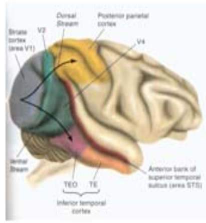
Cognitive Neuroscience : memory lecture 2 -Object and semantic memory in monkeys and humans

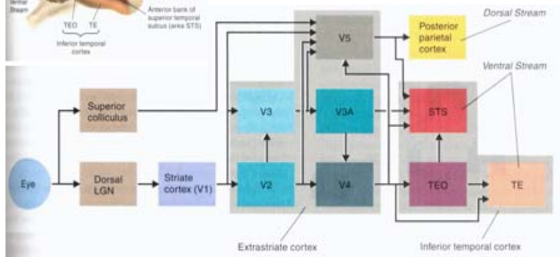
- Temporal Lobe Cortex and object memory
- Inferior temporal cortex consists of the STSv, MTG, ITG and perirhinal cortex.
- Recent anatomical studies have shown that it is divisible into several parts.
  - Seltzer and Pandya (1978) (TE1, TE2, TE3, TEa, TEm)
  - Iwai et al (1987) –amygdala connectivity (D-V dichotomy)
  - Barbas (1985)- orbitofrontal connectivity (D-V dichotomy)
  - Van Essen et al (1990)- PIT, CIT, AIT (D-V dichotomy)
- PRh could be considered just ventral extension……?
- Early lesion studies of IT cortex revealed a role in object memory

Rhinal / perirhinal lesion studies

- Squire papers (included parahippocampal cortex)
- Murray et al (1989) rhinal lesions SocNs Abs
- Gaffan & Murray (1992) two choice visual discrimination. Retention impaired, new learning intact. Learning DMS impaired
- Murray Gaffan & Mishkin (1993) Stimulus-stimulus association learning
- Meunier, Bachevalier, Mishkin & Murray (1993) peri/rhinal and DMS
- Eacott Gaffan & Murray (1994) DMS, many versus few stimuli
- Buckley Gaffan & Murray (1997) no effect of perirhinal lesion on colour discrimination, replication of effect on DMS. Compared with MTG lesion
- Buckley & Gaffan (1997) Effect of perirhinal lesion on two choice discrimination learning if length of list or number of foils varied
- Buckley & Gaffan (1998a) Digitised images of different views of objects
- Buckley & Gaffan (1998b) Objects in different orientations, transfer from real to digitised objects and reversal effects
- Buckley & Gaffan (1998c) Configural and stimulus-stimulus association learning
- Murray, Baxter, Gaffan (1998) scene learning and object reversals
- Easton & Gaffan (2000) scene & object learning
- Buckley, Booth, Rolls & Gaffan (2001) perceptual impairments using an oddity task
- Bussey, Saksida and Murray (2002) Configural learning with varying overlap
- Hampton & Murray (2002) visual discrimination with altered views of objects



Circuit diagram for visual processing in monkey:



Functional Double Dissociation Between Two Inferior Temporal Cortical Areas: Perihinal Cortex Versus Middle Temporal Gyrus.

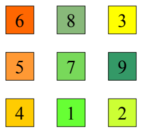
M.J.Buckley, D.Gaffan and E.A.Murray (1997)

– rationale for experiment:

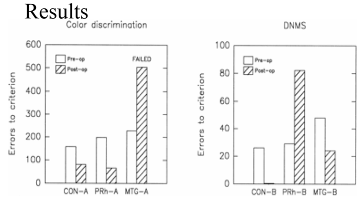
- Horel (1987, 1994) ITG is dissociable from MTG
- MTG cooling/lesions- disrupt colour memory, but not form
- ITG cooling lesions- deficit in DMS
- However is PRH dissociable from MTG?

Colour Discrimination Task

- Green 1 +ve
- Other foils
- Isoluminant
- Hue and saturation



Results



- Summary – Buckley et al (1997)
- MTG lesioned group impaired dramatically on colour discrimination, but not DNMS.

- PRh lesioned group impaired on DNMS, but not colour discrimination

Is there a unique role for perirhinal cortex in resolving feature ambiguity?

