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Impairments in visual discrimination after perirhinal cortex lesions: testing 'declarative' vs. 'perceptual-mnemonic' views of perirhinal cortex function

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Abstract

Two experiments tested the predictions of 'declarative' vs. 'perceptual-mnemonic' views of perirhinal cortex function. The former view predicts that perirhinal cortex lesions should impair rapidly learned, but not more slowly learned, visual discriminations, whereas the latter view predicts that impairments should be related not to speed of learning but to perceptual factors. It was found that monkeys with perirhinal cortex lesions were impaired in the acquisition and performance of slowly learned, perceptually difficult greyscale picture discriminations, but were not impaired in the acquisition of rapidly learned, perceptually easier discriminations. In addition, these same monkeys were not impaired in the acquisition or performance of difficult colour or size discriminations, indicating that the observed pattern of impairments was not due to ceiling effects or difficulty *per se*. These findings, taken together, are consistent with the 'perceptual-mnemonic' view that the perirhinal cortex is involved in both perception and memory, but are not consistent with the 'declarative' view that the perirhinal cortex is important exclusively for declarative memory, having little or no role in perception. Moreover, the results are consistent with the more specific proposal that the perirhinal cortex contributes to the solution of complex visual discriminations with a high degree of 'feature ambiguity', a property of visual discrimination problems that can emerge when features of an object are rewarded when part of one object, but not when part of another. These and other recent findings suggest the need for a revision of prevailing views regarding the neural organization of perception and memory.

Introduction

The perirhinal cortex lies at the interface between the putative 'medial temporal lobe (MTL) memory system' and the ventral visual stream or 'what' pathway. Based on findings from anatomical, physiological and lesion studies, two competing ideas about perirhinal cortex function have emerged. The currently prevailing 'declarative' view stresses a role in declarative memory, and holds that 'the perirhinal cortex is not involved in the perceptual processing of complex visual stimuli.' (Buffalo *et al*., 1998; see also Buffalo *et al*., 1999; Squire, 1992). An alternative, 'perceptual-mnemonic' view is that the perirhinal cortex has a role in visual perception as well as memory, and considers the perirhinal cortex as part of both the MTL and the ventral visual stream, as well as other cognitive systems (e.g. Eacott *et al*., 1994; Buckley & Gaffan, 1998b, 2000; Murray & Bussey, 1999; Buckley *et al*., 2001; Bussey & Saksida, 2002; Bussey *et al*., 2002).

A way to distinguish these two views is to compare the influence of perceptual difficulty and rate of learning on the magnitude of impairments in visual discrimination learning following perirhinal cortex lesions. Rapid learning is thought to be a defining characteristic of declarative memory in both humans and monkeys, whereas slow, incremental learning is thought to depend on a nondeclarative, procedural system (Squire & Zola-Morgan, 1983; Buffalo *et al*., 1999; Squire & Knowlton, 2000; Teng *et al*., 2000; Zola & Squire, 2000). Thus, the declarative view predicts that '... simple two-choice discrimination tasks – that is, ones that are learned quickly by normal animals – are dependent on the medial temporal lobe. More difficult two-choice discrimination tasks... are independent of the medial temporal lobe' (Zola & Squire, 2000). In contrast, the 'perceptual-mnemonic' view predicts that impairments in visual discrimination should be related not to the speed of acquisition, but to perceptual factors. In the present study, therefore, the perceptual difficulty of single-pair discriminations was manipulated by using 'morphing' software to blend together pairs of greyscale picture stimuli to create discriminanda that shared many features. We could then evaluate whether the pattern of deficits following perirhinal cortex lesions was more consistent with the declarative view (impairment on rapidly learned, but not slowly learned, visual discrimination problems) vs. the perceptual-mnemonic view (impairment only on perceptually difficult visual discriminations). If the latter finding were obtained, it would support not only the general predictions of the perceptual-mnemonic view outlined above, but also the more specific proposal that perirhinal cortex is important, not for all perceptually difficult visual discriminations, but only for complex discriminations with a high degree of 'feature ambiguity', a property of visual discrimination problems that

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can emerge when features of an object are rewarded when part of one object, but not when part of another (Murray & Bussey, 1999; Bussey & Saksida, 2002). We thus provided further tests of this more specific proposal by testing the same monkeys on difficult colour discriminations, in which the stimuli are not comprised of conjunctions of features.

The findings suggest, contrary to the declarative view, that the effects of perirhinal cortex lesions depend on the perceptual demands of the task. In a second experiment we conducted an additional test in which we allowed the monkeys to acquire visual discriminations to a high level of accuracy and then examined the effect on performance when perceptual difficulty (feature ambiguity) was systematically increased. In this way we were able to examine discrimination performance unconfounded by concomitant associative (stimulus-reward) learning. Both of these experiments were preceded by simulations using the connectionist network of Bussey & Saksida (2002), thus making concrete the assumptions and predictions of the model.

Experiment 1. Acquisition of single-pair discriminations: manipulating 'feature ambiguity'

This experiment tested the predictions of the perceptual-mnemonic view against those of the declarative view of perirhinal cortex function. The perceptual difficulty of single-pair discriminations was manipulated by blending together pairs of greyscale picture stimuli to create discriminanda that shared many features. Monkeys with perirhinal cortex lesions or unoperated control monkeys were tested on the acquisition of slowly learned, perceptually difficult 'high feature ambiguity' discriminations and rapidly learned, perceptually easier 'low feature ambiguity' discriminations. We have used the term 'feature ambiguity' to refer to a property of visual discrimination problems that can emerge when features of an object are rewarded when part of one object, but not when part of another. In the case of our 'morphed' stimuli, as the pictures are blended together it becomes increasingly difficult to solve the discrimination by 'tracking' a single feature; a much more effective strategy is to use the 'gestalt' impression of the whole picture – the conjunction of all features in the picture – to tell the pictures apart (see, for example, pictures 17 vs. 24 in Fig. 4; the bottom flower is a poor feature on which to discriminate the pictures, yet the pictures taken as a whole are more easily distinguished). The connectionist network of Bussey & Saksida (2002) captures this through the use of conjunctive feature representations, combined with a stringent similarity function on the feature conjunction layer. In other words, feature conjunction units in the network are tuned to specific conjunctions of features, with little generalization to other, similar conjunctions (see Bussey & Saksida, 2002). This assumption seems reasonable, as neurons in anterior regions of the ventral visual stream that show 'configurational selectivity' also show limited generalization (e.g. Logothetis & Sheinberg, 1996), and Baker *et al*. (2002) have recorded from neurons in anterior inferotemporal cortex for which the summed response to individual features of a stimulus is less than the response to the conjunctions of those features, i.e. in which the 'whole is greater than the sum of the parts' (Murray & Bussey, 1999; Bussey & Saksida, 2002; Bussey *et al*., 2002).

In addition, the same monkeys were tested on difficult colour discriminations, which did not share overlapping (and therefore ambiguous) features. This also provided a control for the possibility that differential effects of the lesion on the greyscale picture discriminations might be related to task difficulty or ceiling effects. Finally, a second set of perceptually difficult greyscale picture discriminations was given to controls for possible confounds related to the order of testing.

Materials and methods

Animals

Eight rhesus monkeys (*Macaca mulatta*) were used in the present study. The monkeys were housed individually and were fed a controlled diet of Purina Primate Chow (Purina Mills Inc., St. Louis, MO, USA), supplemented with fruit. Four of these monkeys received aspiration lesions of the perirhinal cortex; the remaining four monkeys were retained as unoperated controls. All monkeys had been trained on a series of visual discrimination problems before entering the present study. The training histories of all eight monkeys were identical. All procedures were approved by the NIMH Animal Care and Use Committee.

