Lesions of the Rat Perirhinal Cortex Spare the Acquisition of a Complex Configural Visual Discrimination Yet Impair Object Recognition

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Rats with perirhinal cortex lesions were sequentially trained in a rectangular water tank on a series of 3 visual discriminations, each between mirror-imaged stimuli. When these same discriminations were tested concurrently, the rats were forced to use a configural strategy to solve the problems effectively. There was no evidence that lesions of the perirhinal cortex disrupted the ability to learn the concurrent configural discrimination task, which required the rats to learn the precise combination of stimulus identity with stimulus placement ("structural" learning). The same rats with perirhinal cortex lesions were also unimpaired on a test of spatial working memory (reinforced T maze alternation), although they were markedly impaired on a new test of spontaneous object recognition. For the recognition test, rats received multiple trials within a single session in which on every trial, they were allowed to explore 2 objects, 1 familiar, the other novel. On the basis of their differential exploration times, rats with perirhinal cortex lesions showed very poor discrimination of the novel objects, thereby confirming the effectiveness of the surgery. The discovery that bilateral lesions of the perirhinal cortex can leave configural (structural) learning seemingly unaffected points to a need to refine those models of perirhinal cortex function that emphasize its role in representing conjunctions of stimulus features.

Keywords: configural learning, perirhinal cortex, recognition memory, spatial learning, structural learning

It is widely accepted that in both the monkey and the rat brain, the perirhinal cortex has an important role in object recognition memory (Brown & Aggleton, 2001; Murray & Bussey, 1999; Winters, Saksida, & Bussey, 2008), that is, detecting the repeat occurrence of an object. It is also increasingly likely that this same region has key perceptual functions. It has been proposed that the location of the perirhinal cortex, near the end of a hierarchical sequence of visual (and other sensory) processing areas, reflects its importance for the categorization of complex visual objects (Buckley, 2005; Bussey, Saksida, & Murray, 2005; Eacott, Machin, & Gaffan, 2001; Murray & Bussey, 1999; but see Hampton, 2005). Consequently, it has been argued that some or even all of the apparent mnemonic deficits associated with perirhinal cortex damage in animals are, in fact, essentially perceptual deficits (Bussey & Saksida, 2002; Cowell, Bussey, & Saksida, 2006; Murray, Graham, & Gaffan, 2005; Norman & Eacott, 2004).

One influential description of perirhinal cortex function that emphasizes its perceptual contributions is the perceptual-mnemonic/feature conjunction model (Bussey, Saksida, & Murray, 2002, 2005). In this model, the perirhinal cortex represents conjunctions of stimulus features, and the features are, themselves, represented in more caudal brain regions (e.g., areas V4 and TEO in the monkey). This model and closely related views of perirhinal cortex function (e.g., Eacott et al., 2001) predict that the perirhinal cortex is important for solving those visual problems where the repeat occurrence of the same or very similar visual elements makes the solution ambiguous. Support for this view comes from studies with rats showing that perirhinal cortex lesions disrupt the discrimination of ambiguous stimuli (Bartko, Winters, Cowell, Saksida, & Bussey, 2007a, 2007b; Eacott et al., 2001; Norman & Eacott, 2004; Winters et al., 2008).

Feature ambiguity is maximized in "configural" discriminations because their defining characteristic is that the problem cannot be solved by the presence of any particular element (or feature). To solve a configural task, the subject must discriminate unique combinations of shared elements. For these reasons, the perceptual-mnemonic/feature conjunction model predicts that visual configural tasks will be impaired by perirhinal cortex lesions (Bussey & Saksida, 2002). Previous studies have reported the impact of perirhinal cortex lesions on biconditional visual discriminations, but they found either no deficit (Davies, Machin, Sanderson, Pearce, & Aggleton, 2007) or a borderline impairment (Eacott et al., 2001) on this type of configural task. Such findings are potentially problematic for the perceptual-mnemonic/feature conjunction model. This uncertain situation prompted the present study, which determined the learning performance of rats with perirhinal cortex lesions on a particular class of complex discriminations known as "structural" tasks. Here, the term *structural* refers to learning the location (spatial or temporal) of a specific element with respect to the other elements that make up the same overall scene or event (George & Pearce, 2003; George, Ward-Robinson, & Pearce, 2001). To test this form of learning unam-

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biguously, it is necessary to use a configural task to stop the animals from relying on only the identity of one element or on only the location of one stimulus (without reference to its specific identity) to solve the problem. For these reasons, a structural discrimination takes the form of a configural problem where the solution depends not only on learning that a particular combination of elements is associated with reward but also how these components are put together, or "structured." The "structure" in the present study concerned the spatial location of specific elements.

For comparison purposes, the rats in the present study with perirhinal cortex lesions and their controls were first trained in a rectangular water tank on an elemental visual discrimination (cross vs. circle). This problem was followed by three structural discriminations where, by the final stages, the individual stimulus elements occurred equally in the reinforced (S+) and nonreinforced (S−) compound stimuli, making it a configural task (George & Pearce, 2003; George et al., 2001). The structural property was that the rats were required to learn the spatial disposition of the elements within each compound stimulus to solve the task (see Figure 1). The rats were also given a probe task designed to examine the type of representation used to solve the task.

To test the effectiveness of the perirhinal cortex lesions, we also tested the rats on object recognition (Barker, Bird, Alexander, & Warburton, 2007; Bartko et al., 2007a; Brown & Aggleton, 2001; Ennaceur, Neave, & Aggleton, 1996; Mumby & Pinel, 1994). The present study used a new test of object recognition (Albasser, Poirier, & Aggleton, in press) that combines features of delayed nonmatching-to-sample (Mishkin & Delacour, 1975) with spontaneous exploration (Ennaceur & Delacour, 1988; Steckler, Drinkenburg, Sahgal, & Aggleton, 1998). Finally, all rats were given an initial screening task: reinforced T maze alternation. Whereas this alternation task is highly sensitive to hippocampal system damage (Aggleton, Hunt, & Rawlins, 1986; Rawlins & Olton, 1982), it is typically insensitive to perirhinal cortex damage (Aggleton, Kyd, & Bilkey, 2004; Machin, Vann, Muir, & Aggleton, 2002), thus providing a potential contrast with object recognition. We also intended to include an additional group of rats with hippocampal lesions. Training of this group, however, was stopped because these rats were impaired on the initial elemental discrimination in the water tank. As a consequence, it would have been impossible to determine whether they suffered a selective structural learning impairment. The training of their surgical controls did continue, however, and their data are presented along with those of the perirhinal surgical controls.

Method

Subjects

Eighteen male Lister hooded rats (*Rattus norvegicus*) supplied by Harlan Olac (Bicester, England) were used in this study. All rats were housed in pairs under diurnal conditions (14 hr light/10 hr dark), and water was provided ad libitum throughout the study. At the time of surgery, the rats were 4 months old and weighed from 290 to 360 g. All experiments were performed in accordance with the U.K. Animals (Scientific Procedures) Act 1986 and associated guidelines, and all efforts were made to minimize animal suffering.
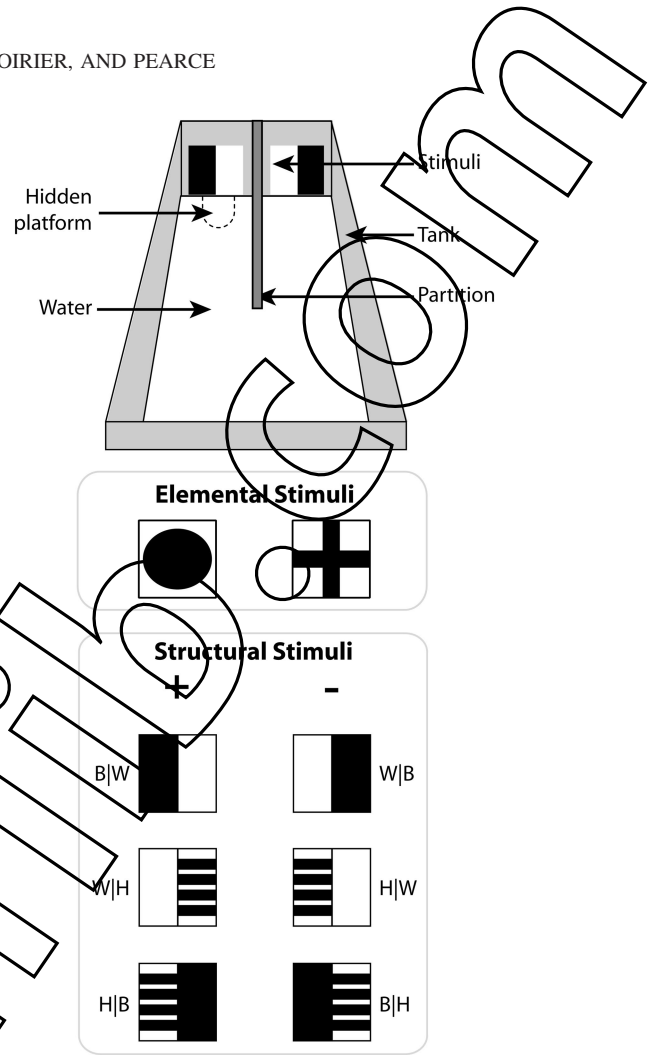