Eacott et al (2001) Elemental and configural discrimination learning following lesions to perirhinal cortex in the rat. Behav Brain Res.

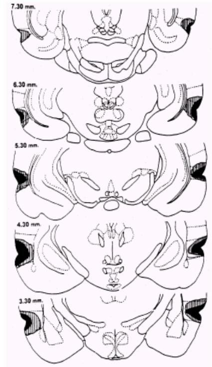
Bussey et al (2002) Perirhinal cortex resolves feature ambiguity in complex visual discriminations. Eur J Neurosci.

Proposals about the functional role of perirhinal cortex

- Recognition memory
  - Support from early lesion experiments using DMS
- Knowledge about objects
  - Precise specification (Gaffan 1994), Gestalt representation (Murray & Bussey 1999)
    - Support from experiments with many discriminanda
      - Eacott et al, 1994
- Possible explanations tested by Eacott et al:
  - 1: fine-grained discrimination needed
    - Therefore detailed discriminations of single elements will be affected
  - 2: Conjunction of features needed
    - Therefore biconditional configural learning should be affected

Experiments 1 to 3 : 'elemental' discriminations between simple stimuli

- Experiment 1:
- 14 controls, 7 perirhinal lesioned before training commenced.
  - Simple two choice discrimination between square (S+) and rectangle (S-)
  - Once this at criterion rectangle is varied in two ways as part of blocks in which original discrimination is intermixed
    - 1) in terms of its width
    - 2) in terms of the size of both square and rectangle



Eacott et al results experiment 1

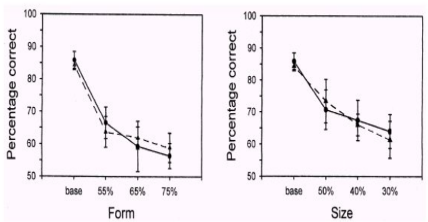


Fig. 2. The figure shows the mean percentage correct in the base discrimination and each transformation in stimulus form (left) and size (right) for the perirhinal group (dashes and triangles) and unoperated group (solid lines and circles) in experiment 1.

Procedure experiment 3

- 19 animals, all that started experiment 1 and survived
- One day of the base discrimination, then did titrating version of the task.
  - Once 3 correct responses made the width of S – became 3% larger(compensated by decrease in area)
  - One incorrect response made width smaller by 1%
  - Difficulty therefore titrated based on individual performance

Eacott et al results experiment 3

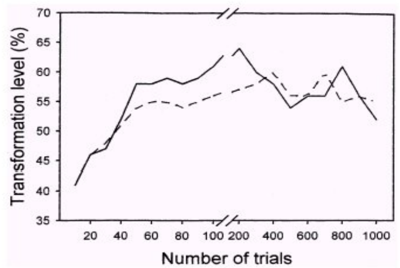
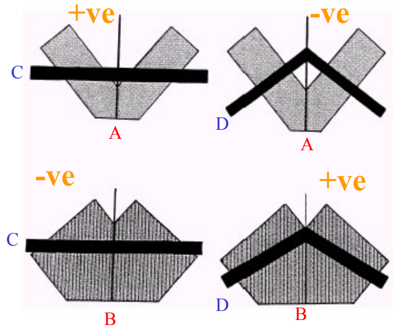


Fig. 4. The figure shows the mean percentage transformation of the S− reached by the perirhinal group (dashes) and sham operated group (solid line) over 1000 trials in experiment 3. Note that increasing levels of transformation make the discrimination increasingly difficult.

Procedure experiment 4

- Three concurrent discriminations
  - First two were four normal computer generated ‘objects’
  - Last pair a biconditional problem with 4 compound objects. There were two shape elements and two line elements. The four compound elements comprised two rewarded and two non-rewarded.

