Individually distinctive odours represent individual conspecifics in rats

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Abstract. Individual recognition implies that a subject has the ability to discriminate between familiar conspecifics on the basis of their idiosyncratic characteristics. In this sense it is likely to be a more complex process than other forms of social recognition which involve classification of conspecifics into broad categories such as group, sex, age, kinship and familiarity. Using a go/no-go discrimination procedure, this study showed that rats, Rattus norvegicus, are indeed able to recognize conspecifics as individuals. Once rats had learned to discriminate a pair of conspecifics, they showed positive transfer on a series of discrimination problems involving novel conspecifics as stimuli. Furthermore, on a reversal test, rats were able to retain the memory of the individual identity of conspecifics to which they were exposed for the first time for at least 24 h. Finally, using the individually distinctive odours of previously discriminated conspecifics in tests clearly demonstrated that rats perceive olfactory signatures as representations of known individuals. Taken together, these results provide evidence for true individual recognition in rats and invite further investigations to gain deeper insight into the cognitive processes used by rats to build up a representation of individual conspecifics.

Olfaction represents the main sensory channel by which rodents recognize conspecifics and acquire knowledge about their social environment (Brown 1979). Social odours provide critical information about the generator of an odour. Such information is pertinent to multiple and distinctive levels of identity such as species, age, sex, status, reproductive condition, group membership, kinship, familiarity and individuality. All of these attributes, except individuality, designate characteristics common to many individuals. In contrast, individuality refers to a set of idiosyncratic traits that are unique and specific to a given individual. Investigating the ability of animals to extract the information contained in social objects (conspecifics or their olfactory signatures) allows the exploration of their capacity to recognize the different levels of identity mentioned above. The term ‘recognition’, however, may cover different operational definitions according to the level of identity (Halpin 1986; Blaustein & Porter 1990). In certain cases, the term ‘recognition’ is used to assess the ability of animals to identify their conspecifics according to different socially relevant characteristics (e.g. male, dominant, group member, non-kin, familiar, etc.). Operationally, such an ability designates the capacity of animals to categorize their conspecifics into social classes. In this context, it is not necessary for the receiver to have had previous exposure to the individual stimulus. In other cases, the term ‘recognition’ is used to assess an animal’s ability to recognize individuals. Such an operation implies that the receiver processes the individually distinctive cues of a known conspecific and matches that signature to a memory trace of this individual. Thus, the receiver discriminates a conspecific on the basis of its idiosyncratic features and as a function of prior familiarization with that individual. This is probably a more selective and complex process than recognition of the general characteristics of conspecifics. Such operational concepts require the distinction between ‘social recognition’ (categorization of known or unknown conspecifics on the basis of their general properties) and ‘individual recognition’ (or even ‘true individual recognition’; recalling the identity of a conspecific on the basis of its idiosyncratic traits; Zayan 1994).
Habituation–dishabituation procedures are commonly used to assess the ability of rodents to recognize previously encountered conspecifics or their signature (Thor & Holloway 1982; Halpin 1986; Brown et al. 1987; Singh et al. 1987; Dantzer et al. 1988; Johnston et al. 1991; Bluthé et al. 1993; Gheusi et al. 1994). Briefly, it consists of exposing the test subject to one individual or its signature during an habituation phase. A decrease in investigation time is usually observed, as a function of time, during this phase. The test subject is then exposed to a novel conspecific (or its signature), or simultaneously to the familiar animal and the novel one during the dishabitation phase. Generally, investigation time increases with respect to the novel stimulus which is interpreted as evidence that the two stimuli are discriminated by the test animal. This procedure is easy to implement. It is based on the spontaneous behaviour of test subjects and represents an ethologically valid technique. Two difficulties are encountered, however. First, a lack of differentiated responses in subjects towards familiar and novel stimuli does not necessarily imply a lack of discrimination. Second, the existence of differential responses in the test subject could be interpreted as assessing either true individual recognition or simply the discrimination between familiar and novel conspecifics. In this case, the subject has to learn to respond specifically to the presentation to one stimulus compared with another. Therefore, in contrast to habituation–dishabitation techniques based on spontaneous behavioural responses of test subjects, operant conditioning procedures involve discrimination learning, imply artificial conditions and require that the animals have a high degree of motivation and an extended number of trials. However, despite its less ecological conditions, the use of operant conditioning techniques represents another way to assess the ability of animals to discriminate between conspecifics. In this case, the subject has to learn to respond specifically to the presentation to one stimulus compared with another. Therefore, in contrast to habituation–dishabitation techniques based on spontaneous behavioural responses of test subjects, operant conditioning procedures involve discrimination learning, imply artificial conditions and require that the animals have a high degree of motivation and an extended number of trials. However, despite its less ecological conditions, the use of operant conditioning procedures eliminates the uncertainty associated with habituation–dishabitation techniques (i.e. whether animals truly discriminate between social stimuli on the basis of their individual characteristics or solely between familiar and novel conspecifics), and thus represents an unambiguous means to assess true individual recognition in test subjects. Schellinck et al. (1991) used such a procedure to demonstrate the ability of Long-Evans rats, _Rattus norvegicus_, to discriminate between urine odours from two individual donors. Because olfaction is the primary sense by which rodents discriminate between conspecifics, most experiments have used scents (i.e. urine, glandular, vaginal or salivary secretions) instead of individuals to assess the subjects’ ability to discriminate classes of conspecifics or individuals (however, for the use of conspecifics as discriminative stimuli in rats, see Husted & McKenna (1966) and Hopp et al. (1985)). However, from a cognitive point of view, it is critical to demonstrate that subjects are able to perceive an individually distinctive signature of a known individual as a representation of this individual. We specifically addressed this question in this paper.