Figure 1.   Upper: Water tank apparatus used for testing the elemental and structural discriminations. Rats were placed in the water facing the near wall; discriminative stimuli were at the far end of the tank. An opaque partition separated the reinforced pattern (S+) from the nonreinforced pattern (S−). (The stimuli depicted are the first pair from the structural discrimination.) A submerged platform was always present underneath the reinforced pattern. Middle: The two stimuli used for the elemental discrimination, circle versus cross. The identity of the S+ stimulus was counterbalanced across the rats. Lower: The compound stimuli used for the structural discrimination task (Stages 1–6). Stimuli were formed from the elements black (B), white (W), and horizontal (H) presented in pairs with specific spatial relationships, for example, B|W, W|H, H|B. Reinforced stimuli are depicted in the left column (S+), and nonreinforced stimuli (S−) are depicted in the right column. Stimuli in the top row were used for Stage 1. Stimuli in the top two rows were used for Stages 2 and 3 of the structural discrimination, and all three rows of patterns were used in Stages 4–6. When all three discriminations were presented concurrently, every element was presented an equal number of times on the left or right of a compound stimulus as an S+ or S−. Thus, to solve the task the rat needed to learn the left and right positions of each specific pair of elements.

Surgery

The 18 rats were divided into two groups. These groups comprised rats with perirhinal cortex lesions (PRh; *n* = 10) and surgical controls (Sham; *n* = 8). All surgeries were performed under aseptic conditions. Rats were first injected with the analgesic

Meloxicam (1.0 mg/kg) and then anesthetized with an intraperitoneal injection of sodium pentobarbital (60 mg/kg), and then placed in a stereotaxic frame (David Kopf Instruments, Tujunga, CA), with the incisor bar set at +5.0 mm to the horizontal plane. A sagittal incision was then made in the scalp, and the skin retracted to expose the skull. A dorsal craniotomy was made directly above the target region and the dura cut to expose the cortex. After every surgery, the skin was sutured together over the skull and antibiotic powder was applied to the wound (Acramide; Dales Pharmaceuticals, North Yorkshire, England). All rats received 5 ml glucose saline subcutaneously and were placed in a heated box until they showed signs of recovery. Paracetamol (for pain relief) and sucrose were dissolved in the rats' drinking water for several days postsurgery.

For the perirhinal cortex lesions (PRh), the temporal muscles were retracted and an area of skull was then removed over the parietal cortex in each hemisphere, approximately 4–7 mm posterior to bregma. The perirhinal lesions were made by injecting a solution of 0.09M N-methyl-D-aspartic acid (NMDA; Sigma Chemical Company Ltd., Poole, U.K.) dissolved in phosphate buffer (pH 7.2) in three sites per hemisphere using a 1-μl Hamilton syringe (Bonaduz, Switzerland). The stereotaxic coordinates of the lesion placements relative to ear-bar zero were anterior–posterior (AP) 3.9, lateral (L) ± 5.9; AP 2.4, L ± 6.2; and AP 0.7, L ± 6.3. The depth (in mm) from bregma at the three sites was −9.3 (most rostral), −9.6, and −9.0 (most caudal). Bilateral injections of 0.20 μl NMDA were made in the most rostral location, and the other two levels each received 0.19 μl NMDA. Injections were made at a rate of 0.10 μl/min with the needle left in place for a further 4 min.

Eight rats served as surgical controls (Sham). Of these, four received the same initial surgical procedure as the rats receiving perirhinal cortex lesions (ShamPRh). The surgery involved the removal of a bone flap and the needle being lowered to the target site (coordinates as above) but without the injection of NMDA. A further four rats received sham surgeries for cytotoxic lesions of the hippocampus (ShamHpc). A bone flap was opened above the parietal cortex and the needle of a 1-μl Hamilton syringe was inserted just into the parietal cortex in 14 tracts in each hemisphere (for coordinates, see Iordanova, Burnett, Good, Aggleton, & Honey, 2009). Once again, no injections were made in any of the tracts.

Reinforced Spatial Alternation: T-Maze

Apparatus. The floor of the maze was made of wood and painted white. Each arm was 70 cm long and 10 cm wide. The sidewalls were made from clear Perspex and were 16.5 cm high. At the end of each arm was a sunken food well, 3.0 cm diameter, 0.75 cm deep. Four metal supports raised the floor of the maze 100 cm above the ground. The maze was located in a 3.0 × 3.0 m² room. From the maze, rats had full view of distal wall cues (1 picture/wall) and extra maze cues such as furniture.

Training procedures. Rats were placed on a restricted diet so that their weights remained around 85% of their free-feeding weight. Pretraining began with five sessions of habituation to the maze with the food wells in all three arms baited with sucrose reward pellets (45 mg; Noyes Reward Pellets, Lancaster, NH). All habituation sessions lasted 5 min, and all rats learned to explore the maze to find the food.

For the alternation task, all rats received six trials per session for a total of six sessions. Trials consisted of a forced "sample" run followed by a "choice" run. Forced turns were made by blocking one of the side arms of the T maze with a metal barrier that fitted into the arms at the junction of the maze. After turning down the "forced" arm, the rat was allowed to eat two sucrose pellets, which previously had been placed in the food well. Rats were then picked up from the end of the forced-choice arm and returned to the start arm, which was the same throughout the experiment. The rats were then given a free choice between the right and left turn arms, receiving a reward (further two pellets) if they turned in the direction opposite to that in the sample run (i.e., nonmatching). The interval between the end of the forced turn and the start of the choice run was around 10 s.

At the start of each session, four rats were taken from the holding room to the experimental room in a sealed box made of aluminum. The box was placed on a table behind the T maze during testing. All four rats were tested concurrently, with each rat having one trial in turn, so that the intertrial interval ranged from 3 to 4 min. Each session contained an equal number of forced right or left turns in a pseudorandom sequence, and every sample run started from the same location.

Structural and Elemental Discriminations: Swim Tank

Training on this task began immediately after T maze alternation. Rats were placed on ad libitum food throughout the task. The training procedure very closely matched that used to study rats with lesions of the fornix and anterior thalamic nuclei (Aggleton, Poirier, Aggleton, Vann, & Pearce, 2009).

Apparatus. All discrimination training took place in a rectangular, gray, fiberglass tank (100 cm long, 62 cm wide, and 62 cm deep). The tank (see Figure 1) was filled to a depth of 32 cm with water made opaque by adding 35 ml of a nontoxic emulsion (opacifier E308; Chesham Chemicals, Harrow, England). Water temperature was maintained at 23–25 °C (± 2 °C). An opaque (gray) Perspex partition wall (62 cm high and 46 cm long) protruded at right angles from the middle of the far wall. A submerged escape platform (0.4 cm thick, 11 cm long, and 9 cm wide, transparent Perspex) was fit onto the end wall and positioned to either the right or left of the central partition wall (see Figure 1). This transparent platform was located 2 cm below the water surface and was not visible. The tank was placed on a table 70 cm above the floor. The room containing the tank was 3 × 3 m with white walls and ceiling, one door, and no windows. The room was visible throughout training. All of the visual stimuli used for the discriminations were black geometrical figures printed on white cards and then laminated to remain waterproof.

Stimuli were attached to the far (goal) wall (see Figure 1) with their bottom edge 1 cm above the water. One stimulus was centered in each of the two goal areas (see Figure 1). One stimulus (elemental or structural) was located on each side of the central partition. Multiple copies of stimuli were used throughout testing to reduce the likelihood of any olfactory cues helping to solve the discrimination. An additional safeguard was that all structural discrimination stimuli could be rotated 180° (inverted) so an S+ stimulus could also be used as an S− stimulus on different trials.

This procedure helped ensure that the rats could not use any unintended local cues to discriminate the test stimuli.

Training procedures. All rats were first pretrained (two sessions) to find the hidden platform in the absence of any test stimuli. During pretraining, the escape platforms were present under both the right and left sides of the end (goal) wall, and each rat received 30 trials (60 s maximum) to locate either of the platforms. Any rat requiring more than 60 s was guided to the platform by following the experimenter's finger (this only occurred in pretraining). Rats were conveyed to the test room in their home cages.