Surgery

Bilateral aspiration lesions of the perirhinal cortex ($n = 4$) were performed with sterile procedures under visual control with the aid of an operating microscope. Dexamethasone sodium phosphate (0.4 mg/kg, i.m.) and an antibiotic (Di-Trim, 0.1 mL/kg, 24% w/v solution i.m.; Syntex Animal Health Inc, West Des Moines, IA, USA) were administered for 1 day before surgery to reduce swelling and to prevent infection, respectively. On the day of surgery the monkeys were restrained with an injection of ketamine hydrochloride (10 mg/kg, i.m.) and anaesthetized with isoflurane (1–3%, to effect). The animals received an intravenous drip of isotonic fluids containing an antibiotic (Cefazolin), and heart rate, respiration rate, body temperature, blood pressure and expired CO_2 were monitored closely throughout the procedure. After draping the animal to establish an aseptic field, a coronal incision was made. The skin and underlying galea were retracted. The zygoma was removed to allow access to the portion of the cranium overlying the ventrolateral surface of the frontal and temporal lobes. Then the temporalis muscle was reflected and a large bone flap was taken, extending rostrally to the orbit, ventrally to the base of the temporal fossa and caudally to the auditory meatus. The dura was first cut over the frontal and anterior temporal lobes. Using a supraorbital approach, the frontal lobe was gently retracted from the orbit with a brain spoon, the rhinal sulcus was identified and the rostral part of the perirhinal cortex was removed with a small-gauge sucker. This part of the lesion extended along the rostral face of the temporal pole from the lateral fissure to the floor of the temporal fossa and included the cortex lining the lateral bank of the rhinal sulcus, together with about 2–3 mm of the cortex lateral to the sulcus. The medial boundary of the lesion was the fundus of the rhinal sulcus. After this part of the removal was completed, the dura was sewn over the frontal lobe, and was cut again over the lateral temporal lobe. The monkey's head was now tilted at an angle of 120° from vertical, thereby allowing a subtemporal approach for ablation of the caudal half of the perirhinal cortex. Mannitol was administered at this time (25%; 30 mL i.v. over 30 min) to reduce brain volume and increase accessibility of the ventromedial cortex, which was retracted from the base of the temporal fossa. The lesion was continued caudally from the first ablation, along the lateral bank of the rhinal sulcus, to include the cortex lining the lateral bank as well as about 2–3 mm of cortex lateral to the sulcus. The medial boundary of the lesion was the fundus of the rhinal sulcus. After the removal was completed, the dura was sewn and the bone flap was repositioned and held in place with Vicryl sutures.

At the completion of surgery, the galea was closed with Vicryl sutures and the skin was closed with surgical steel staples. Dexamethasone sodium phosphate (0.4 mg/kg, i.m.) and an antibiotic (Di-Trim, 0.1 mL/kg, 24% w/v solution, i.m.; Syntex Animal Health Inc) were administered for 1 week following surgery to reduce swelling and to prevent infection, respectively. Monkeys also received acetamino-

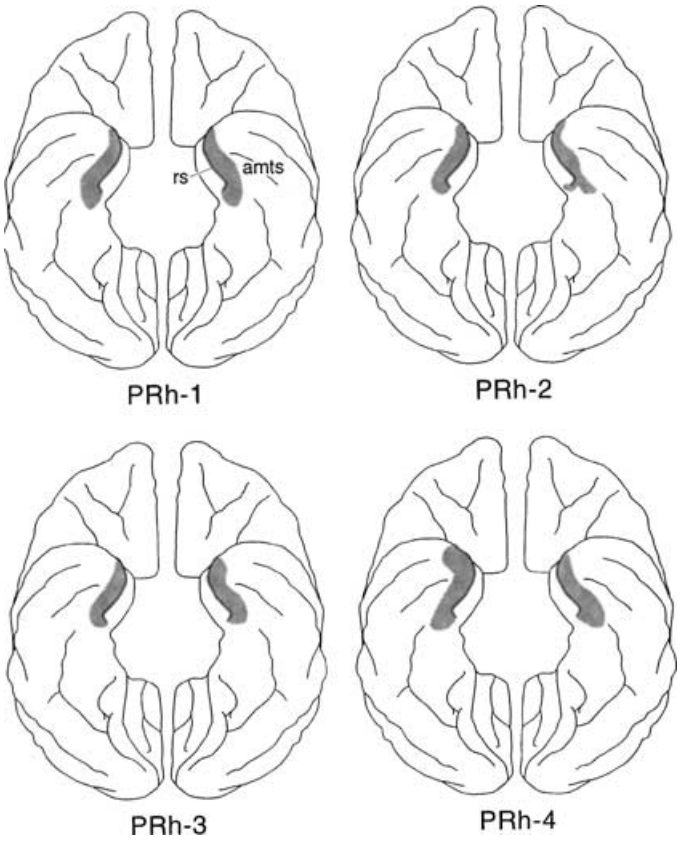

FIG. 1. Ventral views showing the extent of the perirhinal cortex (PRh) lesion in monkeys PRh-1, PRh-2, PRh-3, and PRh-4. Shaded regions indicate the location and extent of the lesion reconstructed from individual coronal MR images from each of the four operated monkeys. rs, rhinal sulcus; amts, anterior middle temporal sulcus.

phen (40 mg) or Banamine (flunixin meglumine, 5 mg) as an analgesic for 3 days following surgery.

Lesion assessment using magnetic resonance imaging

Location and extent of the perirhinal cortex lesions were evaluated using magnetic resonance (MR) images obtained at 1 mm intervals from each of the four monkeys (see Fig. 1). The lesions were plotted from digitized coronal MR images onto standard sections of a rhesus monkey brain at 1 mm intervals. The volumes of the lesions were then measured using Scion Image software (Scion Corporation, Frederick, MD, USA).

A detailed description of the lesions is provided elsewhere (Bussey *et al*., 2002). The lesions were generally as intended, with the estimated damage to perirhinal cortex averaging 92% (range 79–96) of the total volume of this region. The monkey with the smallest lesion, case 2, had sparing of the deepest portion of the lateral bank of the rhinal sulcus bilaterally. As for inadvertent damage, there was minimal involvement of entorhinal cortex, area TE, and areas TF/TH.

Simulation methods

Connectionist model

This section provides a brief overview of the connectionist network (see Fig. 2). Details of the network are provided elsewhere (Bussey & Saksida, 2002).

The network consists of three layers of continuous units: a 'feature' layer; a 'feature conjunction' layer; and an 'outcome' node. The feature layer corresponds to cortical regions caudal to the perirhinal

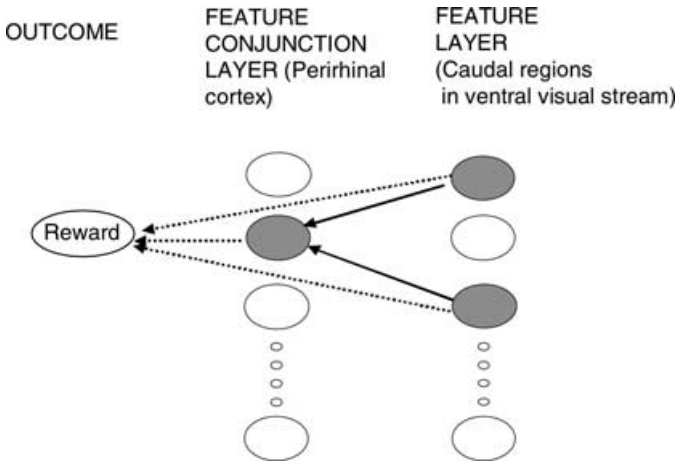

FIG. 2. Diagram of the connectionist network of Bussey & Saksida (2002). The network consists of two layers of units, the feature layer and the feature conjunction layer, as well as an outcome unit representing a consequent event (e.g. reward). The feature layer is connected to the feature conjunction layer through a set of fixed weights. Active units are shown in grey. Both the feature layer and the feature conjunction layer are fully connected to the reward node. The weights between each of the layers and the reward unit are adjustable via an associative mechanism. Connections from two units in the feature layer are shown; in fact 10 of the possible 100 units in the feature layer were used to represent a complex stimulus. The feature conjunction layer represents perirhinal cortex and the feature layer represents more caudal regions of the ventral visual stream. See Bussey & Saksida (2002) for the computational details of the model.

cortex, the feature conjunction layer corresponds to perirhinal cortex, and the outcome node represents the outcome of a trial (reward or nonreward). Upon presentation of a novel stimulus, weights between units in the feature layer and units in the feature conjunction layer are adjusted such that a particular feature conjunction unit becomes fully activated each time that stimulus is presented subsequently. In addition, upon completion of a trial, weights on the links between active feature layer units and the outcome node, and between active feature conjunction layer units and the outcome node are adjusted via the Rescorla–Wagner (delta) rule (Rescorla & Wagner, 1972).

Presentation of a stimulus causes 10 units in the feature layer to become activated to a level between 0 and 1. Because of the connections between the feature layer and the feature conjunction layer, activity in the feature layer leads to a pattern of activation on the units in the feature conjunction layer. Any feature conjunction layer unit may be activated by presentation of the stimulus, depending on the similarity of the stimulus to the pattern of weights between the feature layer and the given feature conjunction unit. A stringent similarity rule operates on the feature conjunction layer, such that feature conjunction layer units are activated only if they match the input very closely. In other words, feature conjunction units in the network are tuned to specific conjunctions of features, with little generalization to other, similar conjunctions (see Bussey & Saksida, 2002). All active feature layer units and feature conjunction layer units become associated with the outcome node (i.e. the weights on the connections between them increase) to an extent dependent on their degree of activation and whether or not reinforcement occurs. Response probabilities, based on these connection weights, are calculated for the feature layer and for the feature conjunction layer, the former representing the response as predicted by cortical regions caudal to perirhinal cortex and the latter representing the response as predicted by perirhinal cortex.

