

Research report

Do discrimination tasks discourage multi-dimensional stimulus processing? Evidence from a cross-modal object discrimination in rats

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Abstract

Neurobiologists are becoming increasingly interested in how complex cognitive representations are formed by the integration of sensory stimuli. To this end, discrimination tasks are frequently used to assess perceptual and cognitive processes in animals, because they are easy to administer and score, and the ability of an animal to make a particular discrimination establishes beyond doubt that the necessary perceptual/cognitive processes are present. It does not, however, follow that *absence* of discrimination means the animal cannot make a particular perceptual judgement; it may simply mean that the animal did not manage to discover the relevant discriminative stimulus when trying to learn the task. Here, it is shown that rats did not learn a cross-modal object discrimination (requiring association of each object's visual appearance with its odour) when trained on the complete task from the beginning. However, they could eventually make the discrimination when trained on the component parts step by step, showing that they were able to do the necessary cross-modal integration in the right circumstances. This finding adds to growing evidence that discrimination tasks tend to encourage feature-based discrimination, perhaps by engaging automatic, habit-based brain systems. Thus, they may not be the best way to assess the formation of multi-dimensional stimulus representations of the kind needed in more complex cognitive processes such as declarative memory. Instead, more natural tasks such as spontaneous exploration may be preferable.

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1. Introduction

The last few years have seen a great increase in interest in how an organism's knowledge about the world is encoded by neurons in the form of complex, internal representations. A challenge for neurobiologists lies in finding ways to determine what an animals "knows," as a necessary prerequisite for finding out how such knowledge is encoded. To this end, discrimination tasks, where an animal has to choose between a rewarded and an unrewarded stimulus, have historically been a favoured method of assessing perceptual and cognitive capabilities, by the argument that if an animal can make a particular discrimination then it must possess the necessary perceptual/cognitive processing. For example, Pavlov used a failure of visual discrimination to conclude that the occipital lobes are necessary for vision [11].

Discrimination tasks are easy to administer and score, and provide ready data in the form of easily quantified learning

curves. In cases where the difference rests upon a single, uni-modal feature, discrimination tasks have thus provided a useful means of assessing such perceptual capabilities as size, luminance and orientation perception. Recently, however, neurobiologists have been turning their attention to more complex, "cognitive" kinds of representation, and in this case the picture in discrimination tasks becomes less straightforward. When the stimuli are complex, the animals may need to process more than one kind of information (and perhaps more than one sensory modality) simultaneously, using what is known as "configural processing" [12] in order to make a correct judgement. If animals cannot learn discriminations between complex stimuli, it can no longer simply be assumed that they are unable to perceive the differences between the stimuli: it may be simply that the animals failed to discover which were the stimuli upon which they should base their discrimination. It is not, in fact, known how animals solve such configural problems [8], or even *if* they necessarily always solve them.

As an illustration of this difficulty, we have recently shown that an apparent shape discrimination task, requiring simultaneous processing of both height and width (i.e., aspect ratio) of

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visual figures, turned out to be solved by rats wherever possible on the basis of uni-modal features such as luminance in a restricted part of the figure [9]. Somewhat surprisingly, in our task the animals preferred to solve the problem by means of two simultaneous featural discriminations than by one single, complex (configural) one. Although they eventually mastered the configural task, this required thousands of trials, and it is questionable whether such a task could be said to probe natural neurobiological processing capabilities.

Our shape experiment suggested that rats were disinclined, or alternatively unable, to process the discriminative stimuli configurally. However, it could be that the difficulty the animals experienced in that task was a specific difficulty with the visual stimuli used, inasmuch as the stimulus dimensions (height versus width) were very closely related. Accordingly, the present study used stimuli where the dimensions to be combined were very different, one being visual and one being olfactory. Rats were given a configural object-discrimination task in which the animals had to combine information about the “colour” (black, white or grey: more accurately termed luminance) of the objects with that about the odour (lemon, orange or apple) in order to make the discrimination. Arguably, this should be an easy task because in the real world, objects have multimodal attributes and are processed, probably even by rats, through more than one sensory modality [13]. Indeed, the original motivation of this experiment was to find a task requiring multi-modal object processing, as a first step towards elucidating the site of such integration. In fact, it was found that rats had difficulty making a multi-modal discrimination when this was presented as a straightforward biconditional problem (such as “choose the black–lemon object or the white–orange one but not the white–apple or black–orange”). Control tests explored the ability of animals to learn combinations of featural discriminations (black versus white, apple versus lemon, etc.) using the same object set.

Experiment 1 found that the rats were able to learn the featural problems as pairs of concurrent discriminations in the two modalities (olfaction and vision) easily and with no differences between the rate of learning of the olfactory and visual problems. However, they were unable to learn the configural discrimination, suggesting that although they could discriminate the objects via either olfaction *or* vision, they could not discriminate using both together. In the second experiment, a new group of rats was trained on the featural subcomponents of a configural discrimination before being required to combine these subcomponents to perform the full configural (biconditional) discrimination. They were able to eventually do this, indicating that they were indeed able to make the necessary cross-modal association. However, it seems likely, on the basis of the results from Experiment 1, that the animals solved the task as a set of separate conditional featural discriminations rather than as a true configural one. When these results from integration across sensory modalities are considered together with those from the shape discrimination study [9], which required integration within a single sensory modality, the conclusion seems to be that rats are reluctant to base their discriminations on such integrated representations. It is suggested that simultaneous discrimination tasks encourage animals

to make featural rather than configural comparisons between stimuli, and are thus not the best choice of task for assessing higher order perceptual or cognitive processes such as object processing.