Throughout all discrimination training, there was only one escape (submerged) platform, which was located directly underneath (see Figure 1) the midline of the reinforced stimulus (S+). The S+ appeared equally often in the right and left goal areas in a random order with the constraint that an S+ could not appear in the same goal location on more than three consecutive trials. If a rat swam to the S+, it was allowed to sit on the platform for 10 s before being removed and briefly placed in a dry box. Whenever a rat swam to the incorrect goal location (S−, no platform), it was allowed to carry on swimming so that it could return around the partition wall to finally reach the platform on the other side of the tank, that is, the rat self-corrected itself. An incorrect trial was recorded if a rat's snout came within 20 cm of S−. The next trial began after 20 s. Each trial began with the rat gently lowered into the water facing away from the goal areas and close to the start wall.

Elemental discrimination training. Following two pretraining sessions (as described above), all rats were first trained to select between a black cross and a black circle. The cross was 28 cm long and the arms were 7.5 cm wide; the circle had a 21-cm diameter (see Figure 1). Both stimuli were printed on a white background on a card measuring 28 × 28 cm. The stimuli were counterbalanced so that for half the rats, the S+ throughout was the cross; for the remainder, the S+ throughout was the circle. The training procedure was as described above. The first session was split across 2 consecutive days, each comprising 10 trials. Thereafter, the remaining 14 sessions each contained 20 trials.

Structural discrimination training. All rats were trained both sequentially (seven stages) and concurrently on three discrimination problems, each of which comprised mirror-image stimuli (see Figure 1). It was only by Stage 6 of training (see Table 1) that the rats were required to discriminate concurrently all three sets of structural discriminations when the stimuli were presented in equal numbers of trials and in a completely intermingled order. Thus, it was only in Stage 6 that the rats could be unambiguously assumed to rely on structural (configural) information, although it is quite feasible that structural learning had occurred long before this stage. Training continued on the elemental discrimination (cross vs. circle, five trials per session) throughout all stages on this task to encourage the rats to choose flexibly between the two sides of the water tank.

The rats were progressively trained on three structural discriminations in which the S+ and S− were mirror images of each other. The rats did not start structural discrimination 2 until the entire cohort had mastered structural discrimination 1 (and likewise for structural discrimination 2). This method was selected as it ensured that every rat in each group had exactly the same degree of exposure to the various stimulus types. This training feature was important as some of the discriminations (e.g., going from Stage 1 to Stage 2) involved reversal learning if the rats were relying on elemental cues at this initial stage of training.

Training was also concurrent in that training on the previous elemental discrimination continued during the acquisition of structural discrimination 1 (see Table 1). Likewise, training on both the elemental discrimination and structural discrimination 1 continued during the acquisition of structural discrimination 2. Again, during acquisition of structural discrimination 3, the rats continued training on all previous discriminations. These concurrent training procedures were necessary to ensure that by the end of the final discrimination (Stage 6; see Table 1), each individual element was placed equally to the left or the right of a compound stimulus as either an S+ or an S−. Consequently, the rat needed to learn the relative spatial position of each element if it was to be able to perform over 50% on all three discriminations concurrently.

Table 1

Stages of Training for the Three Structural Discriminations

Stage	Structural discrimination	Presentation
1	Problem 1 (B|W+ W|B−)	20 trials on Problem 1 and 5 trials elemental task (Cr vs. Ci); 4 sessions
2	Problem 1 and Problem 2 (W|H+ H|W−)	15 trials (5 blocks of 3) on Problem 2, 5 trials on Problem 1, and 5 trials elemental task; 7 sessions
3	Problems 1 and 2	10 alternate trials each of Problems 1 and 2, and 5 trials elemental task; 3 sessions
4	Problems 1, 2, and 3 (H|B+ B|H−)	15 consecutive trials of Problem 3, with 5 trials each of the three other discriminations (Problem 1, Problem 2, elemental task); 12 sessions
5	Tasks 1, 2, and 3	8 trials on each structural discrimination (Tasks 1–3) each in a single block, 5 trials elemental task; 8 sessions
6	Problem 1, 2, and 3	8 trials of all three problems randomly intermixed, 5 trials elemental task; 4 sessions
7 (Probe)	B|W+ vs. H|W−; B|W+ vs. B|H−; W|H+ vs. W|B−; W|H+ vs. B|H−; H|B+ vs. H|W−; H|B+ vs. W|B−	24 trials in which the S+ and S− from the structural discrimination were re–paired, 5 trials elemental task; 4 sessions

Note. B = black; W = white; H = horizontal; S+ = reinforced compound stimuli; S− = nonreinforced compound stimuli. The elemental discrimination (cross [Cr] vs. circle [Ci]) was presented (5 trials per session) throughout all stages. The choice of the S+ stimulus for the elemental discrimination was counterbalanced across all subjects, but for the structural discriminations, all rats received the reward contingencies depicted above. Whereas Stages 4–6 included all three structural discriminations, only Stages 6 and 7 (probe) unambiguously tested structural learning.

The three stimuli used for the three structural discriminations (see Figure 1 and Table 1) were a black rectangle (B), a white rectangle (W), and a rectangle containing black and white horizontal stripes (H). The horizontal stripes were 2.5 cm wide. Each of these rectangular stimuli was 28 cm high and 14 cm wide. When combined side-by-side, the two rectangular stimuli formed a square, compound stimulus that was 28 cm wide and 28 cm high (see Figure 1). The six patterns formed by joining the rectangles side-by-side were as follows: black left of white, B|W; White left of Black, W|B; white left of horizontal, W|H; horizontal left of white, H|W; horizontal left of black, H|B; and black left of horizontal, B|H.

Stage 1 contained 25 trials per day (see Table 1). Rats received 20 trials on the first structural discrimination (B|W+ vs. W|B–), that is, a pair of mirror-imaged stimuli. For all rats, B|W was the S+ (i.e., black to the left of white). Intermingled among these 20 trials were five additional trials of elemental discrimination (cross vs. circle). Training required just four sessions.

Stage 2 introduced the second structural discrimination (W|H+ vs. H|W–). During each session, rats received 15 trials of this discrimination, with W|H as the S+ for all rats (see Table 1). Rats were given five blocks of three consecutive trials of W|H+ versus H|W– during each session. In between these blocks, the rats received a single B|W+ versus W|B– trial (making five trials per session). Likewise, the rats also received five trials per session of elemental discrimination (cross vs. circle). Thus, each session contained 25 trials. Training continued for seven sessions.

Stage 3 consisted of three sessions in which the rats now received 10 trials per session of both B|W+ versus W|B– and W|H+ versus H|W–, during which the two discriminations were on alternate trials. Five intermingled trials of elemental discrimination were also given (cross vs. circle), making 25 trials in total.

Stage 4 introduced the third and final structural discrimination (H|B+ vs. B|H–). Each session comprised 30 trials in which the rats received five trials of each of the three previous discriminations (B|W+ vs. W|B–, W|H+ vs. H|W–, cross vs. circle), along with 15 consecutive trials of the third structural discrimination (H|B+ vs. B|H–). These 15 trials were placed in the middle of every session. Training continued for 12 sessions.

In Stage 5, the rats received equal numbers of trials of the three concurrent structural discriminations. Each discrimination was presented in a block of eight trials. These blocks were separated by a total of five trials on elemental discrimination, making 29 trials per session. All rats received eight sessions.

Stage 6 completed the acquisition phase, as now the three structural discriminations were presented in an intermingled order. Again, there were eight trials of each of the three structural discriminations and five trials of elemental discrimination (29 in total). All rats received four sessions.

Stage 7 (probe) consisted of a series of four probe sessions that explored the ways in which the mirror-image stimuli had been discriminated. For these sessions, the compound (mirror-image) pairs of elements that had been used throughout Stages 1–6 (e.g., W|H+ vs. H|W–) were re-paired, although the individual S+ and S– stimuli remained constant (e.g., now W|H+ vs. B|H–). Rats that had learned the unique compound—for example, approach white to the left of horizontal bars (W|H+), avoid white to the right of horizontal bars (H|W–)—should find the probe straightforward as all of the individual S+ and S– stimuli were unchanged. In contrast, any rat that had learned a conditional solution on the basis of combining pairs of S+ and S– stimuli into one global visual array—for example, if white–horizontal–horizontal–white (W|H H|W), then go left (or if H|W W|H go right)—would find this probe particularly difficult. For the probe, rats received 29 trials per session, five of which were for elemental discrimination. For the remaining 24 trials, the three structural discriminations were re-paired so that the S+ and the S– stimuli remained unchanged, and the combinations were changed to remove all of the mirror images. This created six trial types: B|W+ versus H|W–, B|W+ versus B|H–, W|H+ versus W|B–, W|H+ versus B|H–, H|B+ versus H|W–, and H|B+ versus W|B–.