The monkey experiments in the present study consist of simultaneous discrimination learning tasks. In this type of task, two objects are presented simultaneously and the monkey must indicate a choice by

selecting one of the two objects. Similarly, in the simulations using the network, on a given simulation trial two stimuli are presented, in this case sequentially, and the network is reinforced for responding to one and not reinforced for responding to the other. For each simulation, two groups of networks are tested. Group Control consists of intact networks as described above; Group Lesion consists of networks that have had the feature conjunction layer, representing perirhinal cortex, removed.

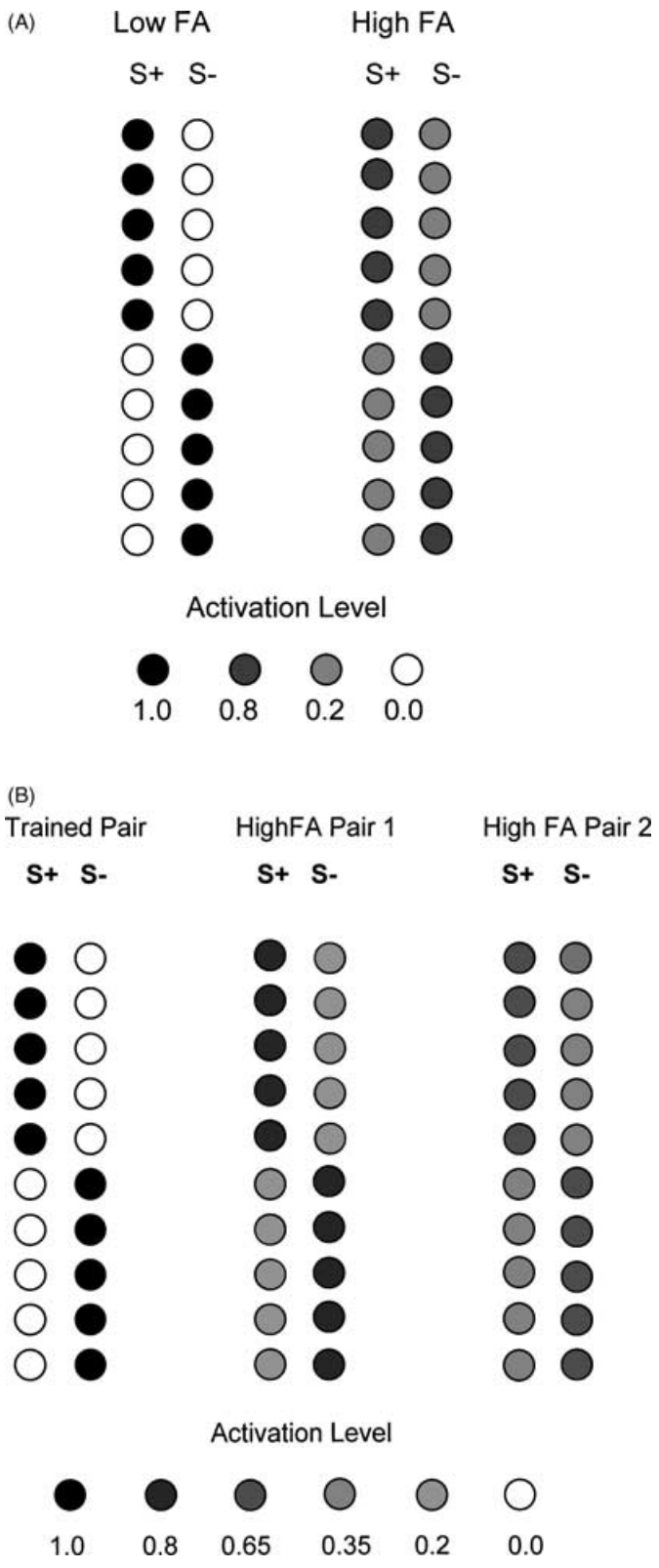

FIG. 3. Diagram illustrating how representations in the network are 'morphed' (blended) together. (A) Representations used for the simulations in Experiment 1. The left panel shows the representation of a pair of stimuli with low feature ambiguity (FA). In this example, all feature layer units are either fully activated (1.0) or fully inactivated (0.0), and the S+ and S– have no activated units in common. In the high feature ambiguity stimulus pair, the units that were fully activated in the low feature ambiguity pair become less activated (i.e. they 'fade out' from an activation level of 1.0 to a level of 0.8), whereas the units that were inactivated become more activated (i.e. they 'fade in' from an activation level of 0.0 to a level of 0.2). This process parallels the way that picture stimuli were morphed together using the image morphing program (see Fig. 4). (B) Representations used for the simulations in Experiment 2. The left panel shows the representation of a 'Trained pair' of stimuli with low feature ambiguity (FA). In this example, all feature layer units are either fully activated (1.0) or fully inactivated (0.0), and the S+ and S– have no activated units in common. In High Feature Ambiguity Pair 1, the units that were fully activated in the Trained Pair become less activated (i.e. they 'fade out' from an activation level of 1.0 to a level of 0.8), whereas the units that were inactivated become more activated (i.e. they 'fade in' from an activation level of 0.0 to a level of 0.2). In High Feature Ambiguity Pair 2 the representations are further blended, with units taking on activations of 0.65 and 0.35. This process parallels the way that picture stimuli were morphed together using the image morphing program (see Fig. 4).

Stimuli

Inputs to the network (stimuli) were vectors consisting of activation values for the 100 units in the feature layer. Units could take on activation values ranging between 0 and 1, with 0 representing a complete lack of activation and 1 representing maximum activation. Thus the vector {1,1,0.5,0,. . .,0} represents a stimulus with units 1 and 2 fully activated, unit 3 partially activated, unit 4 inactive, and so on.

For the current experiment two pairs of stimuli were created. The first (low feature ambiguity) pair of stimuli was created by selecting and activating 10 of the 100 possible units in the feature layer for each stimulus such that there was no overlap in activity between the two stimuli. The second (high feature ambiguity) pair was created by 'morphing' the activations of the initial discriminanda to make the patterns more similar, i.e. by increasing the activation of relatively inactive units and decreasing the activation of relatively active units comprising each stimulus representation (see Fig. 3A for stimulus activation details). Thus the representations of the stimuli changed during morphing in the same way that the picture stimuli changed when processed by the image morphing software.

Procedure

Two groups of four networks each were initialized (for details see Bussey & Saksida, 2002): Group Control consisted of intact networks whereas group Lesion consisted of networks with the feature conjunction layer removed to simulate the effect of a lesion in perirhinal cortex. Each network was trained on a pair-wise discrimination using the low feature ambiguity pair for 24 blocks of 200 trials. Each network was then reinitialized, and subsequently trained on a pair-wise discrimination using the high feature ambiguity pair for 24 blocks of 200 trials.

Behavioural methods

Test apparatus and materials

Monkeys were trained and tested in an automated apparatus consisting of an IBM compatible computer linked to a 15-inch colour monitor fitted with a touch-sensitive screen (Microtouch Systems, Woburn, MA, USA) and an automatic pellet dispenser (BRS/LVE, Laurel, MD, USA). Reward pellets (190 mg banana flavoured; Noyes, Lancaster, NH, USA) were delivered through a copper tube into a food cup located directly below the centre of the monitor. During each test session, the

monkey was seated in a primate chair inside a test cubicle. The monkey's head was approximately 230 mm from the monitor screen.

Visual stimuli consisted of rectangular grayscale images, approximately 4 cm × 4 cm, presented at two locations, one on the left and one on the right side of the monitor screen, set approximately 8 cm apart from centre to centre.

Testing procedure

Monkeys were tested for the ability to learn to discriminate pairs of stimuli. In each pair, one stimulus was arbitrarily designated as the S+, and the other the S–. On each trial, two stimuli appeared on the monitor screen. The stimuli remained on the screen until the monkey made a response by touching one or the other. Touching the S+ resulted in offset of the stimulus display concomitant with delivery of a reward pellet. Touching the S– resulted in offset of the stimulus display with no reward delivery. Whether the S+ was on the right or left on a given trial was determined by a pseudorandom series. In each test session a given pair of stimuli was presented for a total of 96 trials; there was 10 s between each trial. A different pair of stimuli was presented in each daily session. The same stimulus pairs were used for all monkeys.