Stimuli experiment 4



•Three concurrent discriminations

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Eacott et al results experiment 4

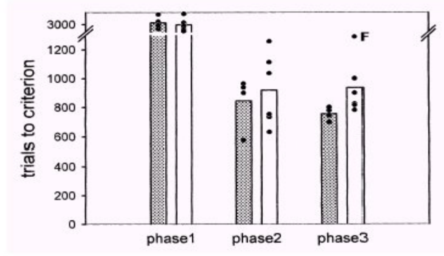


Fig. 6. The figure shows the mean number of trials to criterion for the perirhinal (open bars) and sham operated (shaded bars) in the three phases of learning the compound discrimination in experiment 4. The circles represent the scores of individual animals. An *F* beside a score indicates that this animal failed to reach criterion.

Eacott et al conclusions

- Perirhinal lesions do not cause a general impairment in visual discrimination learning, even when fine discrimination is needed
- Rather, perirhinal cortex is necessary for discriminating between objects that have an overlap of features.

Bussey et al’s computational model

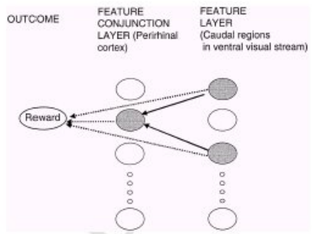


FIG. 3. Diagram of the connectionist network of the companion paper, Bussey & Saksida (2002). The network consists of two layers of units, the feature layer and the feature conjunction layer, as well as an outcome node representing a consequent event (e.g. reward). The feature layer is connected to the feature conjunction layer via 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. These weights 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 photographic stimulus (or ‘feature’). The feature conjunction layer represents perirhinal cortex and the feature layer represents more caudal regions of the ventral visual stream. See the companion paper, Bussey & Saksida (2002), for the computational details of the model.

Bussey et al procedure

- Eight monkeys, four with perirhinal lesions
- All extensively pre-trained in other visual discrimination tasks
- 3 levels of feature ambiguity in sets of stimuli
- Only four pairs of stimuli in a set, each set used for two days
- Four different stimulus sets at each level
- Each animal therefore gives 24 days data
  - C.f. Buckley & Gaffan, see later

Levels of 'feature overlap'

- Minimum

feature

object

–+ve A B A B C D C D

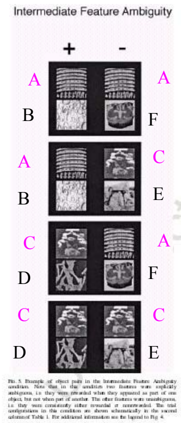
– -ve E F G H E F G H

Each feature was either rewarded or unrewarded

Levels of 'feature overlap'

- Intermediate
  - +ve A B A B C D C D
  - -ve A F C E A F C E

Two of the features were ambiguous, rewarded in one object but not in another

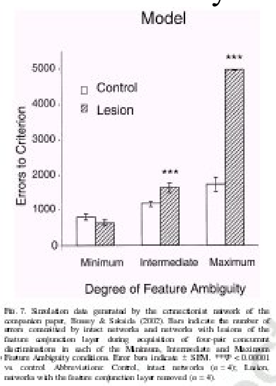


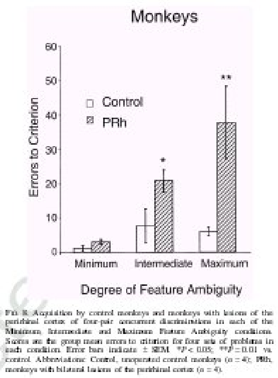
Levels of 'feature overlap'

- Maximum
  - +ve A B A B C D C D
  - -ve A D C B A D C B

All of the features are ambiguous, rewarded as part of one object but not as part of another

Bussey et al results





•Conclusions - In both monkeys and model, a perirhinal lesion or a lesion in the 'feature conjunction area' produced a deficit in configural learning.

•This suggests that the perirhinal cortex contains complex conjunctive representations of object features.

Bussey et al – convincing?

- Stimuli are problematic. The two clipart pictures do not make up an object in any meaningful way.
- The minimum condition is trivially easy for experienced monkeys, with or without perirhinal damage.
- The criterion is very low. 80% is unusual for monkeys, 90% far more usual. For criterion to be only 8 correct out of 10 consecutive trials with a pseudorandom sequence it is likely that criterion could have been reached by chance. In the intermediate condition criterion could have been achieved using the non-ambiguous stimuli on many occasions.