Spontaneous Object Recognition: Bow-Tie Maze

Apparatus. The rats were tested in a bow-tie shaped maze made of opaque Perspex (see Figure 2). The apparatus was 120 cm long, 50 cm wide, and 50 cm high. Each end of the apparatus was triangular, the apices of which were joined by a narrow corridor (12 cm wide). There was an opaque guillotine door in the middle of the corridor that could be raised by the experimenter. The far wall of each triangle contained two recessed food wells, 3.5 cm in diameter and 2 cm deep. The food wells were separated by a short,
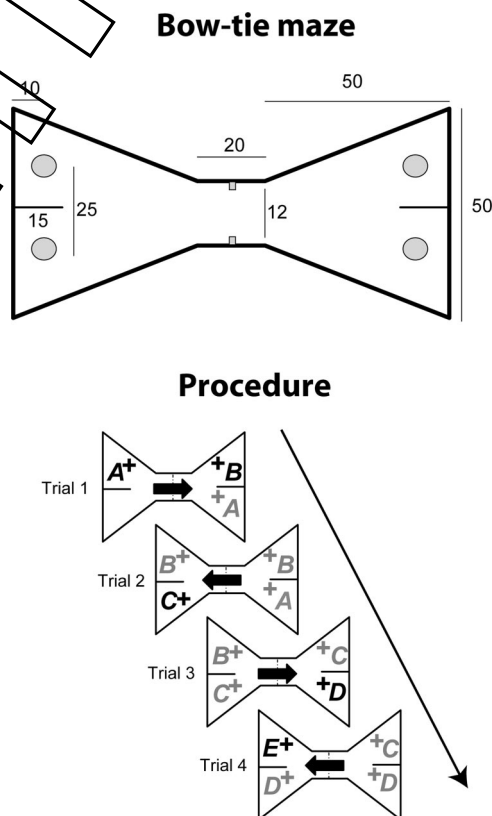
Bow-tie maze

Procedure

Figure 2. Object recognition memory. Upper: Shape and dimensions (in cm) of the bow-tie maze when viewed from above. Food wells are shown in gray. Lower: Illustration of the general test procedure showing the presentation order of the objects. All objects are rewarded (+). The arrows show the direction of the rats' movements. Letters in black print represent novel objects; gray letters represent familiar objects.

opaque dividing wall that protruded 15 cm from the middle of the end wall. These food wells were covered by objects in the experiment proper.

Objects. The study used identical pairs of different junk objects with various shapes, textures, sizes, and colors. Each object was large enough to cover a food well (3.5 cm diameter) but light enough to be displaced. Any object with an obvious scent was excluded. The objects were divided into two separate sets of 21 pairs of objects.

Pretraining. Pretraining began 1 week after completion of the structural discrimination. Following pretaining, which lasted 8 days, all rats would run from one side of the maze to the other and displace an object positioned over the two food wells to reach food rewards. On Day 1, pairs of rats were placed in the apparatus for 30 min, during which they explored the maze freely and ate sucrose pellets scattered on the floor and in the food wells (45 mg; Noyes Purified Rodent Diet, Lancaster, NH). On Days 2 and 3, rats were pretrained singly in the maze for 20 min, during which they were rewarded for shuttling between the two goal areas. From Day 4, the central guillotine door was used to control the movement of the rat from one side of the maze to the other. From Day 6, up to three pairs of different objects were introduced in the maze. By the end of pretraining (Day 8), all rats would readily push these same three objects, which covered the food wells, to access the food rewards. These three pairs of objects were not used in the experiment proper.

Test protocol. All rats received two sessions (5 days apart), each of 20 trials, during which the rat was exposed to two objects (one novel, one familiar) on every trial (see Figure 2). A single sucrose pellet was placed in the well under every object before each trial. All objects had duplicate pairs so that identical objects were used for consecutive trials. Rats were videorecorded throughout the two test sessions.

At the start of each test session, the rat was placed on one side of the maze, where a single object (object A) covered a food well that contained a sucrose pellet (see Figure 2). The rat was contained in that part of the maze (with object A) for 1 min. After min, the central guillotine door was raised, and the rat ran to the opposite side of the maze. There, the rat had a free choice between object A, which was now familiar, and a novel object B (Trial 1). Both objects A and B covered baited sucrose pellets and were concurrently available to the rat for a total of 1 min (see Figure 2). The guillotine door was then raised (Trial 2) to reveal object B (now familiar) and object C (novel). This procedure continued so that Trial 3 comprised object C (familiar) versus object D (novel), for 20 trials and, hence, 21 sets of objects. Baiting of both the novel and familiar objects was designed to encourage the rats' exploration of the test objects, but could not affect the validity of the behavioral test, which relied on the *differential* exploration of both objects. The placement of the novel object varied from left to right according to a pseudorandom schedule, and different sets of objects were used for the two sessions. In addition, the order of the particular objects used in the test was reversed for half of the rats from both groups. A consequence of this counterbalancing procedure is that the novel object in any given pair is reversed; for example, for half of the rats in the trial of B versus C, it is C that is novel (see above), but for the other half, it is B that is novel.

Analysis of behavior: Object recognition. Exploration of an object was defined as directing the nose at a distance < 1 cm from the object or touching it with the nose or the paws. Turning around or sitting on the object was not counted. The duration of exploration was determined by holding down a key pad on a computer during the bursts of exploration recorded on videotape. Exploration times could then be examined for individual trials and summed across the 20 trials. Two measures of discrimination behavior were calculated (Ennaceur & Delacour, 1988). The first measure (D1) was the difference in exploration time for novel versus familiar objects, that is, the exploration time devoted to the novel object minus the time devoted to the familiar object. Thus, the "cumulative D1" was the sum of the exploration times devoted to the novel objects across 20 trials minus the sum of the exploration times for the familiar objects. The second measure (D2) used the difference in exploration time (i.e., D1), but then divided D1 by the total amount of exploration given to both the novel and familiar objects. The resulting D2 index can vary between +1 and −1, with a positive ratio showing a preference for novel objects and a ratio of zero corresponding to no preference.

Statistical Analyses

Group comparisons typically used parametric tests (*t* tests and analysis of variance [ANOVA]). When significant interactions were found, we analyzed the simple effects for each group as recommended by Winer (1971) using the pooled error term. Nonparametric statistics were applied when the results were based on a constricted range (e.g., limited trials or ceiling effects). Group comparisons used the Mann–Whitney *U* test. Throughout, the probability level of <.05 was treated as significant.

The study comprised one experimental group (PRh) and two control groups (ShamPRh and ShamHpc). For all analyses, the two control groups were first compared with each other (two-tailed *t* test or ANOVA). When the two control groups did not differ, we combined them to form the Sham group and then compared that with the PRh group. There were, however, a number of occasions when the ShamPRh group outperformed the ShamHpc group (*p* < .05). When this occurred, we conducted additional analyses in which the PRh group was compared with only the ShamPRh rats to help ensure that a lesion-induced deficit had not been masked by the poorer performance of the ShamHpc rats. Only those occasions when it was necessary to perform these extra analyses are reported.

Results

Histology

The lesion reconstructions used the nomenclature and area boundaries described by Burwell (2001). One PRh rat became ill and was removed from the study. In the remaining rats (*n* = 9), the perirhinal cortex lesions were extensive and removed almost all of the target region (see Figure 3). One consequence was that the lesions typically extended ventrally to involve dorsal and superficial parts of the piriform cortex and lateral entorhinal cortex, often in both hemispheres. Most of the lesions involved the entire rostrocaudal extent of the perirhinal cortex, although in three cases there was limited, unilateral sparing of the perirhinal cortex at its most rostral border. In one case, there was some bilateral sparing in the upper part of area 36, that is, above the rhinal sulcus (see
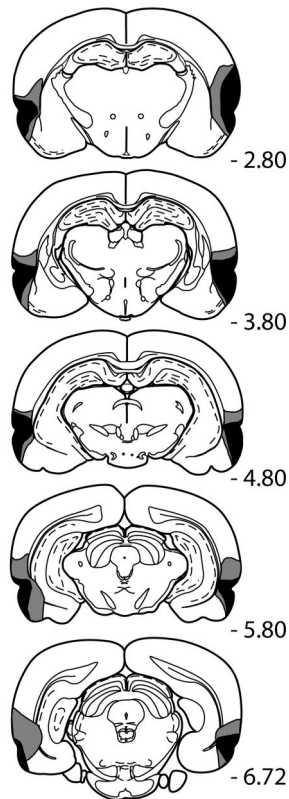
Perirhinal lesions

Figure 3. Coronal sections depicting the extent of cell loss in the animals with the smallest (dark gray) and largest (light gray) perirhinal cortex lesions. The numbers refer to the approximate distance (in mm) of the section caudal to bregma. The sections are modified from *The Rat Brain in Stereotaxic Coordinates*, 3rd ed., by G. Paxinos & C. Watson, 1997, San Diego, CA: Academic. Copyright 1997 by Elsevier Science. Adapted with permission.

Figure 3). In seven cases, the perirhinal cortex lesion extended medially to cross the external capsule and caused a very restricted patch of cell loss in that part of caudal CA1 immediately adjacent to the fundus of the rhinal sulcus. In six cases, this localized CA1 damage was bilateral; in one other, the cell loss was unilateral. In two cases, there was unilateral damage to the lateral nucleus of the amygdala.