High vs. low feature ambiguity discriminations

Problems were of two types: low feature ambiguity and high feature ambiguity. Stimuli used for the 'Low feature ambiguity' discriminations were greyscale photographs and drawings obtained from a commercially available clip-art collection ('Masterclips'; IMSI, San Rafael, CA, USA). Complex pictures of this type elicit selective responses from neurons in perirhinal cortex (Erickson *et al*., 2000). Stimuli used for the 'high feature ambiguity' discriminations were greyscale photographs and drawings, obtained from the same source, that had been blended together using a commercially available image morphing program (Gryphon Software Corporation, San Diego, CA, USA). The morphing software was used as a means of systematically manipulating feature ambiguity; images generated in this way had more features in common than did the original pair. To create each pair of stimuli, two pictures were morphed together to create a series of 40 new images, the first images in this series consisting mostly of features from picture 1, the latter images consisting mostly of features from picture 2. For each discrimination problem, the 14th and 27th images from this series were chosen to be the 'High feature ambiguity' test pair. A representative subset of images generated by the morphing software, including sample Low and High Feature Ambiguity test pairs, is shown in Fig. 4. Each monkey was trained on five problems of each type. The type of discrimination (high or low feature ambiguity) tested in a given session was determined by a pseudorandom series.

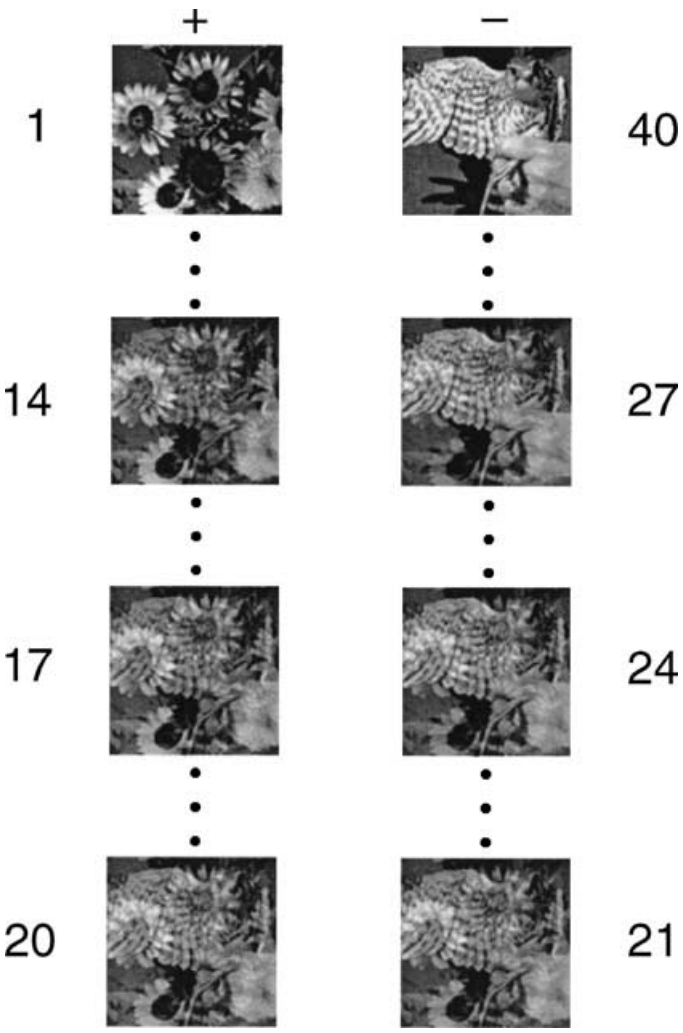

FIG. 4. Example of greyscale picture stimuli. To create each pair of stimuli, two pictures were 'morphed' (blended) together to create a series of 40 new images, the first images in this series consisting mostly of features from picture 1, the latter images consisting mostly of features from picture 2. The numbers next to an image indicate the position of the image in the series. In Experiment 1, for example, the 14th and 27th images were chosen to be the high feature ambiguity test pair. The original images, numbers 1 and 40, were used as the low feature ambiguity test pair. The + and – indicate that the images on the left, in this example those most similar to the photograph of the sunflowers, were the correct (rewarded) images in the pair, whereas those on the right were incorrect (unrewarded).

Difficult colour discriminations

Data were collected from 10 colour discriminations that were of the same difficulty as the difficult picture discriminations in Experiment 1, on which monkeys with perirhinal cortex lesions were significantly impaired (i.e. the mean control scores were <85%, averaged across the session). Stimuli were coloured squares of the same size as the greyscale picture stimuli used in Experiment 1. Colours were created using Adobe Photoshop (Adobe Systems, Inc., San Jose, CA, USA) by varying hue, while keeping saturation and brightness constant across all discriminations. In addition, each pair of colours was matched for luminance.

High feature ambiguity discriminations: retest

To test that a lack of impairment on the colour discriminations could not be attributed to recovery of function, we again tested greyscale picture discriminations, made perceptually difficult by increasing feature ambiguity as described above. Data were thus collected from 10 additional picture discriminations that were of the same difficulty as the difficult picture discriminations used above.

Data analysis

Percentage correct scores for each block of eight trials were averaged across discriminations and analysed using analysis of variance (ANOVA) with appropriate transformations to ensure homogeneity of variance (Howell, 1987).

Results

Simulation results

Low feature ambiguity discriminations

Networks lacking the feature conjunction layer (group Lesion) were unimpaired in discrimination problems with low feature ambiguity

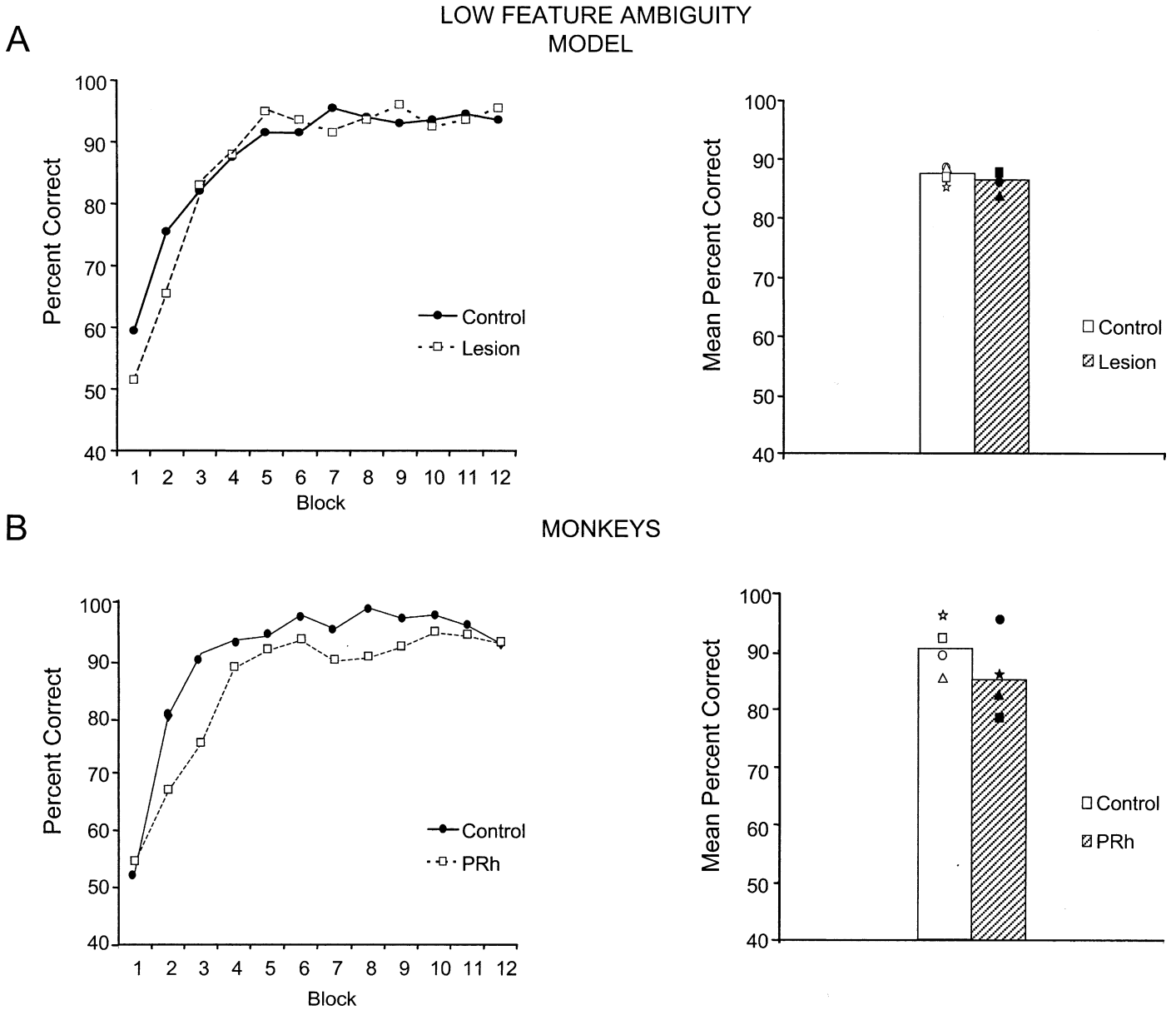

FIG. 5. (A) Simulation of the acquisition of discriminations of stimuli with low feature ambiguity, using the connectionist network of Bussey & Saksida (2002). The left panel shows the acquisition curves for intact networks (Control), and networks in which the feature conjunction layer was removed (Lesion). The right panel shows the mean percentage correct responses for the session. Filled square, L-1; filled star, L-2; filled circle, L-3; filled triangle, L-4; open square, CON-1; open star, CON-2; open circle, CON-3; open triangle, CON-4. There were no significant differences between the groups. (B) Acquisition of discriminations of stimuli with low feature ambiguity, by intact monkeys (Control) and monkeys with lesions of perirhinal cortex (PRh). The left panel shows acquisition curves; the right panel shows the mean percentage correct responses for the session. Filled square, PRh-1; filled star, PRh-2; filled circle, PRh-3; filled triangle, PRh-4; open square, CON-1; open star, CON-2; open circle, CON-3; open triangle, CON-4. There were no significant differences between the groups.