We had several aims in the present study. First, we examined the ability of rats to discriminate conspecifics (i.e. only on the basis of their idiosyncratic cues) using an instrumental learning procedure. Second, once the subjects had learned to discriminate between two conspecifics, we assessed whether they showed positive transfer on a series of novel discriminations using previously unknown conspecifics as stimuli and whether they formed lasting representations of previously discriminated conspecifics. Third, we asked whether a rat could transfer from a learning task involving presentation of live conspecifics to a test phase in which only the individual’s olfactory signature was presented.

**GENERAL METHODS**

**Subjects**

We used adult male Wistar rats (Charles Rivers, France) weighing 250 g at the start of the experiment. They were housed individually in polycarbonate cages (40 \( \times \) 20 \( \times \) 16 cm) in an environmentally controlled room at 22 \( \pm \) 2°C with a 14:10 h light:dark cycle (lights on at 0730 hours). All behavioural training was conducted during the light phase of the cycle. Training was initiated after the rats had been on a progressive food deprivation schedule for at least 7 days and had reached 85% of their free-feeding weight. Following each training session the rats were given 8–10 g of standard laboratory chow.
(Extralabo-M25). This food-restriction schedule was continued throughout the experiment.

Apparatus and Preliminary Training

Behavioural testing took place in a modified operant chamber \((25 \times 23 \times 21 \text{ cm})\). A sample opening \((6 \times 6 \times 4 \text{ cm})\) was centred on one wall of the chamber \(4 \text{ cm}\) above the floor at the opposite side to the food pellet chute. Lights \((2.8 \text{ W})\) were mounted on the roof of the chamber and on the roof of the sample recess. Head introductions (nose pokes) into the sample opening were detected by photoelectric cells. All procedural events were controlled and recorded by a microcomputer linked to a SPIDER event controller (P. Fray, Cambridge, U.K.).

Training rats to discriminate conspecifics individually involved a preliminary procedure in which the subjects learned to obtain a food pellet reinforcement by breaking the photobeam. We gradually increased the amount of time each subject was required to keep its nose in the sample opening within a session from 250 ms to 3 s for five 50-trial daily sessions. No reinforcement was delivered if the rat failed to hold its nose in the opening for the required length of time. The start of each trial was signalled by the illumination of the recess. A 6-s delay starting when food was delivered was imposed between trials. During this delay all lights were extinguished. Nose pokes into the recess during the delay restarted this inter-trial delay. Individual discrimination training began on the day following completion of the preliminary training.