Inspection of the brains of the Sham control rats revealed that one ShamHpc rat had appreciable bilateral damage to that part of the parietal cortex immediately above the dorsal hippocampus. This rat was removed from all analyses. Aside from the expected tract marks, there was nothing remarkable about the brains of the remaining seven Sham cases, with the exception of one other ShamHpc case (with a small patch of unilateral atrophy in the parietal cortex). These histological analyses left a final Sham control group of seven rats (ShamPRh = 4, ShamHpc = 3) and a PRh group of nine rats.

T Maze Alternation

All rats received six sessions (36 trials), and every rat performed well above chance. There was no evidence that the PRh group

differed from the Sham control group ($t < 1$). The group mean correct scores ($\pm SEM$) were PRh = 31.33 (0.82) and Sham = 30.86 (0.55).

Elemental Visual Discrimination

Both the PRh and Sham groups rapidly learned the cross versus circle discrimination (see Figure 4) so that by Session 8 they were making extremely few errors. Training persisted, however, to ensure that this basic discrimination was overlearned. Not surprisingly, there was a highly significant effect of session, $F(13, 182) = 78.54$, $p < .001$, but there was no evidence of a group difference ($F < 1$) or a Group $\times$ Session interaction, $F(13, 182) = 1.24$, $p = .25$.

Training on the elemental discrimination task persisted throughout structural discrimination training. Comparisons using the total correct trials accumulated over Stages 1–7 (215 trials per rat) showed that the performances of both the Sham and PRh groups remained close to ceiling throughout (mean percentage correct, Sham = 97.4%, PRh = 94.9%). As a consequence, the group comparisons employed nonparametric statistics. There was no evidence that the PRh group was impaired on performing the cross versus circle discrimination when it was tested concurrently (Stages 1–7) with the three structural discriminations ($U = 25.5$, $p = .28$).

Structural Visual Discriminations

Figures 5, 6, and 7 depict the mean performance of the two groups of rats (PRh and Sham) across the six acquisition stages of configural learning. All rats were eventually able to master the concurrent structural discrimination task, and there was no evidence that perirhinal cortex lesions impaired acquisition. Although on a few of the 14 individual discriminations (when separated by stage) there was evidence that the ShamPRh group outperformed the ShamHpc group, there was no evidence that the scores of the PRh rats ever differed from those of the ShamPRh rats.
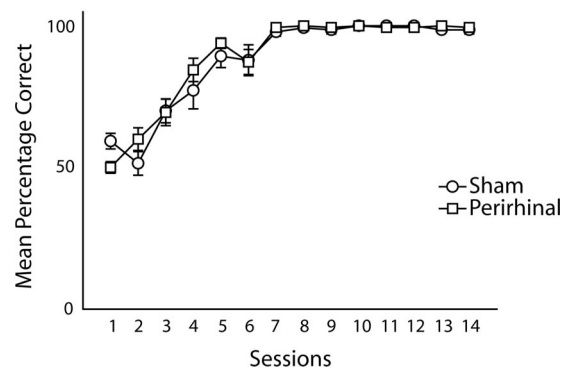
Elemental Discrimination

Figure 4. Elemental discrimination (circle vs. cross). Mean performance of the perirhinal lesion (PRh, square) and sham control (Sham, circle) groups. The vertical bars show the standard error of the mean (although when small, they are obscured by the symbols).
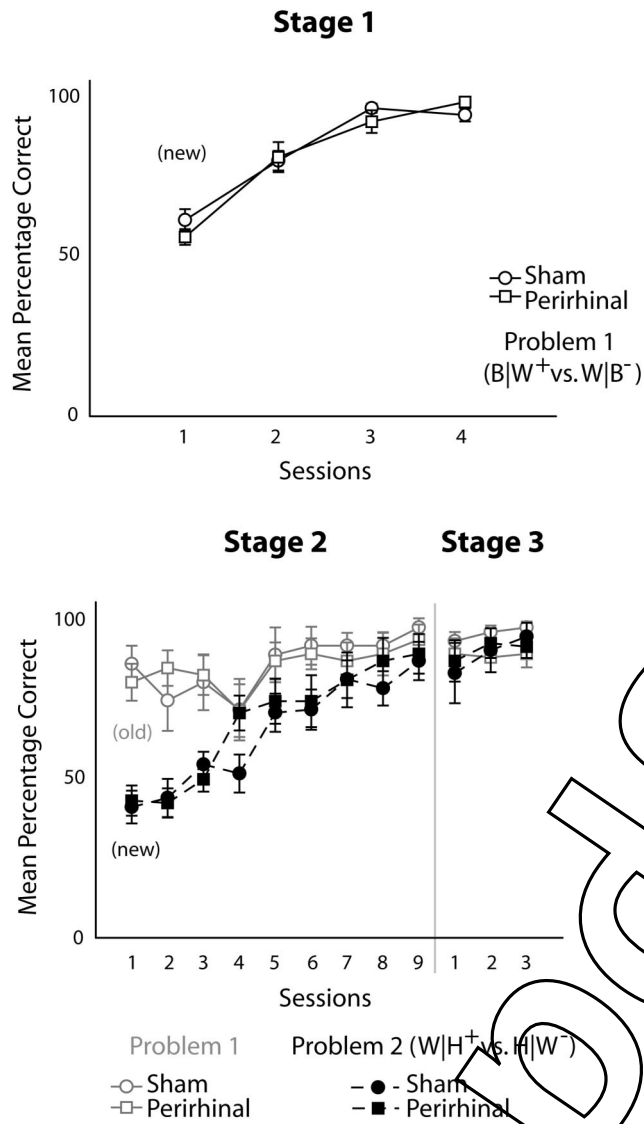
Stage 1

Stage 2   Stage 3

Figure 5. Structural discrimination learning, Stages 1–3. Mean performance of the perirhinal lesion (PRh, square) and sham control (Sham, circle) groups. The upper graph shows performance on the first discrimination (B|W vs. W|B). The lower graphs (Stages 2 and 3) show performance on the second (new) discrimination (Task 2, W|H vs. H|W) while testing on the previous discrimination (B|W vs. W|B) continued ("old," light gray). The vertical bars show the standard error of the mean (although when small, they are obscured by the symbols). B = black; H = horizontal; W = white.

Stage 1: B|W+ versus W|B–. Figure 5 shows the rapid acquisition (effect of session), $F(3, 42) = 59.0$, $p < .001$, of the first structural discrimination. There was no group difference ($F < 1$) and no Group $\times$ Session interaction ($F < 1$).

Stages 2 and 3: B|W+ versus W|B– and W|H+ versus H|W–. Concurrent testing on the first discrimination (B|W+ vs. W|B–) continued throughout Stages 2 and 3 (see Figure 5), but there was no still evidence of a group difference: Stage 2, $F < 1$; Stage 3, $F(1, 14) = 2.24$, $p = .16$.

A slightly more complex pattern of results emerged for the new structural discrimination in Stage 2 (W|H+ vs. H|W–). Here, evidence was found for a difference in overall performance between the ShamPRh and ShamHpc groups, $F(1, 5) = 10.32$, $p = .024$. Consequently, comparisons for this discrimination (W|H+ vs. H|W–) were made only between the PRh group and the ShamPRh group (the better performing control group). There was, however, still no evidence of a perirhinal lesion effect ($F < 1$) or of a Lesion $\times$ Session interaction ($F < 1$), although there was the expected effect of session, $F(8, 88) = 18.53$, $p < .001$, reflecting acquisition of the new discrimination. By Stage 3 (three sessions, 10 trials on each discrimination per session), the two control groups did not differ on the W|H+ versus H|W– discrimination, $F(1, 5) = 2.69$, $p = .16$; therefore, their results are grouped together (see Figure 5). Subsequent comparisons with the PRh group again failed to show evidence of a lesion-induced deficit ($F < 1$).

Stages 4–6: B|W+ versus W|B– W|H+ versus H|W– and H|B+ versus B|H–. These three stages progress from the first, concurrent introduction of the third structural discrimination (H|B+ vs. B|H–; see Figure 6) to eventually testing all three discriminations in a completely intermixed order (Stage 6; see Figure 6). As a consequence, Stage 6 provides the most rigorous test of task acquisition and performance. From Figure 6, it can be seen that the profiles of acquisition and performance for the PRh and Sham groups appear very similar across these three stages, with no suggestion of a perirhinal lesion deficit.

For the purpose of clarity, the results for Stage 6 (full structural task) are described first. The discriminations were fully intermingled in this stage; therefore, the initial comparisons used the total scores from all three structural discriminations (see Figure 7, left). Because the ShamHpc rats made more errors than the ShamPrh rats ($p < .05$), comparisons were made between the PRh and ShamPRh groups. No evidence was found for a perirhinal lesion effect on Stage 6 ($F < 1$), nor was there an interaction with session, $F(3, 33) = 2.07$, $p = .12$.