(Fig. 5A). ANOVA with Group as between-subjects and Block as within-subjects factors revealed no significant main effect of Group ($F_{1,6} = 1.45$, $P = 0.27$), a significant main effect of Block ($F_{11,66} = 74.4$, $P < 0.0001$) and no significant Group–Block interaction ($F_{11,66} < 1$).

High feature ambiguity discriminations

In contrast to the above result, networks lacking the feature conjunction layer were significantly impaired in the discrimination problems with high feature ambiguity (Fig. 6A). ANOVA with Group as between-subjects factor and Block as within-subjects factor revealed a significant main effect of Group ($F_{1,6} = 508.6$; $P < 0.0001$), a significant main effect of Block ($F_{11,66} = 36.0$, $P < 0.0001$) and a significant Group–Block interaction ($F_{11,66} = 5.52$, $P = 0.0001$). Analysis of simple effects revealed a significant difference between the performance of Control and Lesion groups at Blocks 2 to 12 ($P < 0.001$).

Behavioural results

Low feature ambiguity discriminations

As shown in Fig. 5B, monkeys learned the low feature ambiguity discriminations at a rapid rate, attaining a mean score above 80% correct by the end of the first two 8-trial blocks. This rate of learning is appropriate for testing the view that '. . .an object discrimination that takes only 10–20 trials to learn. . . should be expected to be more

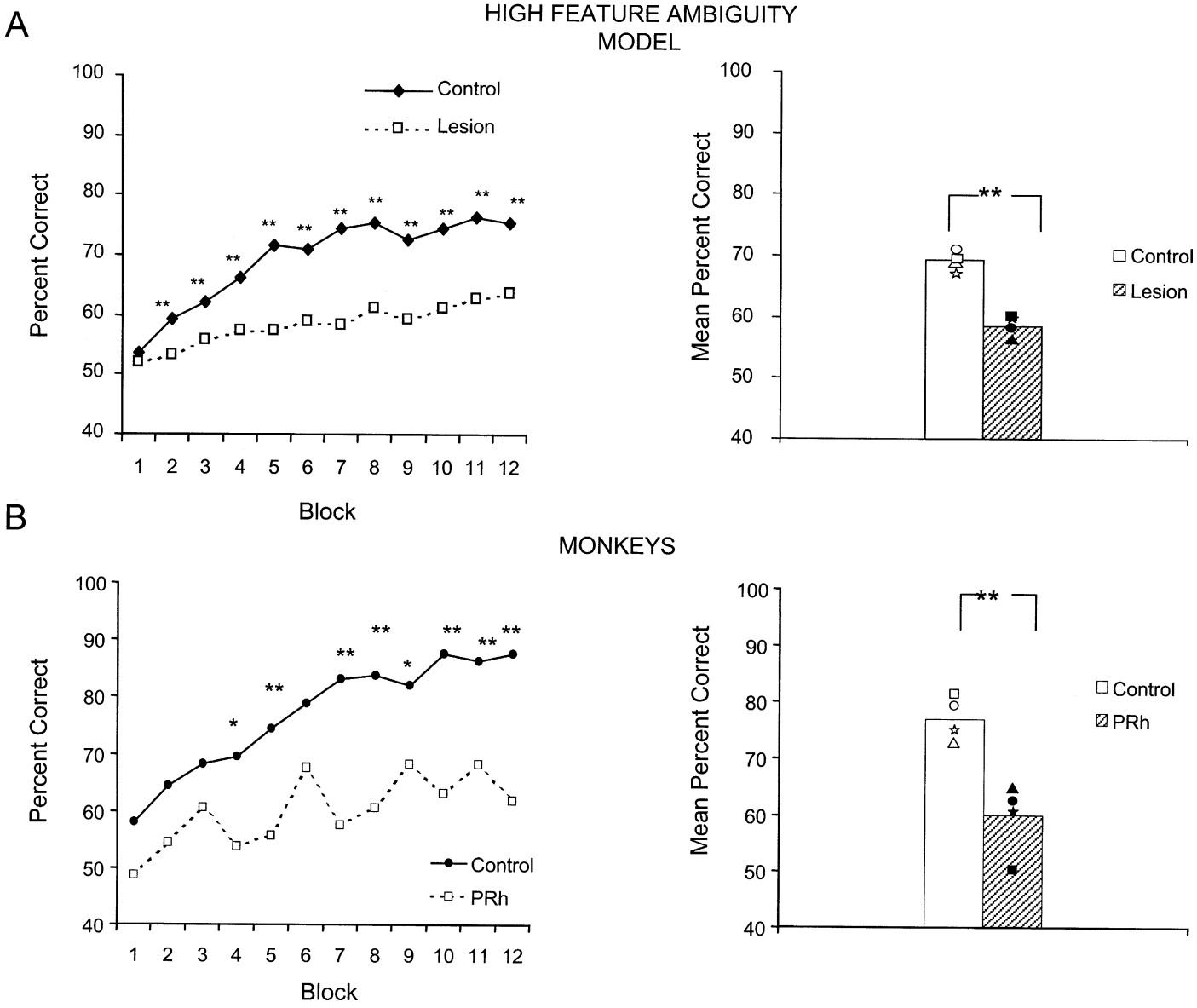

FIG. 6. (A) Simulation of acquisition of discriminations of stimuli with high feature ambiguity, using the connectionist network of Bussey & Saksida (2002). The left panel shows the acquisition curves for intact networks (Control), and networks in which the feature conjunction layer was removed (Lesion). The right panel shows the mean percent correct responses for the session. Filled square, L-1; filled star, L-2; filled circle, L-3; filled triangle, L-4; open square, CON-1; open star, CON-2; open circle, CON-3; open triangle, CON-4. Asterisks indicate significant differences between the groups; $^{**}P < 0.01$. (B) Acquisition of discriminations of stimuli with high feature ambiguity, by intact monkeys (Control) and monkeys with lesions of perirhinal cortex (PRh). The left panel shows acquisition curves; the right panel shows the mean percent correct responses for the session. Filled square, PRh-1; filled star, PRh-2; filled circle, PRh-3; filled triangle, PRh-4; open square, CON-1; open star, CON-2; open circle, CON-3; open triangle, CON-4. Asterisks indicate significant differences between the groups; $^{*}P < 0.05$; $^{**}P < 0.01$.

sensitive to the effects of medial temporal lesions than a discrimination that takes 300–500 trials to learn.' (Buffalo *et al.*, 1999).

As predicted by the simulation results, monkeys with perirhinal cortex lesions were unimpaired in discrimination problems with low feature ambiguity (Fig. 5B). ANOVA with Group as between-subjects factor and Block as within-subjects factor revealed no significant main effect of Group ($F_{1,6} = 1.36$, $P = 0.29$), a significant main effect of Block ($F_{11,66} = 26.2$, $P < 0.0001$) and no significant Group–Block interaction ($F_{11,66} = 1.1$).

High feature ambiguity discriminations

As expected, these problems proved more difficult than the problems with low feature ambiguity. Although control monkeys obtained a mean score of $90.3 \pm 3.0\%$ correct responses on problems with low feature ambiguity, their mean score on problems with high feature ambiguity was $76.9 \pm 2.1\%$ correct responses. In contrast to the lack of impairment on low feature ambiguity visual discriminations, and as predicted by the simulation results, monkeys with perirhinal cortex lesions were significantly impaired in the discrimination of visual stimuli with high feature ambiguity (Fig. 6B). ANOVA with Group as between-subjects factor and Block as within-subjects factor revealed a significant main effect of Group ($F_{1,6} = 24.0$; $P = 0.003$), a significant main effect of Block ($F_{11,66} = 8.2$, $P < 0.0001$) and a significant Group–Block interaction ($F_{11,66} = 1.89$, $P = 0.05$). Analysis of simple effects revealed a significant difference between the performance of intact and operated groups at Blocks 4, 5, and 7 to 12 ($P < 0.05$).