2. Experiment 1

2.1. Materials and methods

2.1.1. Subjects

All experimenting took place under license from the UK Home Office under the Animals (Scientific procedures) Act, 1986. Male Lister hooded rats weighing 250–350 g ($n = 16$) were food deprived to 90% of their free-feeding weight. Behavioural testing was conducted during the light phase of the day. The rats were assigned to groups that are described more fully in the sections on experimental procedure, below. The groups were:

- Config ($n = 4$),
- Elem1 ($n = 4$),
- Elem2 (same) ($n = 4$),
- Elem2 (diff) ($n = 4$).

2.1.2. Apparatus

The experiments took place in UCL’s Central Biological Services facility. The apparatus was situated in a sparsely furnished room containing the rack of home cages, a chair and a sink, and consisted of a wooden Y-maze situated on a raised circular platform 1 m from the floor. The arms of the maze were always in the same position in the room and the same arm was always used as the start arm. Small steel plates were fixed to the other two arms at 20 cm from the central choice point, and served to anchor the magnetic objects.

2.1.3. Objects

The objects consisted of black, white or grey cardboard cubes, 6 cm square, five faces of which each possessed 25 small perforations to facilitate odour dispersal. Set into the topmost face of each cube was a steel food well 1.5 cm in diameter and 2 cm deep, covered by a lid possessing a rubber handle. The food reward consisted of a twig of cereal (Kellogg’s All-Bran). The remaining face of the cube was surfaced with magnetic vinyl tape to allow rapid attachment to and removal from the steel plate. At the start of each training session the cubes were filled with cotton fabric that had been scented with six drops of lemon, apple or orange odour essence (Amphora Aromatics, Bristol, UK). Each cube always contained the same odour and four replicate sets were used during training so as to discourage the rats from learning to choose on the basis of unique uncontrolled cues. The replicate cue sets, labelled A, B, C and D, were varied each day as follows (Discrimination 1/Discrimination 2): A/B, B/A, A/C, C/A, B/C, C/B, A/D, D/A. A new cue set was therefore introduced on days 4 and 8 for Discrimination 1 trials and days 3 and 7 for Discrimination 2 trials. When the same stimulus combination occurred in both types of trial, these were drawn from different cue sets to prevent these rats from gaining an added advantage by increased exposure to individual objects during one training session.

2.1.4. Pretraining

Pretraining took place over five days and its purpose was to familiarise the animals with the maze and the procedural aspects of the task. The animals learned to retrieve food from a steel well set into a single junk object (wax tomato), positioned in the same location on the maze arms as the subsequent training objects, and the left–right location of which was varied randomly. On the last pretraining day, the lid of the food well was introduced and gradually moved further over the mouth of the well, until the rats were comfortable with removing it to obtain the reward.

2.2. Experimental procedure

This experiment used concurrent simultaneous object discriminations to compare the learning of uni-modal (or “elemental”) discriminations with the