Selective perceptual impairments after perirhinal cortex ablation

Buckley, Booth, Rolls and Gaffan (2001)
Selective perceptual impairments after perirhinal cortex ablation. Journal of Neuroscience.

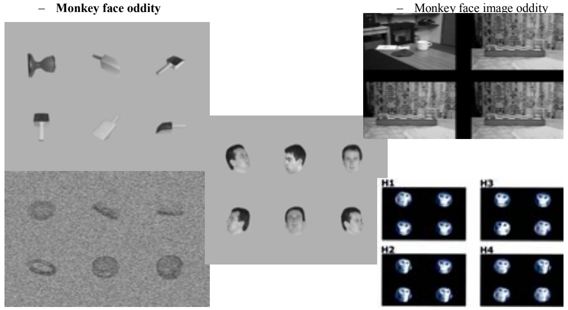
Why did they use an oddity task?

•Previous studies have concentrated on **memory** performance after rhinal/perirhinal lesions

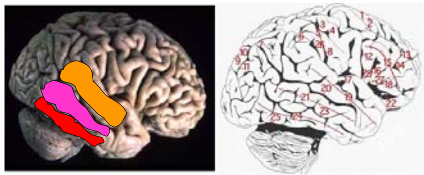
•Exception is Eacott et al (1994) tasks A & D which used simultaneous match to sample

•Debate over division of TE / rhinal into memory / perception (Squire vs everyone else)

- **Impaired**
  - **Object oddity reacquisition**
  - **New post-op object oddity**
  - **Degraded object oddity**
  - **Human face oddity**
  - **Scene oddity**
  - **Monkey face oddity**
- Unimpaired
  - New post-op image oddity
  - Colour oddity
  - Shape oddity
  - Human face image oddity
  - Size oddity
  - Monkey face image oddity

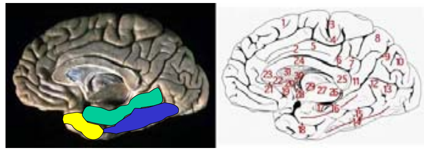


Lateral surface of right cerebral hemisphere



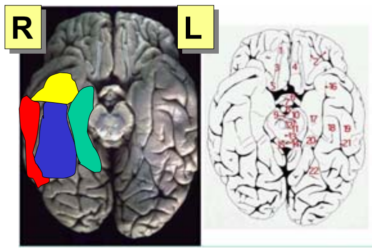
- Superior temporal gyrus
- Middle temporal gyrus
- Inferior temporal gyrus

Medial surface of right cerebral hemisphere



- Parahippocampal gyrus
- Fusiform gyrus
- Rhinal gyrus

Inferior surface of the brain (after transection of midbrain and removal of cerebellum)



- Fusiform gyrus
- Rhinal gyrus
- Inferior temporal gyrus
- Parahippocampal gyrus

Kanwisher et al. view

- Processes involved in face recognition may be qualitatively different from those involved in the recognition of other kinds of objects.
  - Behavioural evidence: Disruption of recognition performance that results when a face is presented upside-down is considerably greater than the analogous inversion cost for the recognition of objects (Yin, 1969).
  - Neuropsychological double dissociation between face and object recognition (Newcombe et al, 1994)

Imaging studies

- A focal region in the fusiform gyrus (Fusiform face area or FFA) responds selectively to faces, compared to a great variety of other stimuli (Kanwisher et al, 1997)
- Cat and cartoon faces activate FFA as much as human faces (Kanwisher et al., 1997).
- Kanwisher (1998): FFA may be involved in **face detection** but not in **face recognition.** FFA may simply be triggered by the presence of a face, but may not itself carry out the processes involved in discriminating between faces.