**EXPERIMENT 1: INDIVIDUAL DISCRIMINATION LEARNING**

To ensure that subjects would learn to discriminate between individual conspecifics and not between classes of conspecifics, paired-stimulus conspecifics were same-aged, unrelated adult male rats fed on the same diet and housed in the same conditions. Furthermore, to preclude any differences between stimulus conspecifics in terms of degree of familiarity with the test subjects, stimulus conspecifics were unknown to the test subjects before the beginning of discrimination training.

**Methods**

We used 14 male rats in this experiment. All animals served both as a test subject and as a stimulus. Each experimental subject was presented with the same pair of stimulus conspecifics throughout the discrimination training phase of the experiment, but different subjects were presented with different conspecific stimuli. Discrimination training was based on a successive discrete-trial go/no-go procedure. One daily session consisted of 50 trials with two equiprobable trial types (see below) presented in random order. During each trial, test rats were exposed to one of the stimulus conspecifics behind the wire mesh of the recess. Each stimulus rat was placed in a compartment with a wire-mesh front. Compartments were located on a swivelling platform which could be rotated in order to position each compartment in front of the sample opening during each trial (see Gheusi et al. 1994, for details). At the rear of each compartment a small fan ensured that the odours were projected towards the experimental subject. The location of each stimulus rat in one of the two compartments was randomized from session to session. One stimulus conspecific was arbitrarily designated as positive \((S^+, \text{ rewarded})\) and the other designated as negative \((S^-, \text{ unrewarded})\). At the beginning of a trial, the recess and house lights came on, signalling the presence of a stimulus rat. As soon as the photocell beam was broken, indicating that the subject had started to sample the stimulus rat, we initiated a timer, measuring the duration of the nose poke. If the positive stimulus was presented, a 3-s nose poke (go response) was rewarded with a food pellet. No reward was given whatever the duration of the nose poke during the presentation of the negative stimulus. Rats therefore learned to maintain nose pokes for at least 3 s during the presentation of the positive conspecific and to withdraw rapidly from the recess (no-go response) during the presentation of the negative conspecific. No correction procedure was used. Positive and negative conspecifics were presented in random order. The house and recess lights remained on after the test subject had broken the photobeam and were extinguished as soon as it withdrew its nose from the sample opening. All responses were followed by a 6-s inter-trial interval. We assessed discrimination performance on the basis of the percentage of correct responses during each session. A score of 80% or more of correct responses in three successive sessions was the criterion for learning to
discriminate between two individuals. Overall performance, go performance (go responses/S+ presentations) and no-go performance (no-go responses/S− presentations) were separately measured. We used a two-way analysis of variance (stimulus × sessions) to assess differences between response performance during the presentation of each stimulus conspecific over the discrimination training.

**Results**

On the basis of the criterion of 80% or more correct responses in each of three consecutive daily sessions, all 14 subjects learned to discriminate between two conspecifics. Six rats met the learning criterion within nine sessions, four required 10 sessions and four 11 sessions. Subjects performed at chance-levels during the initial sessions and gradually increased their performance until reaching criterion ($F_{8,104}=42.71$, $P<0.001$; Fig. 1). This improvement occurred especially after session 4 (pair-wise comparisons of sessions (Newman–Keuls): $P_S<0.05$ between each session 1–4 versus each session 5–9, but $P_S>0.05$ within the first four sessions).

**EXPERIMENT 2: SERIAL INDIVIDUAL DISCRIMINATIONS AND MEMORY FOR INDIVIDUALS**

In this experiment we investigated whether rats could transfer the rules they had learned during a first discrimination task to a series of six different pairs of conspecifics. Lasting memory for individuals was assessed on a final problem requiring reversal discrimination learning of the conspecifics presented during the previous problems, and thus providing a measure of the test subjects’ memory for individuals and their valence.

**Methods**

We used 21 male rats in this experiment. Each animal served both as a test subject and as a stimulus, and was submitted to a series of six different discrimination problems involving six pairs of conspecifics. Each problem was separated by 24 h. All stimulus conspecifics were unknown to the test subjects before their first presentation. None of the stimulus conspecifics was used more than once in a series assigned to a given subject but served as stimulus in the series of the other test subjects. Procedures were identical to those described in experiment 1. For each problem, criterion performance was set at 90% correct responding within a block of 20 consecutive trials (18 correct responses). We used a 90% criterion in this experiment (instead of 80% previously) because we considered that the procedural aspects of the task were already mastered during the discrimination of the first stimulus pair, leaving only the specific discrimination to be learned. A minimum of 50 trials was given on each problem. If criterion performance was not met within a single session (50 trials), training continued for a maximum of 250 trials.