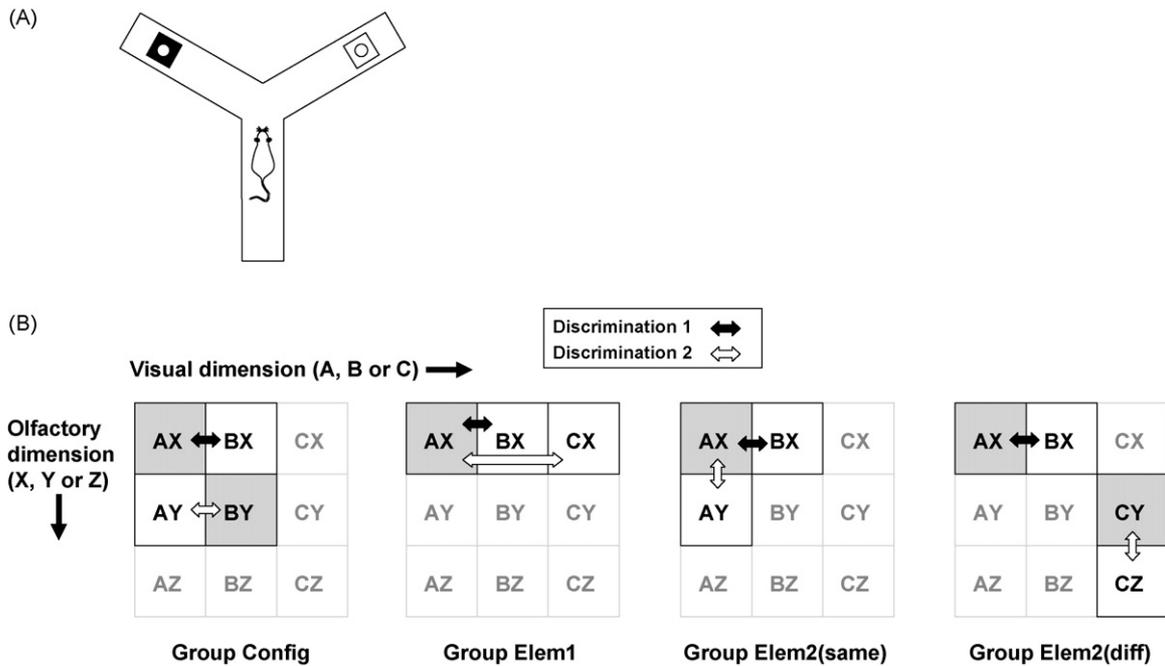


Fig. 1. (A) Diagram of the Y-maze showing the position of the objects. (B) Problems learned by the four groups in Experiment 1. The logic of the problems is shown graphically by expressing the possible stimulus combinations as items in a Latin square, with arrows depicting the pairs of discriminations being made in each condition. Each object (represented by one of the items) consisted of one of three possible visual elements (black, white and grey, marked A–C) paired with one of three possible odours (marked X–Z). The presented stimulus combinations are outlined in black and of these, the rewarded stimulus combinations for this example are shaded (although because of counterbalancing, half the rats were rewarded the other way around from what is shown here). Group Config learned two problems with two positive objects, each element of which (A vs. B and X vs. Y) was rewarded and non-rewarded equally, but the unique combination of which was rewarded on every trial in which it was presented. The remaining (Elem) groups were presented with various types of elemental discrimination. Group Elem1 learned two discriminations in one modality, either vision (as is shown) or olfaction, the positive stimulus element being the same on every trial. Group Elem2 (same) learned two discriminations in two modalities but the rewarded stimulus combination was the same in both types of trial. Group Elem2 (diff) learned two discriminations in two modalities, the rewarded stimulus combinations being different for the two types of trial.

learning of a stimulus compound (the “configural” discrimination). The objects were the cardboard cubes described above and for any trial, the relevant stimulus dimension for discrimination was either the visual appearance of the cubes (black, white or grey), their odour (lemon, apple or orange) or a combination. On any given trial the two objects used differed only in one sensory modality, while the other was kept constant. The principal aim of the experiment was to determine whether rats could solve an olfactory-visual conditional discrimination, in which an elemental stimulus in one modality was needed to determine the correct stimulus in the other modality. Success in this configural task would indicate that rats could form cross-modal, configural object representations.

Performance of the group presented with the conditional discrimination was compared with that of three groups learning various combinations of elemental discrimination. The logic of the experiment is shown in Fig. 1.

The design of this task was as follows: each object consisted of two possible visual elements (black, white or grey) paired with one of three possible odours (orange lemon or apple). Group Config learned two problems with two positive objects, each element of which (one of the colours and one of the odours) was rewarded and non-rewarded equally, but the unique combination of which was rewarded on every trial in which it was presented. The remaining (Elem) groups were presented with various types of elemental discrimination. Group Elem1 learned two discriminations in one modality, either vision or olfaction, the positive stimulus element being the same on every trial. Group Elem2 (same) learned two discriminations in two modalities but the rewarded stimulus combination was also the same in both types of trial. Group Elem2 (diff) learned two discriminations in two modalities, the rewarded stimulus combinations being different for the two types of trial.

The rationale for the above design is as follows: because the conditional task given to the Config rats consisted essentially of two simultaneous discriminations in two different modalities, control rats were given tasks that tested their performance on simple discriminations either in one modality (to estab-

lish baseline performance in this apparatus) or in two (to ensure that rats could learn simultaneous discriminations in two modalities). Each elemental group was therefore given two simultaneous discriminations, the differences between the groups being the number of stimulus elements the rats needed to learn about, and the number of dimensions (olfaction, vision or both). The two elemental discriminations differed from those given to the group Config rats in that on any one of the problems, only the visual appearance of the objects or their odour was relevant (but never both). Thus, these rats could, in principle, learn to solve each task on the basis of only a uni-modal discrimination.

The four groups comprised three that were presented with elemental discriminations, designated Elem1, Elem2 (diff) and Elem2 (same), and a fourth group presented with a configural discrimination (group Config). The problems given to the four groups are as follows (the numbers refer to the number of relevant stimulus dimensions; see Fig. 1 for a summary).

2.2.1. Group Elem1

Rats in this group were presented with two simple discriminations in either vision (two rats) or olfaction (two rats), where the stimuli in the non-discriminated modality were identical (and hence irrelevant). The same positive object was presented in both Discrimination 1 and Discrimination 2 trials but the negative objects differed. An example of the problem given to an Elem1 rat is:

	Discrimination 1	Discrimination 2
Form:	AX+ BX–	AX+ CX–
Example:	(black–lemon)+ (white–lemon)–	(black–lemon)+ (grey–lemon)–

This problem could, in principle, be solved by learning a single rule: for example, “always choose black”.

2.2.2. Group Elem2 (diff)

These rats were presented with two discriminations in two stimulus modalities. The positive objects in the two discriminations differed in both odour and colour (hence “diff”). One discrimination was in the olfactory modality (where the visual appearance of the objects was identical and irrelevant) and the other was in the visual modality (where the odour of the objects was likewise identical and irrelevant). For example:

	Discrimination 1	Discrimination 2
<i>Form:</i>	AX+ BX–	CY+ CZ–
<i>Example:</i>	(black–lemon)+ (white–lemon)–	(grey–orange)+ (grey–apple)–

These problems could be solved by learning two simultaneous rules: “always choose black” (if it is available) and “always choose orange” (if available).