Gauthier et al. view

- The putative “face area” may be the result of our extensive experience with faces.
- Expert subjects recognising non-face objects showed similar effects to those obtained with faces (Gauthier et al., 1997).
- Therefore, the activation obtained in the FFA may likewise depend on a subject’s expertise with a given object category.
- Activation of the middle fusiform “face area” increases with expertise in recognizing novel objects. (Gauthier et al., 1999)

Gauthier et al 1999

- 5 subjects were trained with novel objects called greebles until they reached expertise (about 7 hours over at least 4 days).
- Expertise criterion: Categorisation of the greebles at the individual level as well as that at the family level.
- 1 scan before exposure to the greebles. 3 scans at different times during training. 2 scans after they reached criterion.

Task

- Upright and upside-down faces.
- Upright and upside-down greebles.

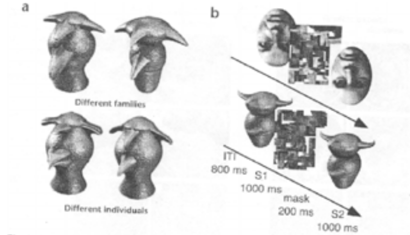


Fig. 1. Greebles and sample trials from the sequential-matching task. (a) Two greebles from different "families", as defined by the shape of the large central part, as well as two individual greebles from the same family, differing only in the shape of the smaller parts. (b) Design of sample trials in the sequential-matching task used in the fMRI experiments. Stimuli were presented for 1 s, separated by a brief (200 ms) pattern mask to prevent matching from retinal

Hypothesis

- Expertise training with upright greebles would lead to an increase in activation for upright minus activation for inverted greebles in the face-specific but not comparable change for faces.

Interpretation

•Unlike Kanwisher’s results, Gauthier’s results suggest that the FFA is implicated in recognition at the individual level because training at this level led to an expertise effect.

•Subjects shift from feature-based to more configural processing as they become experts.

•The face-selective area in the middle fusiform gyrus may be most appropriately described as a general substrate for subordinate-level discrimination that can be fine-tuned by experience with any object category.

Discussion

- Unlike Kanwisher, the results in this study suggest that the FFA is implicated in recognition at the individual level because training at this level led to an expertise effect.
- Subjects shift from featured-based to more configural processing as they become experts.
- The face-selective area in the middle fusiform gyrus may be most appropriately described as a general substrate for subordinate-level discrimination that can be fine-tuned by experience with any object category.

- **General reference**
- Gazzaniga MS (1995) The cognitive neurosciences. MIT Press
- Chapters: 53, 30 and pp751-753.
- Gazzaniga MS (2000) The new cognitive neurosciences MIT press
- Chapters : 27, 51, 52, 53, 57
- **Research papers**
- Murray & Mishkin (1998) Journal of Neuroscience, 18, 6568-6582
- Gauthier et al (1999) Nature Neuroscience, 2, 568-573.
- Kanwisher et al (1997) Journal of Neuroscience, 17, 4302-4311.
- Zola et al (2000) - Impaired memory in monkeys after damage limited to
- the hippocampal region. The journal of Neuroscience, Jan 1 2000, 20(1):
- 451-463.
- Bussey et al (2002) Eur J Neuroscience 15, 365-374.
- Eacott et al (2001) Behavioral Brain Research 124, 55-70.
- Hampton & Murray (2002) Behavioral Neuroscience, 116, 363-377.
- Buckley et al (2001) J. neurosci, 24, 9824-9836.
- Murray & Bussey (1999) Trends in Cognitive Science, 3, 142-150
- Levy & Goldman-Rakic (1999) Journal of Neuroscience, 19:5149-5158
- Gaffan, Parker & Easton (2001) *Neuropsychologia,* **39**, 51-70.
- Parker, Wilding & Akerman (1998) Journal of Cognitive Neuroscience, 10, 691-703.
- Parker & Gaffan (1998) European Journal of Neuroscience, 10, 3044-3057
- And for the very keen – this paper is being heavily cited but the whole thing is rather long
- Aggleton & Brown (1999) ; Episodic memory, amnesia and the hippocampal - anterior thalamic axis and all commentaries, *Behavioral & Brain Sciences*, 22, 425-489.