Further analyses of Stage 6 involved taking the poorest discrimination score (from any of the three structural discriminations) for each rat for each session in Stage 6. If the rats had mastered all three discriminations using a structural solution, the score on even the poorest discrimination should still be above chance, that is, above 16, because the rats received four sessions with eight trials on each discrimination. One-sample t tests (two-tailed) showed that both the PRh and Sham groups still performed above chance across their poorest individual discrimination taken from each session (maximum = 32; PRh, $M = 26.2$, $SD = 2.22$; Sham, $M = 24.3$, $SD = 3.59$, ps $< .001$). Furthermore, the scores of the Sham and PRh groups did not differ from one another, $t(14) = 1.34$, $p = .103$ (one-tailed). The same lack of difference was found when only the PRh and ShamPRh groups were compared on this measure ($t < 1$).

Detailed statistical analyses are not provided for Stages 4 and 5 as they were transitional in reaching the full structural task (Stage 6). The profiles of performance on the three discriminations were, however, very consistent with those seen in previous structural learning tasks using the same procedures (George et al., 2001; Sanderson, Pearce, Kyd, & Aggleton, 2006). Separate analyses of the scores from Stage 4 for the three concurrent discriminations found no evidence of a lesion effect, highest $F(1, 14) = 1.77$, and
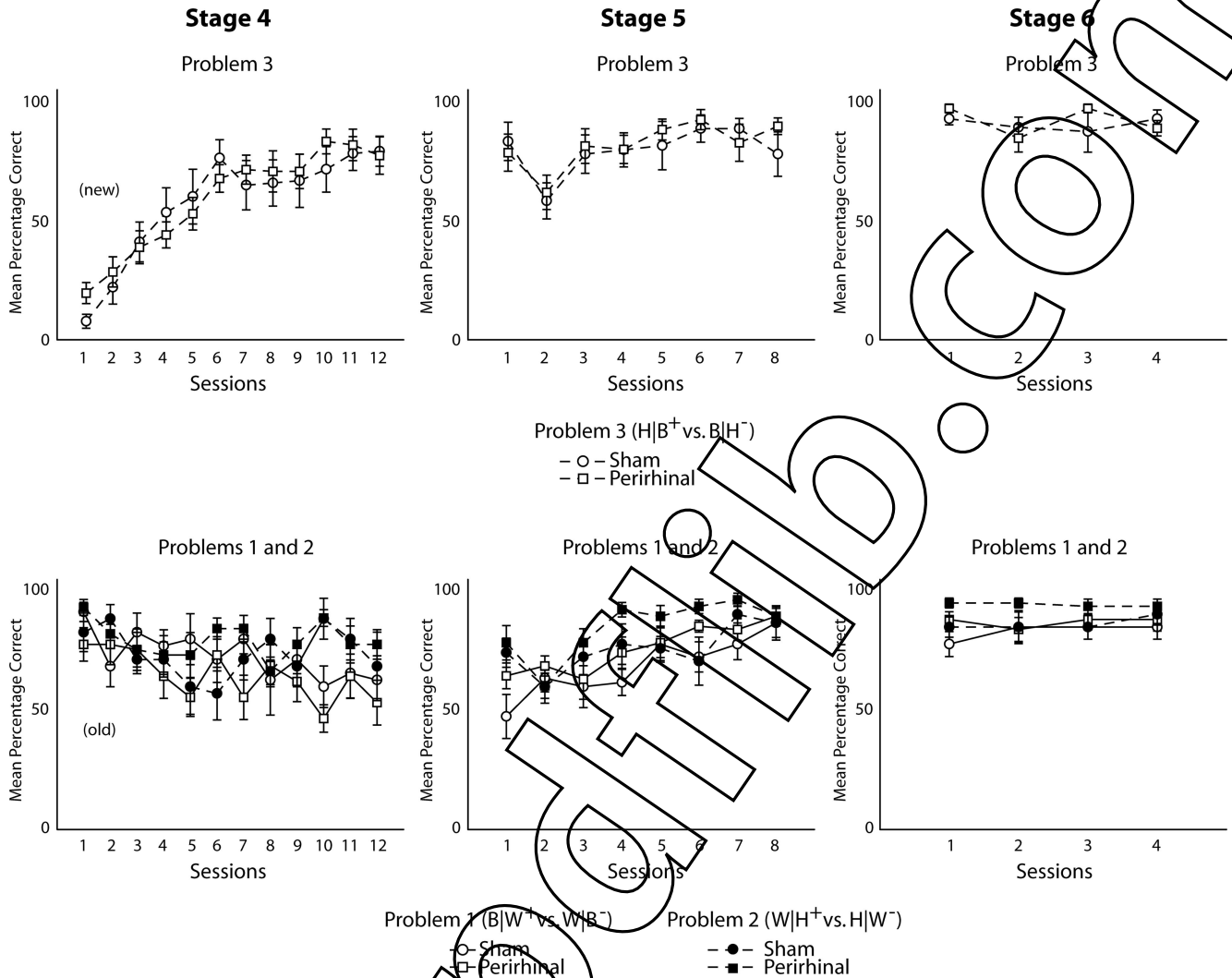
Figure 6. Structural discrimination learning, Stages 4–6. Mean performance of the perirhinal lesion (PRh, square) and sham control (Sham, circle) groups. The upper graphs show performance on the third (new) discrimination (H|B vs. B|H). The lower graphs show concurrent performance on the previous two structural discriminations (Tasks 1 and 2). In Stage 6, all three discriminations were equally intermingled within a session so that the rats had to solve the full configural task. The vertical bars show the standard error of the mean (although when small, they are obscured by the symbols). B = black; H = horizontal; W = white.

no interactions with session. The same pattern was found for Stage 5, where the PRh group did not differ from either the Sham or the ShamPRh group, highest $F(1, 14) = 3.05$, $p = .1$. Finally, there were no significant interactions between session and group for any of the discriminations in Stages 4 or 5, highest $F(7, 98) = 1.23$.

Stage 7: Recombination probe. In the final set of four sessions (Stage 7), the S+-S– pairs were recombined so that now none of the discriminations involved patterns that were mirror images of the pattern in the adjacent arm, but the three S+ stimuli remained the correct choice (see Figure 7, right). The rats readily transferred to this new condition, with little change in performance, so that their overall scores stayed well above chance. The ShamPRh group outperformed the ShamHpc group ($p < .05$); therefore, only analyses using the ShamPRh group are reported. There was no evidence of a difference in perfor-

mance between the ShamPRh and PRh groups ($F < 1$) or any interaction ($F < 1$). Finally, comparisons were made across the last session of Stage 6 and the first session of Stage 7 to see how rats initially coped with the recombination of the S+ and S– stimuli. Here, there was no group or session effect (both Fs < 1), although there was a small, but nonsignificant, difference in profiles, Group × Session interaction, $F(1, 11) = 4.20$, $p = .065$, as the PRh group seemed less affected by the change in stimulus pairings.

Spontaneous Object Recognition

All rats received two sessions, each of 20 trials. The pattern of results (see Figure 8) was very similar for both sessions as the PRh
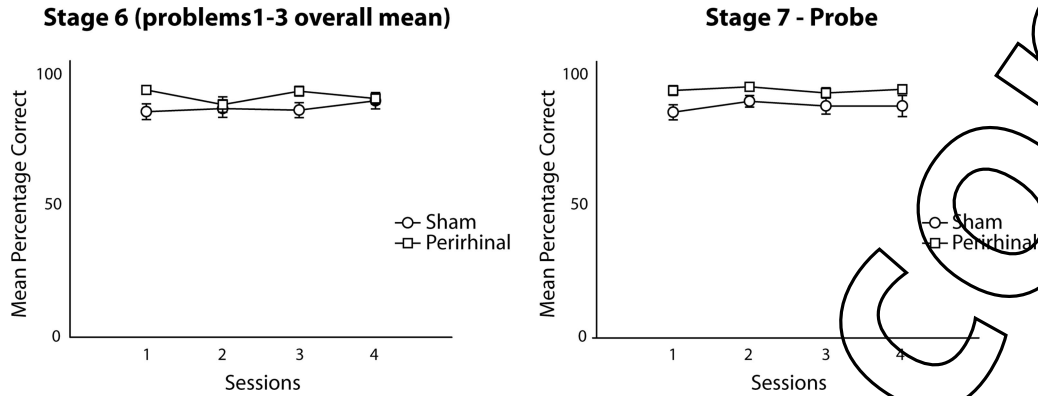
Figure 7. Structural discrimination learning. Left: Mean performance of the perirhinal lesion (PRh, square) and sham control (Sham, circle) groups on Stage 6 across all three concurrent, structural discriminations. Right: Stage 7 (probe). Mean performance when the compound stimuli were re-paired to give novel combinations of S+ with S– stimuli. Performance of both groups remained above chance. The vertical bars show the standard error of the mean (although when small, they are obscured by the symbols).

group was significantly impaired at preferentially exploring the novel objects when compared with the Sham rats.