Twenty-four hours after completing the sixth novel discrimination problem, rats were retested with the same sixth pair of conspecifics but the valence of the stimuli were reversed (problem R). Thus, the conspecific that had previously served as the $S^+$ stimulus was now the $S^−$ stimulus and the conspecific that previously served as the $S^−$ was now the $S^+$. We recorded the number of trials and the number of errors to criterion. We also recorded the number of errors within the first 20 trials. We used a one-way analysis of variance with repeated measures to
assess differences in response performance during the six successive discrimination problems. We used the Student t-test for paired samples to assess statistical significance of differences between the performance of test subjects on problem 6 and their performance on reversal learning.

**Results**

The rats improved markedly from the initial acquisition to the sixth discrimination pair in terms of the number of trials to criterion ($F_{5,100}=172.79$, $P<0.001$; Fig. 2a), the number of errors to criterion ($F_{5,100}=149.28$, $P<0.001$; Fig. 2b) and the number of errors in the first 20 trials ($F_{5,100}=8.40$, $P<0.001$; Fig. 2c), indicating that they learned more rapidly to discriminate between conspecifics over the successive problems. Post hoc analyses (Newman–Keuls) showed that both problems 1 and 2 required significantly more trials than all other subsequent problems to meet the criterion ($P<0.01$). Similarly, rats committed significantly more errors before achieving criterion during the first discrimination task than across subsequent problems ($Ps<0.001$), as well as during the second discrimination compared with problems 4–6 ($Ps<0.05$). On the basis of the same index, tasks 2 and 3 were found to differ from problem 6 ($Ps<0.05$). Taken together, these results showed that the improvement of the test subjects over the problem series mainly occurred following problem 2. They clearly support the conclusion that once rats have acquired the procedural aspects of the task, they use those cognitive skills to achieve rapid discrimination between individual conspecifics and specific association for individuals and their valence. We assessed reversal performance by comparing the performance between session 6 and the last problem (R). Rats required significantly more trials to reach criterion during reversal learning than during the immediately previous acquisition ($t_{20}=2.67$, $P=0.01$). In addition, rats made more errors during the entire session of the reversal problem ($t_{20}=3$, $P<0.01$) as well as in the first 20 trials ($t_{20}=3.66$, $P<0.01$). These results indicate that rats had more difficulty in acquiring a reversed discrimination than a novel discrimination. Thus, the decrease in performance on reversal discrimination reveals that test subjects remember the previously discriminated individuals over 24 h.

**Figure 2.** Changes in performance for each of a series of two-conspecifics discrimination problems. The first six discrimination problems (□) involved six different pairs of conspecific stimuli. Session R (■) denotes valence reversal of the two conspecifics presented in session 6. (a) Mean number (+SEM) of trials to criterion. (b) Mean number (+SEM) of errors to criterion. (c) Mean number (+SEM) of errors in the first 20 trials.

**Figure 3** shows the learning curve for one representative subject in each of the different tasks.
EXPERIMENT 3: INDIVIDUAL RECOGNITION USING INDIVIDUALLY DISTINCTIVE SIGNATURES

Experiments 1 and 2 provide evidence that rats are able to discriminate between individuals on the basis of their idiosyncratic characteristics, but do not specify the relative contribution of the different sensory systems used by rats in the learning paradigm. Since stimulus conspecifics were presented behind a wire mesh, visual, acoustic, or olfactory cues or a combination of those might have formed the basis of the discrimination. In the present experiment we focused on the role of individually distinctive olfactory signatures in triggering representation for known individuals in rats. This choice was based on a large body of literature reporting the role of odour cues in individually distinctive identity in mice, *Mus musculus*, and rats (Singh et al. 1990; Boyse et al. 1991; Brown & Schellinck 1992). Technically, this experiment was based on the reversal learning procedure used in the previous experiment. We assessed the ability of rats to recognize individuals only on the basis of their odours by exposing test subjects to the olfactory signatures (soiled bedding) of previously discriminated conspecifics in a reversal discrimination task. We predicted that if individually distinctive odours are sufficient cues to represent individuals for rats, then test subjects should perform poorly (below criterion level) on a reversal discrimination task involving individual odours of previously discriminated individuals, whereas good positive transfer would occur when the bedding of the previously positive stimulus remained positive.