2.2.3. Group Elem2 (same)

Subjects in this group were also given two discriminations in two different sensory modalities. However, although the rats were presented with two discriminations, the positive cue was the same in both discriminations. The irrelevant stimulus in one trial type became the positive stimulus in the other, for example:

	Discrimination 1	Discrimination 2
<i>Form:</i>	AX+ AY–	AX+ BX–
<i>Example:</i>	(black–lemon)+ (white–lemon)–	(black–lemon)+ (black–apple)–

Although these rats were presented with two discriminations in different modalities, they could, in principle, be solved by learning the single rule “always choose the black–lemon cube,” which requires the formation of a cross-modal association. Alternatively, the rats could learn two rules: for example, “always avoid white” and “always avoid apple”. The purpose of this group was to determine whether these rats gained any advantage over the Elem2 (diff) rats by virtue of the fact that the same “object” (i.e., stimulus combination) was positive on both sets of trials.

2.2.4. Group Config

This group was presented with a configural task, in the form of a conditional discrimination in one modality whose conditions were set by a stimulus in the other. Two rats were given a conditional visual task, for example:

	Discrimination 1	Discrimination 2
<i>Form:</i>	AX+ BX–	BY+ AY–
<i>Example:</i>	(black–orange)+ (white–orange)–	(white–apple)+ (black–apple)–

The other two rats were given a conditional olfactory task, such as:

	Discrimination 1	Discrimination 2
<i>Form:</i>	AX+ AY–	BY+ BX–
<i>Example:</i>	(white–apple)+ (white–orange)–	(black–orange)+ (black–apple)–

This task could only be solved by a rule referring to both stimulus modalities at once, and would thus require cross-modal object processing. Although such processing has been established for transient stimuli such as lights and tones, it has not been well established in the domain of object-processing.

The experiment was conducted in two replications containing one to three rats from each group. Training began the day after the final pretraining day. On this day, but on no others, the rats were allowed to correct their mistakes. On each trial a rat placed at the outside end of the start arm ran to the centre of the maze, chose one of the two cued arms, approached and partially mounted the cue, and grasped the handle of the lid of the food well in its forepaws or teeth and displaced it. If the choice was correct and the food well contained reward, the

rat was allowed to consume it before being removed from the maze and returned to its home cage. Removal of the lid was always counted as a choice. Rats were permitted to climb over the cue to explore the rest of the arm, provided they did not remove the food lid. On the first two days, rats were removed from the maze if they failed to make a choice after 10 min.

The objects were counterbalanced, with the exception that orange never had to be discriminated from lemon. Rats were run sequentially, in a different order each day, and so the inter-trial interval ranged from 40 min (at the beginning of training) to 10 min (when they were proficient). The rewarded arm was varied from trial to trial and from rat to rat on each trial, with no runs of more than three trials to the same side for a given rat. Because each trial involved a stimulus element common to both objects that was irrelevant for that trial type but possibly relevant for the other, the two types of trial were intermixed to prevent the rats from learning to ignore the irrelevant cue. The 10 Discrimination 1 and 10 Discrimination 2 trials were therefore interspersed unpredictably so that no more than three trials of the same type occurred in a row, making 20 trials in total for each rat on each day. Training proceeded for eight days, except for two rats from group Config in which training was continued on to 20 days.

2.3. Results

The results of Experiment 1 are shown in Fig. 2. All groups appeared to learn at a similar rate except for group Config in which none of the rats improved above chance performance, even for the two rats that underwent 20 days of training (400 trials). This was verified by two-way ANOVA (groups \times two-day blocks) which showed a main effect of group ($F(3,12) = 21.9$, $p < 0.001$), a main effect of block ($F(3,12) = 22.3$, $p < 0.001$) and a significant interaction ($F(3,12) = 5.4$, $p < 0.001$). Pairwise comparisons (t -tests) revealed a significant improvement between blocks 1 and 4 for groups Elem1 (mean errors declined from 0.45 to 0.11 ($t(3) = 3.52$, $p < 0.05$)), Elem2 (same) (mean errors declined from 0.46 to 0.13 ($t(3) = 15.51$, $p < 0.001$)) and Elem2 (diff) (mean errors declined from 0.41 to 0.11 ($t(3) = 3.07$, $p < 0.05$)) but a slight but significant *worsening* for group Config (mean errors increased from 0.48 to 0.58 ($t(3) = -2.94$, $p < 0.05$)). Training continued out to 20 days for two of the Config rats, with no improvement in performance (Fig. 2).

Although the group sizes (and hence statistical power) were low, it seems that group Elem1, in which one positive element was paired against either of two negative elements, learned no faster than that Elem2 (diff) that were required to learn two completely separate feature discriminations ($F(1,7) = 0.1$, NS). Similarly, groups Elem2 (same) and Elem2 (diff) did not differ in their rate of learning ($F(1,7) = 3.90$, NS). Comparison of the visual and olfactory subcomponents of the tasks in rats given elemental discriminations showed that both types of task were learned at a similar rate ($F(1,7) = 0.1$, NS; Fig. 2B). Thus, in general it seems that the elemental versions of the task were learned easily but the configural version, in which information from one modality was needed to inform the comparison in the other, was not learned.