The PRh and Sham groups of rats did not differ (see Figure 8, left) on the total amount of object exploration: Session 1, $t(14) = 1.25$; Session 2, $t < 1$. However, as clearly seen in Figure 8, the Sham rats showed a consistent pattern of preferring the novel object in each pair, so that their cumulative D1 scores (novel minus familiar exploration times) increased to a mean that was greater than 100 in both test sessions. In contrast, the PRh rats showed a much smaller cumulative preference (Session 1, $M = 31.2$ s, Session 2, $M = 40.4$ s), which differed significantly from the Sham group: Session 1, $t(14) = 4.79$, $p = .00028$; Session 2, $t(14) = 3.63$, $p = .0027$. Despite this very clear lesion effect, the cumulative D1 scores of the PRh rats were still above chance: one-sample t test, Session 1, $t(8) = 3.073$, $p = .015$; Session 2, $t(8) = 2.96$, $p = .018$. Analyses using the cumulative D2 ratio (cumulative D1 divided by the cumulative total time spent exploring both objects) gave exactly the same pattern of significant results.

Further analyses looked at the potential impact of proactive interference. For this reason, we calculated the individual D2 ratios across the first two trials in Sessions 1 and 2. From the start of recognition testing, the Sham group outperformed the PRh group: one-tailed t test, Session 1, $t(14) = 2.434$, $p = .014$; Session 2, $t(14) = 1.978$, $p = .034$. Moreover, only Sham rats performed above chance across the first two trials of Session 1: one-sample t test, Sham, $t(6) = 3.436$, $p = .014$; PRh, $t(8) = 0.169$, $p = .87$. Both groups, however, were above chance at the beginning of Session 2: one-sample t test, Sham, $t(6) = 6.493$, $p = .001$; PRh, $t(8) = 4.731$, $p = .001$.

Discussion

Rats with extensive, cytotoxic lesions of the perirhinal cortex were not only unimpaired in their acquisition of an elemental visual discrimination (cross vs. circle) but also learned at a normal rate a configural discrimination that required rats to combine element identity with element placement (structural discrimination). Such structural discriminations require the rat to demonstrate learning the specific spatial configuration of the specific elements

within a compound stimulus. While the same rats also performed normally on a reinforced T maze alternation task, they were markedly impaired on object recognition. This recognition deficit helps confirm the effectiveness of the perirhinal cortex lesions (Ennaceur et al., 1996; Mumby & Pinel, 1994; Winters et al., 2008) and provides a contrast with the spared configural learning. Because the pattern of results appears to be in conflict with the perceptual-mnemonic/feature conjunction model of perirhinal cortex function (Bussey et al., 2002, 2005), it is first important to confirm whether the structural discrimination was indeed configural and, hence, whether solution of the task actually required learning conjunctions of visual features. This property of the discrimination is critical as the perceptual-mnemonic/feature conjunction model assumes that feature ambiguity is greatest in configural tasks (Bussey & Saksida, 2002), that is, such tasks should be especially challenging for animals with perirhinal cortex lesions.

The initial stages of structural discrimination training (Stages 1–3) do offer possible conditional solutions using only elemental features. In the case of Stage 1 (see Figure 1, upper), a rat could learn the following rule: If leftmost element in water tank is black, then approach; if leftmost element in tank is horizontal, then avoid. Such conditional solutions are, however, of no use by Stage 6, which was specifically designed to tax configural learning. For this stage, the three discriminations B|W+ versus W|B–, W|H+ versus H|W–, and H|B+ versus B|H– were presented concurrently and in an intermingled order. As can be seen (see Figure 1), no individual element (black, white, or horizontal) can solve the task as all three occur equally in the S+ and S– stimuli. Likewise, the overall task cannot be solved by learning the left or right location of an individual element as these also occur equally in the S+ and S– stimuli. Critically, the scores from the discrimination on which each rat individually performed poorest on a given day remained above chance when all three discriminations were presented concurrently (Stage 6). This result shows that the rats had not acquired a conditional elemental solution as this strategy might solve two but not all three discriminations concurrently.
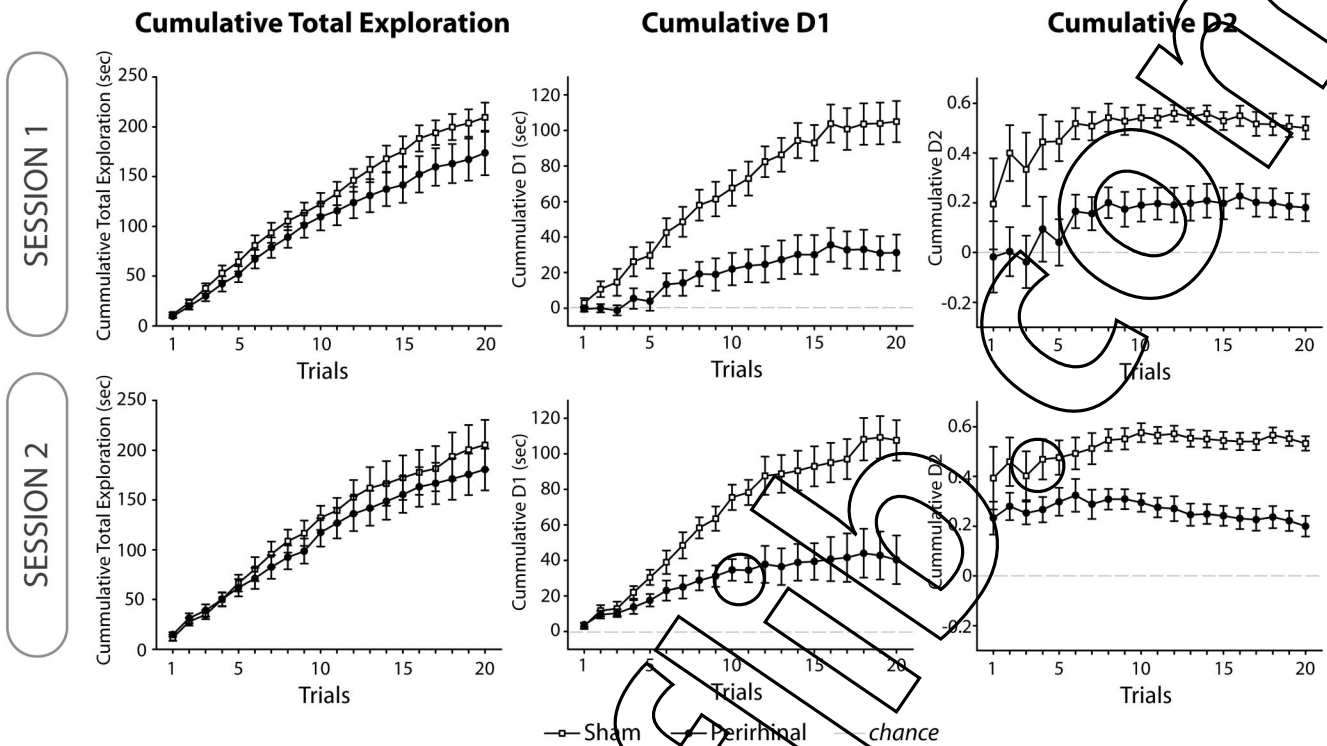
Figure 8. Object recognition. Six graphs depicting the mean performance from Session 1 (upper row) and Session 2 (lower row). Session 1 (upper): left, cumulative total exploration times for all objects; middle, cumulative D1 score; right, cumulative D2 score. Session 2 (lower): left, cumulative total exploration times for all objects; middle, cumulative D1 score; right, cumulative D2 score. Black symbols show the performance of the perirhinal lesion group, white symbols show the performance of the Sham control group. The vertical bars show the standard error of the mean (although when small, they are obscured by the symbols).

Evidence that the rats had not found unintended cues to solve the configural task comes from the impact of introducing new training stages. Initial group performances were significantly *below* chance for the new discriminations introduced at the start of Stage 2 and Stage 4 (see Figures 5 and 6), a pattern seen in previous, comparable studies (Aggleton et al., 2009; Sanderson et al., 2006). This initial "poor" performance shows that the rats had not learned some unintended cue from the experimenter, that is, a "clever Hans" effect. Rather, this pattern of responding is consistent with an interim conditional solution. Finally, the probe test (Stage 7) again shows that the rats had learned the specific combinations of elements in each compound stimulus and their relative positions. It is important to note that the probe test shows that the rats could not have learned a conditional solution on the basis of global features on the far (goal) wall; for example, if white across the middle of the goal wall (BW|WB), go left (see Figure 1, upper). Thus, detailed examination of the performance patterns only seems to confirm that all rats had acquired a visual configural task involving element identity and location.