To test more stringently the apparent differential effects of perirhinal cortex lesions on high and low feature ambiguity discriminations, data from these two tasks were combined for analysis. ANOVA revealed a significant Group–Task interaction, ($F_{1,6} = 7.51$, $P = 0.03$). This analysis underscores a clear impairment in the operated group on the high, but not the low, feature ambiguity discrimination.

Difficult colour discriminations

Control monkeys scored a mean of $70.4 \pm 8.5\%$ correct responses on difficult colour discrimination problems. Thus, as intended, the difficulty level matched that of the high feature ambiguity problems. As predicted, and as shown previously (Buckley & Gaffan, 1998a; Buckley *et al.*, 1997, 2001), monkeys with perirhinal cortex lesions were unimpaired on difficult colour discriminations. ANOVA with Group as between-subjects and Block as within-subjects factors revealed no significant main effect of Group ($F_{1,6} = 1.50$, P=0.26), a significant main effect of Block ($F_{11,66} = 7.22$, $P < 0.0001$) and no significant Group–Block interaction ($F_{11,66} = 1.17$, $P = 0.32$).

High feature ambiguity discriminations: retest

Following completion of the colour discriminations, a second set of difficult (i.e. high feature ambiguity) picture discriminations was given to test whether the lack of effect of the lesion on difficult colour discrimination may have been due to recovery of function. In line with the discrimination problems of this type presented earlier, control monkeys scored a mean of $76.2 \pm 5.2\%$ correct responses for the 10 problems. Monkeys with perirhinal cortex lesions were again impaired in acquisition of picture discriminations that were made perceptually difficult by increasing feature ambiguity. ANOVA with Group as between-subjects factor and Block as within-subjects factor revealed a significant main effect of Group, $F_{1,6} = 6.60$, $P = 0.04$, a significant main effect of Block, $F_{11,66} = 8.86$, $P < 0.0001$, and a significant Group–Block interaction, $F_{11,66} = 3.23$, $P = 0.001$. Analysis of simple effects revealed a significant difference between the performance of intact and operated groups at Blocks 5 through 12 ($P < 0.05$). Thus the main result reported in Experiment 1 was replicated using a different set of high feature ambiguity single-pair discriminations.

Experiment 2. Performance of single-pair discriminations: increasing the feature ambiguity of previously learned discriminations

In Experiment 1 it was found that lesions of perirhinal cortex disrupted the acquisition of perceptually difficult, high feature ambiguity discriminations, thus confirming the predictions of the perceptual-mnemonic view. In all of the discriminations in Experiment 1 the learning requirements were the same: monkeys learned that an S+ was rewarded whereas an S– was not. That the observed impairments were dependent on the perceptual demands of the task suggests, contrary to the declarative view, that perirhinal cortex lesions can affect perceptual function. However, because in all of the discriminations in Experiment 1 learning was required, it is conceivable that learning and perception interact; perirhinal cortex lesions might disrupt a learning process *per se*, but only in certain perceptually difficult discrimination tasks. In Experiment 2 therefore we examined the performance on visual discriminations in the absence of learning. The perceptual-mnemonic view predicts that once a discrimination is learned under lesion conditions – even when there is no impairment in acquisition – increasing the perceptual difficulty of the discriminanda will yield impairment in discrimination. This was tested in the present experiment by first training monkeys on a perceptually easy, low feature ambiguity greyscale picture discrimination problem and then assessing discrimination performance when the discriminanda were blended together, thereby increasing feature ambiguity and perceptual difficulty. Impaired performance under conditions of greater perceptual difficulty would indicate perceptual impairments in the absence of learning. In addition, as in Experiment 1 we wished also to test further the more specific proposal that perirhinal cortex is important, not for all perceptually difficult discrimination problems, but only for those with a high degree of feature ambiguity (Bussey & Saksida, 2002; Murray & Bussey, 1999). Thus, we tested the same monkeys on easy 'size' discriminations, and then increased perceptual difficulty by making the stimuli more similar in size. It was predicted that although the difficult size discrimination was at least as difficult as the high feature ambiguity morphed picture discriminations, perirhinal cortex lesions would lead to impairments only on the latter task, as only the latter task has a high degree of feature ambiguity. This discrimination also served to test whether impairments in discrimination learning were related simply to task difficulty or to a nonspecific impairment in generalization. It also controlled for the more remote possibility that impairments might result from the altered format of the performance test sessions, which differed slightly from that of the acquisition sessions.

Simulation methods

Stimuli

Three pairs of stimuli were created. The first pair of stimuli (Trained Pair) was created by selecting and activating 10 units in the feature layer for each stimulus such that there was no overlap in feature unit activity between the two stimuli. The second stimulus set (High Feature Ambiguity 1) was created by 'morphing' (blending) the activations of the initial discriminanda to make the patterns more similar, i.e. by increasing the activation of relatively inactive elements and decreasing the activation of relatively active elements in each stimulus. The third stimulus set (High Feature Ambiguity 2) was created by blending the initial set even further (see Fig. 3B for stimulus activation details).

Procedure

Two groups of four networks each were initialized (for details see Bussey & Saksida, 2002): Group Control consisted of intact networks whereas group Lesion consisted of networks with the feature conjunction layer removed to simulate the effect of a lesion in perirhinal cortex. Each network was trained to a criterion of 90% correct responses over two consecutive blocks of 10 trials on a pair-wise discrimination using the first stimulus set described above. Both groups were then tested for one block of 10 trials each on the Trained Pair, and on each of the two High Feature Ambiguity Pairs.

Behavioural methods

Test apparatus and materials

Test apparatus and type of materials were identical to those used in Experiment 1. As in Experiment 1, greyscale photographs were blended together using commercially available 'morphing' software (Gryphon Software Corporation) to create a series of 40 images, the first images in this series having mostly features of picture 1, the later images having mostly features of picture 2. Novel stimuli were used. Images 1 and 40 were used for the initial acquisition of the discrimination (the 'Trained Pair'). From the series, the 14th and 27th images were chosen to be High Feature Ambiguity Pair 1, and the 17th and 24th images were chosen to be High Feature Ambiguity Pair 2. Examples are shown in Fig. 4.

Monkeys were first trained to discriminate a single pair of greyscale picture stimuli (the Trained Pair). In each pair, one stimulus was arbitrarily designated as the S+, and the other the S-. With the

exception of number of trials per session, training parameters were identical to those in Experiment 1. Now, rather than receiving 96 trials per session, monkeys were trained to a criterion of 17 out of 20 correct responses. The following day, a reminder session was given in which monkeys were again given the same discrimination problem until a criterion of 17 out of 20 correct had been attained. This was followed immediately by a critical test session in which performance was assessed on the Trained Pair, and on each of the two High Feature Ambiguity Pairs. This procedure was repeated for each of four different sets of picture stimuli, and the data were averaged across the four stimulus sets. During each critical test session monkeys were tested on a 32-trial block of the Trained Pair, a 32-trial block of High Feature Ambiguity Pair 1 and a 32-trial block of High Feature Ambiguity Pair 2. The order in which these three blocks were presented was either Trained Pair first, followed by High Feature Ambiguity Pair 1, followed by High Feature Ambiguity Pair 2 (blocking order 'A'), or High Feature Ambiguity Pair 2 first, followed by High Feature Ambiguity Pair 1, followed by the Trained Pair (blocking order 'B'). To control for potential order effects the blocking order was varied according to an A, B, B, A design; i.e. stimulus set 1 was tested using blocking order A; stimulus set 2 using blocking order B; stimulus set 3, blocking order B; and stimulus set 4, blocking order A. Following each critical test session, monkeys were trained to criterion on the Trained Pair of the stimulus set to be tested the following day, in which again a reminder session was given followed by a critical test session. This 2-day procedure was repeated four times, once for each of the four different sets of picture stimuli.

