), 28 had received ibotenic acid lesions of the hippocampus, and 27 were given sham operations. These rats and an additional 32 rats were tested in Experiment 2 (conducted in three replications), of which 16 had received hippocampal lesions, and the rest received sham operations. The surgical procedures paralleled those described by Honey and Good (1993). The rats were first anaesthetized with Isoflurothane and then placed in a Kopf stereotaxic frame (Kopf Instruments, Tujunga, CA) where, after a scalp incision, the bone over-lying the area of the neocortex directly above the hippocampus was removed. Injections of ibotenic acid (concentration 10 μg/ml; supplied by Biosearch Technologies, Novato, CA) were then made using a 2-μl Hamilton syringe mounted on the stereotaxic frame. The 0.05–0.10-μl injections were made at 28 sites using a KD Scientific electronic pump (Model No. 310) at a rate of 0.03 μl/min. Once the injection was complete, the needle was left in position for 2 min both to encourage diffusion of the ibotenic acid and to restrict the spread of the drug into overlying cortical areas. Sham-operated rats received an identical treatment except that the passage of the needle was limited to the cortex, and no drug was infused. After a postoperative recovery period that lasted a minimum of 2 weeks, rats were gradually reduced to 80% of their ad libitum weights (M = 447 g; range = 300–580 g), at which they were maintained during Experiments 1 and 2. Throughout Experiments 1 and 2, rats were housed in pairs and had free access to water when resident in their home cages. The colony room was illuminated between the hours of 8.00 a.m. and 10.00 p.m., and testing began at approximately 9.00 a.m.
injections of Euthatal, were perfused through the heart, and their brains removed. A cresyl violet stain was used to determine the extent and location of cell loss.

**Apparatus**

In Experiment 1, experimental sessions were conducted in an open-field arena (internal dimensions: floor 100 cm × 100 cm and walls 42 cm high), placed in a room with walls made distinct from one another by the addition of posters and structural features (e.g., the door to the room, wall-mounted electricity supply and sockets). The walls of the arena were constructed from MDF (medium-density fibreboard) painted flat grey, and sawdust was scattered over the floor. Rats' exploratory behaviour was recorded using a video recorder and was subsequently scored using Ethovision computer tracking software (supplied by Noldus Information Technology; Nottingham, UK). The floor of the open-field arena was divided into 36 equally sized zones for the purpose of scoring, and the rats' exploratory behaviour was tracked through these zones using the Ethovision software by identifying the moving rat with respect to the lighter floor of the open field. In fact, the tracking sensitivity of the software could be adjusted so that it tracked a point of the rat (normally the shoulders) close to the snout.

In Experiment 2, experimental sessions were conducted in four standard experimental chambers arranged in a 2 × 2 array. Each chamber (internal dimensions: 24.5 cm wide × 23 cm deep × 21 cm high; supplied by Campden Instruments Ltd., Loughborough, UK) had three aluminium walls, an aluminium ceiling, and a Perspex door that served as the fourth wall. The floors were constructed from stainless-steel rods. On the first day of training, the walls remained plain, but on subsequent days spotted wallpaper was fixed to the three aluminium walls and ceiling of the two upper chambers, and checked wallpaper was fixed to the walls and ceilings of the lower pair of chambers (for a complete description of these wallpapers, see Honey & Watt, 1999). Rats' exploratory behaviour was recorded using a Heiwa VHS movie camera (Model No. TH-650).

**Behavioural procedures**

Experiment 1 was conducted over the course of 2 consecutive days. On both days, each rat was placed in the same corner of the open-field arena with its head facing the wall, allowed to explore the open-field environment for 3 min, and was then removed. On the first day of Experiment 2, rats were placed in a standard (undecorated) operant chamber for 30 min. On each of the next 4 days, rats received the following sequence of events: a single 3-min training trial in one context (A) followed 60 min later by a 3-min training trial in the second context (B), and 1 min later by a 3-min test trial in either A (the remote context; on ABA trials) or B (the recent context; on ABB trials). During the 60-min interval the rats were returned to their home cages, and during the 1-min interval rats were taken out of the experimental room. Half of the rats in each group received ABA trials on Days 1 and 3 and ABB trials on Days 2 and 4, and the remaining rats received ABB trials on Days 1 and 3 and ABA trials on Days 2 and 4. For half of the rats, on Days 1 and 4 the spotted context served as A, and the checked context served as Context B, and on Days 2 and 3 the checked context served as A, and the spotted context as B; for the remaining rats this arrangement was reversed.