2.4. Discussion of Experiment 1

In order to learn which cue to choose, the rats needed information about both objects so that they knew which stimulus dimension was relevant to the task: for example, rats presented with the visual discrimination needed to learn that when the

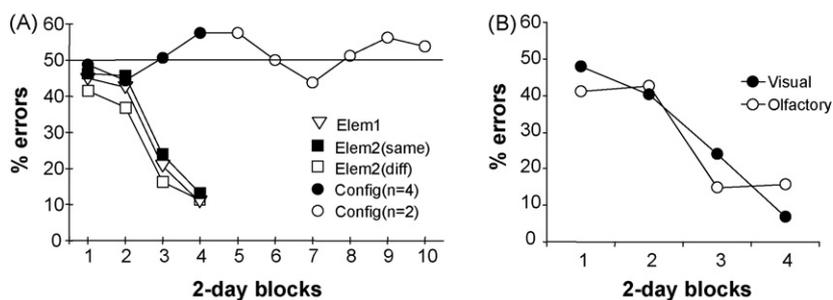


Fig. 2. (A) Learning of the elemental (groups Elem1, Elem2 (same) and Elem2 (diff)) and the configural (group Config) discriminations in Experiment 1. Each data point represents the mean of two days' training (40 trials). The dotted line represents chance performance. All three of the groups learning elemental discriminations in either visual or olfactory modalities, or both, improved their performance significantly over the training period. By contrast, the group learning a configural discrimination failed to improve above chance, even when trained for 20 days ($n=2$). (B) Detailed comparison of learning rate between the olfactory and visual discriminations for rats learning elemental discriminations. Both types of task were learned at a similar rate.

objects were compared, they differed in their visual appearance, and that one of the visual stimuli was rewarded and the other was not. It might have been expected that the Elem2 (diff) rats would take longer to learn the two discriminations than the Elem1 rats, because they were faced with a seemingly more difficult task: they needed to learn that two stimulus dimensions were relevant to problems on this apparatus, without knowing which was to be relevant on any given trial. They also were presented with two positive stimuli instead of one. However, these rats apparently learned just as fast as the rats learning a problem in only one modality. This may be because in addition to having more stimuli to learn about, these rats were presented with more retrieval cues for the discriminations. For example, on the olfactory discrimination trials, they could use the colour of the objects as well as their odours to signal which of the two discriminations they were facing, and conversely for the visual trials.

Rats appeared unable to learn the task for which only a configural solution existed (group Config), even after many days of training. This suggests that either these rats were unable to form the necessary cross-modal association, or that they were unable to use such an association to guide their choices. There are several possible reasons why this may have occurred. The first is that rats may not be able to associate stimuli of different sensory modalities when they belong to objects, because of constraints imposed by the object representation machinery. For example, to recognise that two stimuli belong to the same object, a rat may need to be able to localise them both to a common region in space. Perhaps there exists no mechanism for mapping the spatial location of a stimulus in one modality to that of a stimulus in another. Second, perhaps rats *can* form such associations but the salience of the resulting compound is so low that it is unable to guide choices.

A third possibility is that in this particular task, the rats were unable to determine which were the relevant stimuli for discrimination. Rats in the elemental groups were presented with discriminations in either or both sensory modalities, but only one modality was relevant on any given trial. A rat paying selective attention to any one modality would find that reward and stimulus were consistently associated. However, rats in the conditional group needed to pay attention to stimuli in both modalities together in order to see such a consistency. Perhaps it was the

simultaneous attention to both modalities that was deficient, rather than the formation of associations between them.

This possibility was tested in Experiment 2. Four rats were first trained on two simultaneous problems, one visual and one olfactory, before being asked to combine them into a conditional discrimination where stimuli in one modality (visual) set the conditions for the discrimination in the other (olfactory).

3. Experiment 2

3.1. Materials and methods

3.1.1. Subjects

Male Lister hooded rats weighing 250–350 g ($n=4$) were food deprived to 90% of their free-feeding weight. Behavioural testing was conducted during the light phase of the day.

3.2. Apparatus and pretraining

These were the same as for Experiment 1 except that eight replicate object sets were used during training.

3.3. Experimental procedure

Eight trials per day of the discrimination task were run in the same way as for Experiment 1. Training proceeded in three phases, each of which introduced an additional part of the biconditional discrimination (diagrammed logically in Fig. 3).

3.3.1. Phase 1

In phase 1, rats were trained on a concurrent olfactory and visual discrimination (see table below). For the olfactory discrimination, both objects possessed the colour of the cue that was negative in the visual discrimination, as follows:

	Discrimination 1 (visual)	Discrimination 2 (olfactory)
<i>Form:</i>	AZ+ BZ–	BX+ BY–
<i>Example:</i>	(black–orange)+ (white–orange)–	(white–lemon)+ (white–apple)–

3.3.2. Phase 2

In phase 2, an additional olfactory problem was added: the colour in these objects was different from the colour of the objects in the original olfactory discrimination, and the new olfactory discrimination was the reverse of