**Methods**

We used 15 male rats in this experiment. They were randomly assigned to one of three groups...
(N=5). Procedures were identical to those used in experiments 1 and 2. In the test session, each animal was submitted to two different discrimination problems separated by 30 min. The first discrimination task was identical for the three groups and consisted of discrimination between two conspecifics. The second discrimination task differed for each group. We trained group 1 subjects to discriminate between the olfactory signatures (soiled bedding of the cage) of the two conspecifics that they had discriminated during the first task. The olfactory signature of the S+ individual served as the S+ stimulus and the olfactory signature of the S− individual served as the S− stimulus. Group 2 subjects were also trained to discriminate between the olfactory signatures of the two conspecifics that they had previously discriminated, but the significance of odours was different. Thus, the odour of the S+ individual served as the S− stimulus and that of the individual that had served previously as S− was the S+ stimulus. Finally, group 3 subjects were again exposed to the same individuals that they had discriminated on the first acquisition but the individual that had served as the S+ stimulus was now the S− stimulus and the individual that had served as the S− stimulus was now the S+ stimulus. Only one 50-trial session was run for each discrimination task and a criterion of 80% or more correct responses was used. Individual soiled bedding was collected from the cage of each stimulus conspecific and deposited into a petri dish. Different petri dishes were used for each individual’s soiled bedding. The experimenter wore latex gloves to minimize the transfer of scents. Gloves were not used for more than one individual’s soiled bedding. We used a two-way analysis of variance to assess differences between response performance of the different groups and across the different discrimination tasks.

Results

Figure 4 summarizes the performance of the three groups for the two discrimination tasks. There was a significant difference between the groups (ANOVA: F_{2,12}=100.99, P<0.001), a significant effect of discrimination tasks (F_{1,12}=84.68, P<0.001) and a significant interaction between groups and discrimination tasks (F_{2,12}=14.63, P<0.001). Reversal discrimination of conspecifics or their olfactory signatures markedly affected the performance of groups 3 and 2, while replacing individual conspecifics by their respective signatures did not impair performance in group 1. Post hoc comparisons (Newman–Keuls) revealed that the percentage of correct responses on the first discrimination task (two-conspecific discrimination) did not differ significantly between the three groups. On the second discrimination task, however, group 1 subjects outperformed group 2 and group 3 subjects (Ps<0.001), but no statistical differences were found between group 2 and group 3 subjects.

These results indicate that rats are able to recognize individuals on the sole basis of their olfactory signatures (groups 1 and 2), and that olfaction is sufficient to account for individual recognition (groups 2 and 3). In other words, memory for individuals in rats can be triggered by the individually distinctive odours of these individuals. This suggests that the representation for individuals that rats formed during the first discrimination task includes at least olfactory characteristics, although other factors could of course also be involved.
DISCUSSION

These results indicate that rats have the ability to discriminate and individually recognize live conspecifics in an operant procedure in which they are successively exposed to two conspecifics with differential reinforcement for responses in the presence of each conspecific. Various arguments support the finding that recognition in this study was achieved on the basis of individual characteristics. First, location of stimulus conspecifics in the boxes varied randomly during discrimination training, thus preventing any differences (e.g. subtle differences between the compartments), other than the individual characteristics of the conspecifics, from being used to guide the performance of test rats. Second, since the conspecific stimuli used in this experiment shared their primary social characteristics (sex, age, rearing conditions, diet, familiarity to subjects), only idiosyncratic cues could have been used by test subjects to distinguish them. In experiments 1 and 2, the stimuli used were live conspecifics, and we have no evidence about the information to which test subjects learned to respond. For instance, did they learn to identify, remember and respond to specific cues from each conspecific, or did they learn to associate and categorize the multiple instances of presentations of each conspecific as a single social object? In addition, conspecific stimuli were presented behind a wire mesh and only visual, acoustic or olfactory cues, or some combination of these, could have formed the basis of the discrimination. We have not attempted to specify in this study the relative contribution of each sensory system used by rats in this learning paradigm. This question, however, was partially addressed in experiment 3 in which live conspecifics were substituted by their olfactory signatures. The improvement of the rats’ performance across sessions in experiment 1 suggests that the cues from conspecifics used by the test subjects do vary markedly over time.