**Behavioural measures**

In Experiment 1, the video recordings of rats' exploration of the open field was scored using Ethovision computer tracking software. The open-field arena was divided into 36 equal-sized zones (in a 6 × 6 array), and the exploratory activity of the rats was tracked through these zones. Three types of zone were distinguished: 20 perimeter zones (which were immediately adjacent to the wall), 12 inner zones (which were adjacent to these perimeter zones), and the remaining 4 central zones. Our main focus was on rats' activity in the perimeter zones because the rats spent the majority of the time in these zones. The primary measure of activity was the mean number of entries per zone: the total number of zone entries divided by the number of
zones (20 in the case of the perimeter zones). We also assessed the rats’ tendency to revisit zones they had recently visited by using the standard deviation in the number of times a rat visited each of the 20 perimeter zones. On the one hand, if a rat tended to move around the perimeter without revisiting recently visited zones, then the number of times it visits each of the perimeter zones in the 3-min sessions should be relatively similar, and the standard deviation in zone entries should be correspondingly low. On the other hand, if a rat revisits recently visited zones then there should be substantial variation in the levels of activity in the perimeter zones that they visited. For example, the standard deviation of the numbers of times a rat visits the 20 perimeter zones will be greater if that rat spends all of its time moving between two adjacent zones (i.e., revisiting places recently visited) than if it distributes its exploratory behaviour more evenly across the 20 zones (i.e., does not tend to revisit recently visited zones).

The Ethovision software could not be used to analyse the results of Experiment 2 because rats’ movements could not be tracked effectively against the black-and-white patterned wallpapers used to distinguish the two contexts. Two observers who were blind with respect to the group membership of the rats scored video recordings of the rats’ exploratory activity in Experiment 2. Each occasion on which the rat’s snout moved across (a) a horizontal line (drawn on the video monitor used to present the recordings) that bisected the upper and lower half of each chamber, and (b) a vertical line that bisected the left and right sides of each chamber, was scored as a single activity response. Interobserver concordance for these measures of the activity between two blind observers and V.J.M. was approximately 95%. Pilot work suggested that scoring the first and final 30 s of each training trial provided a sensitive measure of within-session changes in behaviour. During the test, we also scored the first 30 s of each trial; our pilot work indicated that activity during the remainder of the trial was relatively low and variable.

Results

Histological analysis

Of the 44 rats that received ibotenic acid lesions targeted at the hippocampus, 12 had sustained less than 65% cell loss (range 20–65%) and were excluded from the analysis. In addition, 2 rats were found to have extrahippocampal damage to the temporal cortex and were also excluded. All of the remaining lesioned rats (Experiment 1, n = 22; Experiment 2, n = 30; see Figure 1) sustained bilateral damage to both the dentate gyrus and the CA subfields at all dorsal and ventral levels. The range of cell loss in the hippocampus was 70–100%. The majority of rats also sustained cell loss in the subiculum (including the pre- and parasubiculum). This damage was most evident in ventral regions of the subiculum. There was no detectable cell loss in the postsubiculum or in the medial or lateral entorhinal cortex in any of the lesioned rats.