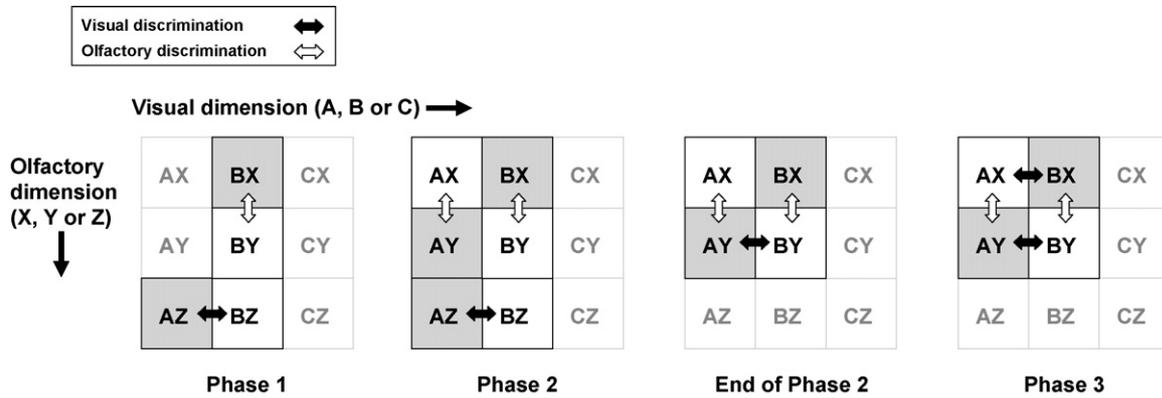


Fig. 3. Problems learned during the three phases of Experiment 2. The presented and rewarded stimulus combinations are shown using Latin squares in the same way as in Fig. 1. Visual trials are shown by solid arrows and olfactory by hollow arrows. In phase 1, rats learned two separate but simultaneous discriminations, one olfactory and one visual. In phase 2, the olfactory discrimination was made conditional upon visual appearance. On the last two days of phase 2 the irrelevant odour of the objects in the visual discrimination was changed so that the visual discrimination now became a subcomponent of the eventual biconditional discrimination. In phase 3, the visual discrimination was now made conditional on the odour of the objects.

that previously learned. In other words, the rats were now presented with a straightforward visual discrimination concurrently with a conditional olfactory discrimination, where the condition was determined by the colour of the objects.

	Discrimination 1 (visual)	Discrimination 2 (olfactory)	Discrimination 3 (olfactory)
<i>Form:</i>	AZ+ BZ– AY ^a + BY–	BX+ BY–	AY+ AX–
<i>Example:</i>	(black–orange)+ (white–orange)– (black–apple) ^a + (white–apple)–	(white–lemon)+ (white–apple)–	(black–apple)+ (black–lemon)–

^a Change of irrelevant odour on last two days of phase 2.

On the last two days of phase 2, the background odour in the visual discrimination was changed to one of the odours in the olfactory discrimination so that the stimulus combination of the negative cue was the same in both cases.

3.3.3. Phase 3

Finally, in phase 3, the visual discrimination was also made conditional: that is, it was reversed conditional upon the odour of the objects (see below). Success in this task requires that the rat learn to associate the visual appearance of the objects with their odour in every trial.

	Discrimination 1 (visual)	Discrimination 2 (olfactory)	Discrimination 3 (olfactory)	Discrimination 4 (visual)
<i>Form:</i>	AY+ BY–	BX+ BY–	AY+ AX–	BX+ AX–
<i>Example:</i>	(black–apple)+ (white–apple)–	(white–lemon) + (white–apple)–	(black–apple)+ (black–lemon)–	(white–lemon)+ (black–lemon)–

3.4. Results

Data were averaged across pairs of days to yield two-day blocks (Fig. 4), and are presented on a phase by phase basis, below.

3.4.1. Phase 1

In this phase, which lasted eight days (four blocks), rats were trained on two concurrent discriminations, one olfactory and one visual. Rats showed significant learning of the task over the four blocks of phase 1 training, as revealed by a significant effect of block ($F(3,9) = 7.16, p < 0.01$).

3.4.2. Phase 2

As expected, introduction of the new olfactory problem, at the start of phase 2, caused a decline in performance from 19% up to 35% errors (paired one-tailed t -test ($t(3) = -4.19, p < 0.05$)). A paired t -test comparing performance on the already-experienced discrimination tasks (1 and 2 combined) with the new discrimination revealed a significant difference ($t(3) = -7.14, p < 0.01$), whereas comparison of performance on the familiar discriminations before and after the introduction of the new problem revealed no change overall ($t(3) = -1.29, NS$). Thus, introducing the new discrimination, while reducing successful performance overall, did not have a deleterious effect on the existing discriminations (see Fig. 5).

Thereafter, performance on the new problem steadily improved, as revealed by a significant effect of block, both for performance collapsed across all three discrimination types ($F(5,18) = 6.47, p < 0.001$; Fig. 4) and for performance on the new problem alone ($F(5,18) = 5.07, p < 0.01$). Improvement on the conditional olfactory subcomponent of the task (that is, the familiar olfactory task together with the new one) was also

significant ($F(5,18) = 7.30, p < 0.001$; Fig. 5). New exemplars of the objects were introduced on days 9 and 10 of this phase (i.e., block 9 overall) and did not affect performance ($t(3) = 0.08, NS$), suggesting that the rats were able to generalise appropriately and had not been responding to characteristics of the individual objects. During the last two days of this phase, the irrelevant odour of the objects during the visual trials was changed to that of the negative cue in the olfactory trials, so that the visual trials became a subcomponent of the eventual biconditional discrimination. As expected, this did not affect performance on the visual discrimination ($t(3) = 0.50, NS$). Thus, it appears by the end of this phase the animals had successfully mastered a conditional olfactory problem (e.g., black–lemon and white–apple