Finally, a control task was given to test the specific prediction of the model that any impairments observed could be accounted for by increased feature ambiguity in the High Feature Ambiguity pairs, rather than being due to difficulty *per se*, or to the deficit emerging only when performance is brought down from ceiling. We chose a size discrimination for this purpose, as two stimuli can be made difficult to discriminate by making them similar in size, which does not increase feature ambiguity as presently defined. Monkeys were first trained, using the method above, to discriminate two square greyscale pictures identical in content but differing in size (4.0×4.0 cm vs. 0.5×0.5 cm). The next day a reminder session was given, followed by a critical test session containing one block of the Trained Pair and two blocks of trials using the same two stimuli made more similar in size (resized Pair 1: 2.8×2.8 cm vs. 1.5×1.5 cm; and resized Pair 2: 2.4×2.4 cm vs. 1.7×1.7 cm). This was accomplished using the same software as was used to create the morph stimuli, by generating a series of 40 images and choosing the 14th vs. 27th images for Resized Pair 1, and the 17th and 24th images for Resized Pair 2. The next day this procedure was repeated, with the blocking pattern reversed to control for potential order effects.

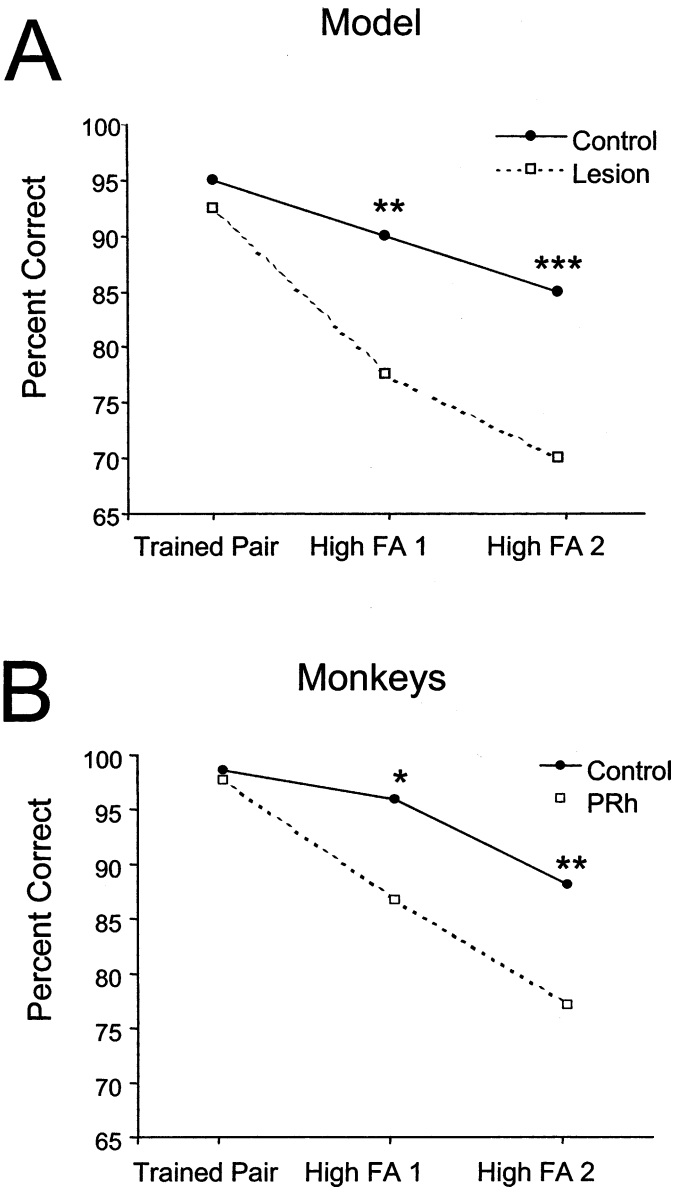

FIG. 7. (A) Discrimination performance of intact networks (Control), and networks with the feature conjunction layer removed (Lesion), on the low feature ambiguity Trained Pair, and on the two High Feature Ambiguity (FA) Pairs (Experiment 2). Asterisks indicate significant differences between the groups; $^{**}P = 0.01$, $^{***}P = 0.001$. (B) Discrimination performance of intact monkeys (Control) and monkeys with lesions of perirhinal cortex (PRh) on the low feature ambiguity Trained Pair, and on the two High Feature Ambiguity Pairs (Experiment 2). Asterisks indicate significant differences between the groups; $^{*}P < 0.05$; $^{**}P < 0.01$.

Results

Simulation results

Acquisition of single-pair discriminations

Both Lesion and Control groups were able rapidly to acquire single-pair low feature ambiguity discriminations, and there was no difference between the groups in their ability to do so ($F_{1,6} < 1$).

Performance test: Increasing feature ambiguity

Networks lacking a feature conjunction layer were significantly impaired when the initially acquired problem was made more difficult to discriminate by increasing feature ambiguity (Fig. 7A). ANOVA with Group as between-subjects factor and Pair as within-subjects factor revealed a main effect of Group ($F_{1,6} = 27.0$; $P = 0.002$, a significant main effect of Pair ($F_{2,12} = 29.8$, $P < 0.0001$) and a significant Group–Pair interaction ($F_{2,12} = 4.85$, $P = 0.029$). Analysis of simple effects revealed no significant effect of Group on the Trained Pair ($P = 0.43$). On discrimination of both of the High Feature Ambiguity Pairs, however, networks lacking a feature conjunction layer were significantly impaired ($P = 0.01$ and $P = 0.001$, respectively).

Behavioural results

Acquisition of single-pair discriminations

As was the case in Experiment 1, perirhinal cortex lesions did not impair the acquisition of rapidly learned single-pair discriminations

($F_{1,6} = 3.3$, $P = 0.12$; mean trials to criterion: Control = 24.8 ± 3.64; perirhinal cortex = 36.4 ± 6.47).

Performance test: increasing feature ambiguity

In contrast to the lack of impairment on the acquisition of easy visual discriminations, and as predicted by the simulation results, monkeys with perirhinal cortex lesions were significantly impaired when these previously acquired stimulus pairs were made more difficult to discriminate by increasing feature ambiguity (Fig. 7B). ANOVA with Group as between-subjects factor and Pair as within-subjects factor revealed no significant effect of Group ($F_{1,6} = 5.11$; $P = 0.06$) a significant main effect of Pair ($F_{2,12} = 38.1$, $P < 0.0001$) and a significant Group–Pair interaction ($F_{2,12} = 4.84$, $P = 0.029$). Analysis of simple effects revealed no group difference on the Trained Pair. On discrimination of both of the High Feature Ambiguity Pairs, however, operated monkeys were significantly impaired ($P < 0.05$ and $P < 0.01$, respectively).

Whereas Experiment 1 showed that acquisition of visual discriminations following perirhinal cortex lesions could be disrupted by increasing feature ambiguity, the present experiment sought to test whether such impairments were restricted to acquisition of new information, or whether the predictions of the perceptual-mnemonic view hold for performance of previously acquired discriminations. The present data appear to confirm this latter prediction. It is conceivable, however, that the differences in discrimination scores of the two groups were due to differences in the rate of learning of new associations between the blended stimuli and reward. Because stimulus pairs were presented in blocks (see Methods), we assessed whether learning occurred within the 32-trial test blocks in either or both of the operated and control groups. The data were thus divided into four-trial blocks for analysis. ANOVA with Group, Pair, and Block as factors revealed no main effect of Block ($F_{7,42} = 1.32$, $P = 0.27$) and no Group–Block interaction ($F_{7,42} < 1$), suggesting that performance differences between groups on the two High Feature Ambiguity Pairs were not because of differences in the rates of new learning during the 32-trial test blocks. It is conceivable, however, that the failure to detect learning differences was due to data from the Trained Pair, in which learning clearly did not occur as both groups were at a very high level of performance, reducing the contribution to the analysis of the data from the High Feature Ambiguity Pairs. Thus to maximize the probability of detecting learning effects, and therefore stringently test our predictions, separate ANOVAs were performed on the eight four-trial blocks of data from each of the two High Feature Ambiguity Pairs separately. For High Feature Ambiguity Pair 1 there was no Group–Block interaction ($F < 1$) and analysis of simple effects revealed no significant effect of Block for either the operated or the control group ($F < 1$). Similarly for High Feature Ambiguity Pair 2 it was found that there was no Group–Block interaction ($F < 1$) and no effect of Block for either the operated or the control group ($F < 1$). Thus, there was no evidence of learning during the test blocks. This analysis indicates that the deficit in discrimination performance was not secondary to an impairment in learning.