Behavioural analysis

Experiment 1. Figure 2 depicts the mean number of entries per zone in the perimeter (left-hand pairs of bars) on Day 1 (upper panel) and Day 2 (lower panel). On Day 1, the mean number of entries per zone was greater in the control group than in the hippocampal group, F(1, 46) = 18.88, p < .001, but on Day 2 there was no such difference (F < 1). The right-hand pair of bars in Figure 2 shows the mean standard deviation of activity in these perimeter zones, and inspection of these scores indicates, what statistical analysis confirmed, that on both Days 1 and 2 the standard deviations were greater in the hippocampal group than in the control group, F(1, 46) = 5.67, p < .05, and F(1, 46) = 5.25, p < .05, respectively. The fact that the standard deviations in perimeter exploration were greater in the hippocampal group than in the control group is consistent with the suggestion that they were revisiting particular areas that they had visited recently. However, it is possible that this pattern of results could be generated if hippocampal rats often and consistently moved from one side of the open field to
the other and thereby frequently visited the perimeter zones on two sides of the open field, but not the other sides of the open field. If this was the case, then hippocampal rats should have higher levels of inner and central zone entries than the control group. On Day 1 the mean numbers of inner zone entries (control $M$: 2.91; hippocampal $M$: 2.98) and central zone entries (control $M$: 2.48; hippocampal $M$: 1.76) did not differ between the groups: largest $F(1, 46) = 2.68$, $p > .10$. Moreover, on Day 2 the mean number of inner and central zone entries was significantly greater in the control group ($M$s: 3.08 and 2.17, respectively) than in the hippocampal group ($M$s: 2.21 and 1.27, respectively); smallest $F(1, 46) = 6.26$, $p < .05$. The difference in the variability with which the hippocampal rats explored the perimeter of the open field does not reflect the fact that they

Figure 1. Histology from Experiments 1 and 2. The maximum (grey) and minimum (black) extent of the lesion in group hippocampal are shown at horizontal sections taken through the dorsoventral extent of the brain. The sections shown are in mm from bregma (clockwise from top left: –3.1, –3.6, –5.6, –7.6, –8.6, –6.6, and –4.6) and are adapted from those in The Rat Brain in Stereotaxic Coordinates by G. Paxinos and C. Watson, 1998. Copyright 1998 by Academic Press. Adapted with permission.

Figure 2. Experiment 1: Mean ($\pm$ SEM) number and standard deviations ($\pm$ SEM) of zone entries on Days 1 and 2 (left-hand pairs of bars in upper and lower figures) and mean standard deviations in levels of activity in the perimeter zones (right-hand pair of bars in upper and lower figures) in control and hippocampal rats.
were more likely to move away from the perimeter than the control rats. Rather it seems more parsimonious to suppose that the control rats were less inclined to revisit recently visited areas around the perimeter, and this tendency both decreased the standard deviations of their exploration of the perimeter zones and contributed to their tendency to explore the inner and central zones.

Figure 3 shows representative exploratory paths from two control rats (RHR040#6 and RHR040#8; upper left and right panels, respectively) and two hippocampal rats (JPR072#19 and JPR072#21; lower left and right panels, respectively). These paths show a trace of the rats’ behaviour across the 3-min trials on the first day of training and are derived from the traces produced by the Ethovision software. Inspection of the upper panels shows that the exploratory paths taken by control rats were orderly, with relatively similar levels of exploration of each of the perimeter zones and rather little exploration of the central zones. Inspection of the lower panels indicates that the exploratory behaviour shown by hippocampal rats was less systematic, with frequent revisits to certain areas (in particular the corners) and little or no exploration of other perimeter zones. Thus, the more qualitative analysis of the exploratory paths shown in Figure 3 complements the automated, quantitative analysis summarized in Figure 2.

Experiment 2 training trials. Table 1 depicts the mean levels of activity in the remote (A) and recent (B) training trials. Inspection of the scores from Days 1 and 2 reveals that the level of activity in the control rats was higher in the first 30 s than in the final 30 s, an effect that was more marked during the recent than the remote training trial. It also reveals that there was little sign of any difference between the levels of activity in the first and final 30 s in the hippocampal-lesioned rats; there was some indication that the level of activity in the remote training trials was higher than that on the recent training trial. An analysis conducted on the activity levels during training trials on Days 1 and 2 revealed no effect of group ($F < 1$), a marginal effect of type of training trial (recent or remote), $F(1, 74) = 3.66, p < .06,$ and

Table 1. Experiment 2: Mean levels of activity during training trials

<table>
<thead>
<tr>
<th>Group</th>
<th>Days 1 and 2</th>
<th></th>
<th>Days 3 and 4</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Remote</td>
<td>Recent</td>
<td>Remote</td>
<td>Recent</td>
</tr>
<tr>
<td>Control</td>
<td>16.32/15.04</td>
<td>17.81/13.02</td>
<td>17.05/13.98</td>
<td>14.70/11.60</td>
</tr>
</tbody>
</table>