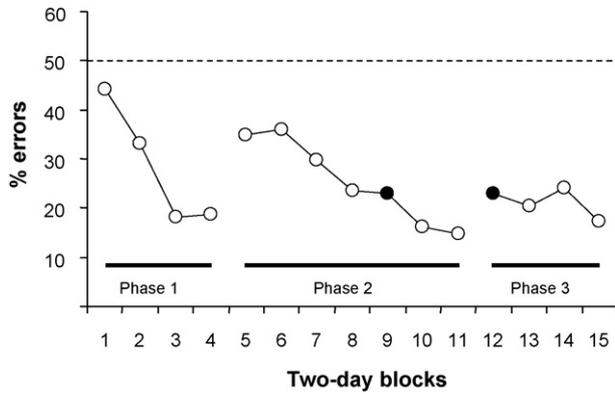


Fig. 4. Total percent errors for the three phases of training in Experiment 2. During phase 1 the rats were trained on a concurrent olfactory and visual problem. In phase 2 the olfactory discrimination was made conditional on the visual appearance of the objects and in phase 3, the visual task was made conditional on the odour of the objects. On both of the two days indicated by each filled symbol, rats were trained with a new exemplars of the objects, to check that they were not responding to unique characteristics of the objects.

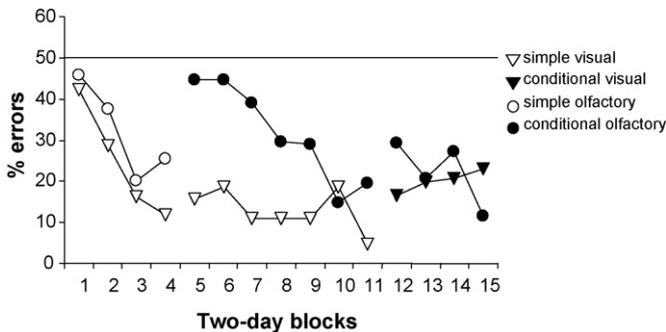


Fig. 5. Comparison of mean performance on the visual and olfactory subcomponents of Experiment 2. When the olfactory task was made conditional, in phase 2, performance on olfactory trials fell to chance but visual performance continued unaffected. When the visual task was made conditional, performance on both types of task worsened slightly but was still considerably better than chance. Thereafter, performance on the visual task continued to deteriorate slightly.

are both rewarded, and white–lemon and black–apple are both unrewarded).

3.4.3. Phase 3

The final step was to add one more problem, which would convert the simple visual discrimination to a conditional visual discrimination and make the whole task truly biconditional. Phase 3 thus consisted of eight days (four blocks) of training where the visual discrimination was conditional on the odour of the objects. New exemplars of all the objects were used for this phase. The positive objects used on the new trial type were the same stimulus type as those already-learned as part of the olfactory discrimination: only the discrimination differed.

Introduction of the final problem, at the start of phase 3, caused a slight decline in performance from 15% to 23% errors, but this was not significant (paired one-tailed t -test ($t(3) = -1.89$, $p = 0.08$)), and it was significantly better than chance ($t(3) = 3.36$, $p < 0.05$).

A paired t -test comparing performance on the already-experienced discrimination tasks (1, 2 and 3 combined) with

the new discrimination revealed no difference ($t(3) = 0.39$, NS), and comparison of performance on the familiar discriminations before and after the introduction of the new problem revealed no change overall ($t(3) = -2.70$, NS). Thus, introducing the new discrimination caused only a very slight decrement in performance of the already-learned discriminations (see Fig. 5). That performance began at better than chance on the new problem, which used familiar objects but simply paired in a novel combination, suggests that the animals were making their choices based on the objects themselves rather than on a comparison between them.

Thereafter, performance on the entire suite of problems remained significantly better than chance on all four blocks (all p 's < 0.001) and also showed slight improvement across the blocks ($F(3,9) = 7.08$, $p < 0.01$). When the familiar discriminations were compared with the new discrimination across the four final blocks there was no effect of discrimination type ($F(1,3) = 1.99$, NS), no effect of block ($F(3,9) = 0.28$, NS), and no interaction ($F(3,9) = 1.76$, NS). Thus, addition of the new problem did not interfere with performance of the old problems. However when the discriminations were divided into olfactory versus visual types, it emerged that while the olfactory discriminations improved (as would be expected, as the rats consolidated the final problem), the visual discriminations showed deterioration, revealed as an olfactory \times visual \times blocks interaction ($F(3,9) = 6.76$, $p < 0.05$). The deterioration of the visual problems explains why performance did not improve more than it did over the last few blocks. Because it occurred despite the fact that the visual problems did not change, it suggests a degree of interference between the new problem and the old. This is despite the fact that the new problem used familiar stimuli possessing the same valence as they did in the other problems. The implications of this interference are discussed below.