The results of experiment 2 show that once rats had learned to discriminate a pair of conspecifics they were also able, in this context, to transfer their discrimination learning remarkably well to successive novel pairs of conspecifics. The results, therefore, strongly suggest that rats can form learning-sets using cues from conspecifics. The use of the term ‘learning-set’ has recently been questioned in the field of olfactory discrimination learning in rats and a debate has ensued concerning the possibility that rats have access to high cognitive processes (see Eichenbaum & Otto 1993; Hall 1993; Lynch & Staubli 1993; Reid & Morris 1993; Slotnick 1993, 1994). Our results cannot contribute to this debate, however, since we did not address specific questions relevant to this topic. We reversed the significance of the original problem in experiment 2 to determine whether rats form a memory of conspecifics that they had discriminated 24 h earlier. They clearly did so, since impaired acquisition of reversal of the original problem was due primarily to the rats committing many errors during early trials.

Studies exploring social and individual recognition have often been conducted by using cues from conspecifics rather than conspecifics themselves. The search for the relevant social cues as well as the ease of testing many of their different aspects have promoted such experimental strategies. Such an approach, however, has largely contributed to our knowledge about the nature and the properties of the cues used by members of different species to signal their identity, but has contributed much less to the analysis of the cognitive processes that support social and individual recognition. Thus, even if subjects accurately perform discrimination tasks by using cues from individuals, it has not been demonstrated that they perceive such cues as representations of these individuals. In this respect, a demonstration establishing that subjects show transfer from individual conspecifics to their individually distinctive cues or vice versa is critical. We specifically addressed this question in experiment 3. In this experiment, rats responded indiscriminately to the individual odours of conspecifics as well as to the conspecifics themselves, thus showing their ability to perceive a clear equivalence between both types of stimuli. This was strongly supported by the poorer performance of rats tested during the reversal task involving the olfactory signatures of the previously discriminated conspecifics. Our results show that individually distinctive signatures represent known individual subjects for rats. To explore the existence of multi-factor representation of individual conspecifics, however, we need further experiments, such as those reported by Johnston & Jernigan (1994), who investigated the ability of hamsters, *Mesocricetus auratus*, to perceive that different sources of scents (i.e. *Animal Behaviour, 53, 5* 942
vaginal and flank scents) belong to the same, known conspecific.

Our results add to the long list of data that have outlined the critical role of the olfactory sense in rats, especially with respect to their social relationships. In addition, they provide strong arguments supporting the idea that, when processing the identification of a conspecific, rats build up an ‘olfactory image’ of this conspecific, as a subset of individually distinctive cues. The ability of rats to recognize individuals on the sole basis of their olfactory signatures provides inferential evidence that they establish an internal representation of these conspecifics when they learn to discriminate between them.

Using comparable discrimination procedures and reversal tests, several authors have examined the ability of rats to discriminate and retain olfactory information (Eichenbaum et al. 1986; Staubli et al. 1986; Lu & Slotnick 1990; Slotnick & Risser 1990; Otto et al. 1991). In this sense, we show in the present experiments that rats can encode socially relevant information in a manner comparable to the way in which they learn and retain non-biological odours. Research on neural structures controlling the acquisition, consolidation and recall of learned olfactory information has provided detailed analyses of the specific role of neurobiological substrates (for a review see Otto & Eichenbaum 1992). However, because the odours used in these studies were pure chemicals, cosmetics, food flavourings or floral perfumes, it is not yet known whether socially relevant cues are also critically encoded and analysed by the same neurobiological pathways or by different pathways which have already been found to support some forms of social recognition (e.g. Kaba et al. 1989, 1994; Brennan et al. 1990; Brennan 1994 concerning research on the detailed analysis of the neural basis of olfactory memory in the context of pregnancy block). Exploring the behavioural and neurobiological aspects of individual recognition in such a way appears to be a major challenge for obtaining insight into the construction of the representation of individual conspecifics and, more generally, into social cognition.

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