*Note:* Mean levels of activity (in responses per minute) during the remote and recent training trials; those scores before and after / are from the first 30 s and final 30 s of each trial, respectively.
no interaction between these factors, $F(1, 74) = 2.23, p > .13$. There was, however, an effect of epoch (first vs. final 30 s), $F(1, 74) = 7.79, p < .01$, an interaction between epoch and group, $F(1, 74) = 6.91, p < .05$, and an interaction between training trial and epoch, $F(1, 74) = 4.13, p < .05$. The three-way interaction was not significant, $F(1, 74) = 1.14, p > .28$. The analysis of simple main effects that was conducted to explore the interaction between epoch and group revealed that there was an effect of epoch in the control group, $F(1, 74) = 8.45, p < .01$, but not in the hippocampal group ($F < 1$) and that there was an effect of group during the second epoch, $F(1, 144) = 4.56, p < .05$, but not in the first epoch, $F(1, 144) = 1.62, p > .20$. Inspection of the scores from Days 3 and 4 in Table 1 reveals that both groups were more active during the remote than the recent training trials and that both were more active in the first than the final 30-s epoch. Analysis of variance (ANOVA) confirmed that there was a main effect of training trial type, $F(1, 74) = 10.39, p < .005$, and epoch, $F(1, 74) = 28.78, p < .001$. There was no effect of group and no significant interactions ($F$s < 1).

Experiment 2 test trials. Figure 4 depicts the critical test results from Days 1 and 2 (left-hand panel) and Days 3 and 4 (right-hand panel). Inspection of the left-hand panel reveals that the levels of activity on the remote and recent test trials were high and similar to one another in both the control and hippocampal rats. ANOVA confirmed that on these test trials there was no effect of group or test trial and no interaction between these factors ($F$s < 1). Inspection of the right-hand panel suggests that the levels of responding were somewhat lower and that whereas rats in the control group showed no more activity in the remote than the recent test context, those in the hippocampal group were more active in the recent context than in the remote context. ANOVA showed that there was no effect of group ($F < 1$), an effect of test trial type, $F(1, 74) = 9.21, p < .005$, and an interaction between these factors, $F(1, 74) = 4.06, p < .05$. Analysis of simple main effects confirmed that there was an effect of test trial in the hippocampal group, $F(1, 74) = 11.27, p = .001$, but not in the control group ($F < 1$), and that there was no effect of group on the remote trial ($F < 1$) and a marginally significant effect of group on the recent trial, $F(1, 148) = 3.61, p = .059$.

Discussion

In the Introduction we identified two short-term behavioural effects, habituation and sensitization, that are a consequence of repeated stimulus presentation. Whether habituation (a reduction in responding), sensitization (an increase in

Figure 4. Experiment 2: Mean (± SEM) levels of activity during the first 30 s of the remote and recent test trials on the first pair of test trials (left-hand panel) and second pair of test trials (right-hand panel) in control and hippocampal rats.
responding) or neither is observed is parameter dependent in control animals (for discussion, see Wagner, 1981). In Experiment 1, hippocampal rats were more inclined to explore a recently visited area of an open field than were control rats. In Experiment 2, hippocampal rats showed greater exploration of a recently presented context than of a remotely presented context, whereas control rats showed similar levels of exploration in contexts that had been presented more or less recently. The supplementary finding that hippocampal rats were less likely than control rats to show a reduction in exploratory activity during the course of presentations of the two contexts during training is consistent with the pattern of test performance. The results of Experiments 1 and 2 provide converging support for the same general conclusion: In rats with hippocampal lesions the balance between the two opposing short-term effects of stimulus presentation—habituation and sensitization—is shifted towards sensitization. Wagner (1981) has presented a formal, general model of animal memory that provides an integrated account of (short-term) habituation and sensitization. The remaining discussion, therefore, focuses on how this model can be applied to the results of Experiments 1 and 2. We begin, however, with an adumbrated description of the model’s central features—in particular, those features that allow it to provide an account of short-term habituation and sensitization.