4. General discussion

This study used an object-discrimination task to explore cross-modal object processing in rats. It was found that rats easily learned concurrent object discriminations where for each discrimination, the attributes of the objects differed in only one of the two relevant sensory modalities (olfaction or vision: e.g., black versus white or lemon versus apple). However, they failed to learn the discrimination when the objects differed only in the unique pairing of the attributes (e.g. black–lemon versus white–lemon *or* white–vanilla): that is, they did not use a cross-modal representation of the objects to tell them apart. Experiment 2 showed that the rats could learn to discriminate based on such pairing if trained on the subcomponents step by step, showing that they had the capacity to make the necessary cross-modal associations, but simply had not used this capacity in Experiment 1. This finding is similar to the results of a previous experiment where the stimuli to be combined were in the same sensory modality [9]. It is concluded that rats try to solve simultaneous discriminations using featural rather than configural differences between stimuli. This finding has implications both for understanding neurobiological representational

processes, and for the practical design of experiments involving complex stimulus processing.

4.1. Why was the configural task so difficult?

There are a number of possible reasons why the discrimination based on combining colour and odour was so hard for the animals. It was necessary to elicit discrimination in order to show that a rat knew about each subcomponent of the stimulus compounds, to demonstrate that they had associated one element with another. Learning about the relevant stimulus dimensions must require a degree of selective attention to these dimensions, and learning about two relevant stimulus dimensions simultaneously (as in the configural task in Experiment 1) may be difficult for rats, especially if on any given trial the objects differ only in one dimension. However, discriminations such as this must occur rarely, if ever, in the natural world. Rats might habitually form multi-modal object representations but have had difficulty in knowing what aspect of these representations was relevant to the task in hand.

It was also necessary, in probe trials, to elicit generalisation from one set of objects to another, identical set, in order to show that it was (for example) blackness and lemonness that the rat knew about, and not some acquired characteristic of the individual cubes. Generalisation across a class of similar objects – probably also an unnatural situation in the wild – may also not be easy for rats to learn, perhaps because they are able to detect olfactory cues that are imperceptible to a human observer, and may normally rely on these to support their discrimination [2]. It may be that the various cubes used as cues in the present experiment appeared very different to the rats, who had to learn to disregard their individual characteristics and attend only to the aspects of their odour and appearance that were shared. Arguing against this is the fact that performance on the simple discriminations did not deteriorate when the objects were replaced with replicas.

A more likely possibility is that the neural systems mediating discrimination normally rely on simple, rather than complex stimuli, and thus do not recruit multi-modal object-processing machinery in tasks such as this. Discrimination tasks seem to engage a kind of memory that is often described as “procedural,” in which the resulting behaviours often look somewhat automatic, and probably rely on the striatally-based “habit” system [3]. By contrast, declarative memory is thought to involve medial temporal lobe structures [14], and it is increasingly coming to be recognised that much of the contribution from these structures to memory derives from their role in formation of complex perceptual representations [10]. In particular, perirhinal cortex has been implicated in the formation of complex, cross-modal object representations [13]. Thus, a plausible explanation for the failure seen here of rats to naturally acquire a configural object discrimination is that the perirhinal cortex (part of the declarative memory system) is not readily recruited in the solving of a simultaneous discrimination (which is, perhaps, normally routed to a feature-based striatal network). One way of addressing this question might be to look at decision times in the two kinds of task – something we did not record in the present experiment.

The present results are comparable with those of another study looking at how rats combine objects with odour in a paired associate task [6]. In that study, rats that had to make compound discriminations – the paired associates – by combining object with odour, object with place or odour with place took around 360 trials to asymptote, which was considerably longer than the 50 trials to criterion of the simple discriminations (object, odour or place). In the present study, rats reached asymptote in the configural task after 240 trials (see Fig. 4), which contrasts with only 60–80 trials for the simple (elemental) discriminations. The point is reinforced that rats seem to make elemental discriminations (relatively) readily but compound discriminations with much more difficulty.

The conclusion is that while rats can in principle learn (albeit with difficulty) to perform a biconditional object discrimination, the nature of the task – a simultaneous discrimination – biased the animals towards trying to find a uni-modal solution to the problem. This conclusion is in accordance with results from a previous study in which the stimuli to be combined belonged to the same sensory modality [9], and suggests that the reluctance of rats to make complex, or “configural,” discriminations is a general one. It seems unlikely that rats do not have multi-modal representations of such commonplace items as shapes and objects: rather, it seems that they do not tend to use such representations to solve discrimination tasks, and it thus follows that discrimination tasks may not be an appropriate tool with which to assess more complex cognitive capabilities of animals.

4.2. Alternatives to discrimination tasks?

If not discrimination, what kinds of tasks could be used instead? Recently, interest has been growing in the use of more “naturalistic” tasks which do not require explicit training of the animals. An example is Ennaceur and Delacour’s spontaneous object exploration task [5], in which animals are presented with either familiar and novel objects, and show preferential exploration of the novel ones. This method has been used to explore quite complex cognitive processes: in, for example, showing that rats can remember what objects they encountered where, and in what context [4]. A related method is to measure rearing, a behaviour that rats exhibit in a novel or altered context [7]. Using this measure we have been able to show that rats can rapidly make spontaneous configural representations of a context [1], of a kind that failed to occur (albeit with objects) in the present, discrimination-based study. Spontaneous behaviour experiments are hard to run because they rely on a small number of observations made in a fairly short space of time: on the other hand, they have the great advantage of exploiting natural processing capabilities. Thus, while configural processing of objects during recognition is a capacity that is probably frequently used in a normal rat’s daily life, it is far from clear that the same could be said for simultaneous configural discrimination. It seems, then, that discrimination tasks, while excellent for studying elemental perceptual processes, are probably not the method of choice for the study of complex cognitive representations.

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