The present study is not the first to examine the impact of perirhinal cortex lesions in rats on visual tests of configural learning. Two previous studies that examined the acquisition of a biconditional task found slightly different results (Davies et al., 2007; Eacott et al., 2001). In one of these studies (Davies et al., 2007), rats were tested in a water tank; using similar training and reinforcement procedures to the present experiment, the authors found no evidence of a biconditional acquisition deficit after perirhinal cortex lesions. Once again, the perirhinal lesions were sufficient to impair object recognition. In a second study (Eacott et al., 2001), perirhinal lesions did impair acquisition of a visual biconditional task, although the deficit was marginal as it was found only for trials to criterion and not for total error score. In both studies, the perirhinal cortex lesions did not disrupt acquisition of a new elemental visual discrimination, as in the present study (see also Machin & Eacott, 1999).

A number of other studies have looked at the impact of perirhinal cortex lesions on other configural tasks (Bussey et al., 2000; Dusek & Eichenbaum, 1998; Iordanova et al., 2009), finding mixed results. A test of negative patterning, which used a combination of light and tone to signal nonreward while their separate presentation signaled reward, found no evidence of an acquisition deficit after perirhinal cortex lesions (Bussey et al., 2000). In contrast, Dusek and Eichenbaum (1998) reported that perirhinal lesions impair olfactory transverse patterning. One possibility is that the importance of the perirhinal cortex depends on the classes of stimuli to be integrated in the configural task. Using a complex discrimination that examined the learning of two-way and three-way configural representations making up an auditory signal (tone or click [*what*?]), visual context (spotted or checkerboard test boxes [*where*?]), and time of day (morning versus afternoon

[*when*?]), Iordanova et al., 2009 found that rats with perirhinal cortex lesions where impaired at acquiring the *what–where–when* conjunction. The same study also found that perirhinal cortex lesions impaired learning the *what–where* but not the *what–when* configural task, leading to the conclusion that the perirhinal cortex is selectively required for those conditional tasks involving visual context. This conclusion (Iordanova et al., 2009) could be accommodated within the perceptual-mnemonic/feature conjunction model if the visual stimuli used to specify context showed high overlap (i.e., ambiguity).

The effectiveness of the perirhinal lesions was tested with object recognition given the importance of this cortical area for normal recognition memory (Brown & Aggleton, 2001). Object recognition after perirhinal lesions in rats has been repeatedly tested using behavioral tasks either based on delayed nonmatching-to-sample (Mumby & Pinel, 1994) or the spontaneous preference for novel over familiar items (Aggleton, Keen, Warburton, & Bussey, 1997; Barker, Bird, Alexander, & Warburton, 2007; Bartko et al., 2007a; Ennaceur et al., 1996; Norman & Eacott, 2004). The present study used a new hybrid test of object recognition (Albasser et al., in press) that combines features of delayed nonmatching-to-sample (Mishkin & Delacour, 1975) with spontaneous exploration (Ennaceur & Delacour, 1988). A potential advantage of the present procedure is that rats can be given many more object recognition trials per session (20 in this case) than in standard spontaneous object recognition tasks (Barker et al., 2007; Ennaceur & Delacour, 1988; Norman & Eacott, 2004; Steckler et al., 1998). Using this new task, it was evident that a clear perirhinal lesion deficit was present even though the retention delay was in practice very short (maximum of 1 min).

This deficit after such a short retention period appears at odds with studies using standard spontaneous exploration tasks with junk objects. Here, deficits associated with perirhinal cortex lesions are found after delays of 15 min and longer, whereas performance at short delays (1 min) can appear spared (Ennaceur et al., 1996; Norman & Eacott, 2004). One possible explanation for the present recognition deficit at short (<1 min) retention delays is that the use of multiple trials and, therefore, multiple stimuli reduced the variance normally associated with the standard one-trial spontaneous recognition task, that is, a deficit would have been reported in previous studies if the method had greater sensitivity to separate the groups when rats with perirhinal cortex lesions are performing above chance. Consistent with this view was the finding that the cumulative discrimination scores of the PRh rats in our study were significantly above chance, albeit at a significantly lower level of discrimination than the control rats. An alternative explanation comes from the perceptual-mnemonic/ feature conjunction model (Cowell et al., 2006; Bartko et al., 2007a). This explanation would argue that in the present study the use of multiple trials within a session leads to high levels of proactive interference between similar features across the various test objects. The consequence is a perceptual deficit that does not require a retention period to emerge. Because the present object recognition study did not attempt to manipulate levels of interference in a systematic way, it is not yet possible to exclude either of these explanations.

Relevant evidence concerning the importance of the perirhinal cortex for discriminating ambiguous stimuli in spontaneous recognition tasks comes from studies where the "novel" objects are composed of the same elements as the sample objects but these elements are now rearranged (Ennaceur & Aggleton, 1994; Ennaceur et al., 1996; Bartko et al., 2007a, 2007b). Such tasks may well tax configural learning, although these same tasks cannot preclude elemental solutions; for example, different angles or faces of the object become exposed, whereas the perceptual properties of a feature might be influenced by a change in the neighboring element. The studies by Bartko et al. (2007a, 2007b) found that rats with perirhinal cortex lesions could perform recognition tasks at near-zero retention delays with standard objects, but that a deficit emerged at "zero" delays when the test stimuli (made of Lego blocks) were designed to have high feature ambiguity by spatially rearranging the component elements of each test stimulus. Curiously, Ennaceur et al. (1996) found the opposite pattern of effects, such that perirhinal lesions impaired performance with normal junk objects (after 15-min retention) but had no apparent effect when the objects were composed of rearranged, familiar elements. Part of the explanation for this unexpected pattern of results probably comes from the performance of the control rats, as they found the configural task more difficult given that they could discriminate novelty after 1 min but not after a 15-min interval, thereby reducing the sensitivity of the task. Even so, the study by Ennaceur et al. failed to find evidence of a specific deficit on a test likely to tax structural learning.

Although the present study does not resolve the underlying nature of the recognition deficit, the findings clearly fail to support a central prediction of the perceptual-mnemonic/feature conjunction model: that the perirhinal cortex is vital for discriminating configural visual stimuli as such stimuli will have maximum ambiguity (Bussey & Saksida, 2002). It should be noted that while the structural task has a spatial component, it also involves discriminating complex visual stimuli that can be distinguished only by the specific combinations of their features (BW vs. HW vs. BH), as in any true configural task. Furthermore, as discussed above, the structural task in the present study was solved configurally, and so would have challenged the discrimination of ambiguous visual stimuli. Even so, rats with perirhinal lesions that were impaired on object recognition could solve this configural task at a normal rate. At first sight, it is tempting to suppose that comparing these two tasks (object recognition and structural learning) is misleading as they vary on many dimensions, most obviously that the recognition task can be described as "single trial," whereas the structural discrimination relied on multiple learning trials. But data used to simulate and support the perceptual-mnemonic/feature conjunction model have often come from discrimination tasks that require multiple acquisition trials (Bussey & Saksida, 2002; Bussey et al., 2002, 2003, 2005). A possible resolution concerns the nature of the elements (black, white, horizontal) used in the structural task. Such stimuli could be expected to be distinguished early in visual processing and so might provide a parallel or different route for combining the different elements with each other and with their relative spatial positions. The problem with this modified account is that it might be difficult to determine a priori what kinds of elements are sufficiently complex to depend on the perirhinal cortex when they are made ambiguous. A further possibility is that the model accurately predicts the performance of monkeys with perirhinal lesions, but may prove less inclusive for rats given cross-species differences in connectivity (Burwell, Witter, & Amaral, 1995).

Previous research has highlighted the importance of the hippocampus for structural learning (Aggleton, Sanderson, & Pearce, 2007; Sanderson et al., 2006), whereas loss of the anterior thalamic nuclei and the fornix appears to have no disruptive effects (Aggleton et al., 2009). The implication is that this form of learning is reliant on corticohippocampal connections. The failure of the perirhinal lesions in the present study to disrupt structural learning signals the potential importance of other routes to the hippocampus that could provide appropriate visual information. One plausible route is via the postrhinal cortex as this region provides parallel, afferent circuitry to the hippocampus (Burwell et al., 1995), and lesion studies show that the postrhinal cortex is required for contextual learning (Burwell, Bucci, Wiig, Saddoris, & Sanborn, 2002), although not for some spatial tasks (e.g., water maze) that are hippocampal-dependent. Another candidate is the retrosplenial cortex. This cortical area provides a potential route for parietal information to reach the hippocampus (Vann, Aggleton, & Maguire, 2009), and loss of the rat retrosplenial cortex disrupts various spatial tasks (Aggleton, in press), including the object-in-place task (Vann & Aggleton, 2002), which might be expected to tax structural learning. Given that there is preliminary evidence implicating the parietal cortex in rat structural learning (Aggleton et al., 2007), it appears that the optimal strategy is to explore the various routes by which parietal information reaches the hippocampal formation. Such routes include both the postrhinal and retrosplenial cortices.

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