Wagner (1981) assumed that the memory node for a stimulus (e.g., a context) consists of a population of representational elements. The model distinguishes between mnemonic activity in these elements that is produced by the presentation of the stimulus itself (primary activity) and a decayed form of that activity (secondary activity) that persists for a limited time once the stimulus has been removed, after which time the elements become inactive once more. The model’s account of (short-term) habituation is based on the assumptions that elements that are in the secondary state (a) cannot be provoked into the primary state, and (b) are less able to generate behaviour than those in the primary state. The result of a recent presentation of a stimulus will be to ensure that some of its elements will be in the secondary activity state upon re-presentation of the same stimulus and to thereby deny the possibility that these elements will be provoked into the primary state of activity (in which they generate vigorous behaviour). Of course, this analysis of short-term habituation, in its turn, provides a basis upon which to anticipate that, under certain conditions, sensitization should be observed. Thus, unless the presentation of a stimulus is capable of activating all of its elements into the primary state of activity, there will be a greater number of elements active on the second of two consecutive presentations of a stimulus than on the first: The first presentation of a stimulus will activate a proportion of its elements into the primary state, when the second presentation of that stimulus arrives it will activate a proportion of the residual, inactive elements into the primary state, and these elements will add to those elements provoked by the first presentation (which have now decayed into the secondary state). According to Wagner’s model, there will thus be two opposing consequences of having encountered a stimulus recently: There will be fewer inactive elements available to be provoked into the primary state of activity (which will tend to result in a diminution of responding), but the total number of active elements will often be greater (and this will tend to augment responding). Depending on the balance of these consequences, habituation, sensitization, or no net effect will be observed.

Wagner (1981) described the conditions under which his model predicts that short-term habituation and sensitization effects should be observed and presented empirical support for these predictions. The question of interest in the present context is: How does hippocampal damage affect the balance of these two opposing effects of recent stimulus presentation? In principle, given the fact that the model’s account of habituation rests on the assumption that primary activity is better able than secondary activity to affect behaviour, then hippocampal damage might change the balance between habituation and sensitization by reducing the contribution of primary activity to
performance. One specific way in which this could be brought about is if hippocampal damage resulted in much more rapid decay of elements from primary to secondary activity (see Honey & Good, 2000a). Under such conditions, the recent presentation of a stimulus will simply add to the number of elements that become active (in the secondary state) when that stimulus is re-presented soon after and, therefore, result in sensitization as opposed to habituation.\(^1\) In more general terms, this analysis supposes that the hippocampus is involved in short-term mnemonic processes and, in particular, in maintaining an active short-term trace of (patterns of) stimulation. This suggestion clearly resonates with the theories of hippocampal function developed in both Olton et al. (1979) and Rawlins (1985).

Irrespective of whether or not one accepts the details of the analysis that have just been outlined, the results of Experiments 1 and 2 show that hippocampal lesions have some intriguing effects on short-term changes in open-field and contextual exploration. These results, when taken together with those of our previous studies of the OR (Marshall et al., 2004; see also, Honey & Good, 2000a, 2000b; Honey et al., 1998), indicate that the hippocampus plays an important and general role in affecting relatively short-term changes in stimulus processing. There is a straightforward link between these effects of hippocampal lesions and other, well-documented effects of such lesions on contextual and spatial learning. For example, revisiting and resampling some aspects of an environment (perhaps at the expense of others) is likely to have a more or less direct impact on assessments of contextual learning (e.g., contextual fear conditioning) and spatial learning (e.g., navigation in the water maze). Of course, one could develop an alternative analysis of the fact that hippocampal lesions result in (a) the sensitization of exploratory behaviour, and (b) the disruption of contextual and spatial learning—namely, that both results reflect the fact that hippocampal rats cannot form an adequate representation of a complex pattern of stimulation (e.g., a context or spatial environment). However, as we have just noted, hippocampal lesions have broadly similar effects to those observed in Experiments 1 and 2 even when the stimuli used are relatively simple and lack an obvious spatial component (see Marshall et al., 2004; see also Honey & Good, 2000a, 2000b; Honey et al., 1998); a parsimonious account of hippocampal function needs to accommodate both sets of findings.

REFERENCES


---

\(^1\) Of course, the absolute levels of responding that a recently presented stimulus will provoke (in hippocampal and control rats) will depend upon the difference between the ability of elements in the primary and secondary states to generate responding and the number of elements that are active in these two states.