Performance test: 'size' manipulation

In contrast to the significant impairment following perirhinal cortex lesions in performance of discriminations made perceptually difficult by increasing feature ambiguity, these same monkeys were unimpaired when a previously acquired 'size' discrimination was made more difficult by making the two discriminanda more similar in size. These results confirm the previously reported finding that perirhinal cortex lesions do not impair difficult size discriminations (Buckley *et al.*, 2001). When tested on discrimination performance with pictures made more similar in size, control monkeys made 95.3 ± 5.4% correct responses on the Trained Pair, 86.7 ± 9.0% on Resized Pair 1 and 78.1 ± 11.7% on Resized Pair 2. Thus, the difficult size discriminations proved to be at least as difficult as the High Feature Ambiguity discriminations in the performance test in the main experiment. Monkeys with perirhinal cortex lesions performed as well as controls on these discriminations, scoring 99.2 ± 0.52% correct on the Trained Pair, 93.75 ± 3.7% on Resized Pair 1 and 74.2 ± 2.4% on Resized Pair 2. ANOVA revealed no main effect of Group ($F_{1,6} < 1$), a significant effect of Pair ($F_{2,12} = 19.4$, $P < 0.0001$), showing that monkeys' performance was significantly worse on the pairs of similar size, and no Group–Pair interaction ($F_{1,6} = 1.3$, $P = 0.30$).

Discussion

The main finding of the present study was that impairments in visual discrimination after perirhinal cortex lesions were related to perceptual factors. In Experiment 1 it was found that monkeys with perirhinal cortex lesions were impaired in the acquisition of single-pair greyscale picture discriminations made perceptually difficult by blending the stimuli together, thereby increasing 'feature ambiguity'. These same monkeys were not impaired on perceptually easier, low feature ambiguity grayscale picture discriminations, or perceptually difficult colour discriminations. In Experiment 2 it was shown that these monkeys were also impaired on performance of visual discriminations when previously acquired perceptually easy discriminations were made more perceptually difficult by increasing feature ambiguity. The same monkeys were unimpaired on difficult 'size' discriminations.

The findings of Experiment 1 are consistent with a perceptual-mnemonic view of perirhinal cortex function (Eacott *et al.*, 1994; Buckley & Gaffan, 1998b, 2000; Buckley *et al.*, 2001; Murray & Bussey, 1999; Bussey & Saksida, 2002; Bussey *et al.*, 2002). They are not, however, compatible with the 'declarative' view that '. . .simple two-choice discrimination tasks – that is, ones that are learned quickly by normal animals – are dependent on the medial temporal lobe. More difficult two-choice discrimination tasks. . .are independent of the medial temporal lobe' (Zola & Squire, 2000; see also Squire & Zola-Morgan, 1983; Buffalo *et al.*, 1999; Squire & Knowlton, 2000; Teng *et al.*, 2000). In Experiment 1 the opposite pattern of results was obtained: the more rapidly acquired, perceptually easy, low feature ambiguity discriminations were spared following the lesions, whereas the more slowly acquired, perceptually difficult, high feature ambiguity discriminations were significantly impaired. This pattern of impairment is inconsistent with the aspects of the declarative view outlined above, but consistent with the perceptual-mnemonic view.

These results are also consistent with the more specific proposal that perirhinal cortex is important, not for all perceptually difficult visual discriminations, but for complex discriminations with a high degree of 'feature ambiguity', a property of visual discrimination problems that can emerge when features of an object are rewarded when part of one object, but not when part of another (for a detailed discussion see Bussey & Saksida, 2002; Murray & Bussey, 1999). Control experiments tested this idea further: monkeys were tested on difficult colour (Experiment 1) and size (Experiment 2) discriminations, which were perceptually difficult but which did not have overlapping features. The monkeys with perirhinal cortex lesions were unimpaired on these discriminations, consistent with our predictions. In addition, this finding indicates that the impairments observed on the high feature ambiguity greyscale picture discriminations were not due to task difficulty *per se*, and that the lack of impairment on low feature

ambiguity greyscale picture discriminations was not due to ceiling effects; performance on the colour and size discriminations was brought down from ceiling, but monkeys with lesions were unimpaired. The size control task also shows that the perirhinal cortex lesion did not disrupt generalization nonspecifically: monkeys with perirhinal cortex lesions were able to generalize normally to the resized stimulus pairs. This finding is consistent with the results of Hampton & Murray (2002), who found that monkeys with perirhinal cortex lesions were able to generalize to shrunken, enlarged and rotated views of objects, even when the discriminations were difficult.

The present study provides clear evidence that perirhinal cortex lesions can disrupt the acquisition of single-pair visual discriminations, and specifies conditions under which such deficits can emerge. Although deficits in single-pair discrimination learning following lesions involving perirhinal cortex in monkeys have been reported previously (Murray *et al*., 1998; Buffalo *et al*., 1999; Baxter & Murray, 2001; Hampton & Murray, 2002), other studies have found no such impairments (Thornton *et al*., 1997). It appears therefore that perirhinal cortex lesions impair single-pair discrimination learning only under certain conditions. The results of the present study suggest that perirhinal cortex lesions can impair complex single-pair discriminations with overlapping (ambiguous) features. Many types of stimulus material will have such ambiguous features; in the present study, for example, even the low feature ambiguity pairs would have had some limited amount of feature ambiguity, and this is perhaps reflected in the slight trend toward an impairment in the low feature ambiguity condition. This interpretation applies not only to single-pair discriminations but to other situations as well. For example, we recently found that monkeys with perirhinal cortex lesions were impaired in the acquisition of four-pair concurrent discriminations when the features the discriminanda were made ambiguous, but not when they were unambiguous (Bussey *et al*., 2002). In that study, rather than blending the stimuli to manipulate the ambiguity of the features, we combined pairs of picture stimuli thereby increasing the 'configural' demands of the task. The results are complementary to those of the present study, indicating a systematic relationship between 'feature ambiguity' and magnitude of impairment.

The results of the present study have implications for the organization of perception and memory in the brain. In Experiment 1, for both the high and low feature ambiguity discriminations the learning requirements were the same: monkeys learned that an S+ was rewarded whereas an S– was not. The observed impairments were dependent not on learning but on the perceptual demands of the task, suggesting that perirhinal cortex has a role in normal perception. However, in Experiment 1, these putative perceptual impairments were observed in the context of a discrimination learning paradigm. It is conceivable, therefore, that learning and perception interact: perirhinal cortex lesions might disrupt a learning process *per se*, but only in perceptually difficult discrimination tasks. A similar caveat applies to a recent study showing that perirhinal cortex lesions can produce impairments in a complex oddity discrimination task (Buckley *et al*., 2001). These authors show, in a similar fashion to the present study, that perirhinal cortex lesions can selectively impair complex visual discriminations. These authors interpret their findings as evidence for a perceptual function of perirhinal cortex; however, the measure of discrimination performance used was the number of trials required to reach criterion and therefore the impairments observed could conceivably have been secondary to impairments in learning. Furthermore, in another recent study, the perceptual difficulty of visual discriminations was manipulated under conditions in which no learning occurred, and under these conditions no deficits were obtained (Hampton & Murray, 2002; note, however, that in that study no attempt was made to manipulate 'feature ambiguity'). In Experiment 2 we therefore examined the effects of manipulating feature ambiguity on the performance of visual discriminations in the absence of learning, by first training monkeys to criterion on a low feature ambiguity greyscale picture discrimination and then assessing discrimination performance when the discriminanda were blended together, thereby increasing feature ambiguity. Monkeys with perirhinal cortex lesions were impaired in performing the discriminations only under conditions of high feature ambiguity. Because no learning was taking place in either the control or lesion group during the critical test sessions, this result cannot be interpreted as an impairment in learning. These results provide perhaps the strongest evidence to date for a contribution of perirhinal cortex to perception. In addition, they provide further evidence contrary to the declarative view, which holds that perirhinal cortex is important for memory, but not visual analysis or perception, whereas regions of the ventral visual stream caudal to perirhinal cortex are important for perception, but not memory (e.g. Squire, 1992; Buffalo *et al*., 1998, 1999). The perirhinal cortex appears instead to be important for both normal memory and normal perception (Buckley & Gaffan, 1998b, 2000; Buckley *et al*., 2001; Murray & Bussey, 1999; Bussey & Saksida, 2002).

In conclusion, the present study shows that perirhinal cortex lesions in monkeys can impair both acquisition and performance of single-pair visual discriminations when the discriminations are made perceptually difficult by increasing 'feature ambiguity'. These results are inconsistent with the prevailing declarative view of perirhinal cortex function. Instead the results provide support for the perceptual-mnemonic view of perirhinal cortex function, based on the idea that, in addition to being a region important for memory that can interact with the hippocampus and other brain regions (Gaffan & Parker, 1996; Bussey *et al*., 2000, 2001; Murray, 2000), the perirhinal cortex can also be considered to be a rostral component of the ventral visual stream, which processes and stores representations of complex visual stimuli (Murray & Bussey, 1999; Bussey & Saksida, 2002; Bussey *et al*., 2002). Thus, perirhinal cortex lesions can lead to deficits that can be characterized as both perceptual and mnemonic, suggesting that 'perception' and 'memory' are unlikely to be neatly organized into anatomically segregated modules in the brain.

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