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The effects of environmental context on laboratory rat social recognition

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Abstract

Moving an animal from the environmental context in which it has learned a particular task to another entirely different context, can reduce performance. We investigated the effect of switching environmental contexts on the ability of adult laboratory rats, *Rattus norvegicus*, to recognize and habituate to repeated presentations of juvenile conspecifics. Adults were exposed to juveniles for four periods of 5 min, separated by a 15-min interval. Rats either received all four exposures in the same context, or the first three in one context and the fourth in a different context. Half the rats in this latter group were familiarised with both contexts prior to testing, the other half had no experience of either. In all groups, the adults reduced their investigation of the juveniles over the three initial exposures. Mild aggression increased over the same period for the context-unfamiliar rats. A significant reduction in investigation by these rats between the third and fourth exposures, when the context was changed, suggested that the context switch further increased habituation to the juveniles. However, the context-familiar rats showed no such change, indicating that the changes observed for the context-unfamiliar rats were due to the effect of context novelty. This was supported by the finding that, during the first exposure, context-familiar adults investigated juveniles more and were more aggressive than those for which the contexts were novel. These results suggest that familiar contextual cues play only a minor role in the short-term social memory of laboratory rats.

Introduction

There is increasing evidence that the environmental context in which an experiment takes place can have a substantial influence on the learning and memory of the subjects involved (e.g. Spear 1973; Bouton & Peck 1989; Bouton & Swartzentruber 1989). Contextual cues play an important role in the ability of human subjects to recall previously learnt information, with information more accurately recalled if the test context is the same as that for training (e.g. Gordon & Klein 1994). The evidence for context specificity in non human animals has often been contradictory, however, and this has resulted in a more confused picture of how environmental context may influence memory formation, retention and recall (e.g. Marlin & Miller 1981; Evans & Hammond 1983). Nevertheless, if contextual cues play a role in non-human animal memory, then this could have important consequences for animal welfare. If both external (e.g. Rodriguez et al. 1993) and internal (e.g. Holloway & Wansley 1973) contextual cues are able to influence animal learning and memory, then aspects of animal memory may be disturbed by routine husbandry procedures. For example, the mixing of familiar conspecifics in the novel context of an unfamiliar pen may lead to a failure of social recognition, and subsequent inappropriate aggression. It is, therefore, of both fundamental and applied interest to investigate the influence of context specificity on animal learning and memory.

Social memory, the ability to form, retain and refer to information related to a conspecific, is a key area for trying to determine if, and to what extent, contextual cues might be involved. For instance, in social memory and recognition research there may be difficulties in determining whether a subject is recognizing an individual conspecific independently of the context in which that individual has been introduced (e.g. Falls & Brooks 1975; Snowdon & Cleveland 1979; Waas & Colgan 1994). To investigate this issue we used a social recognition test based on a natural propensity of laboratory rats to investigate other individuals. In this test the duration of investigation of a conspecific declines with the repeated presentation of that conspecific to the subject animal (e.g. Sekiguchi et al. 1991). This habituation is taken as an indication that the conspecific is recognized, because dishabituation occurs when a novel conspecific is presented.

Previous investigations of whether habituation shows context specificity, have revealed conflicting results. Some researchers have found that habituation does successfully transfer across contexts (e.g. Marlin & Miller 1981); others have observed dishabituation following context change (e.g. Evans & Hammond 1983). Such studies have been criticized, however, for being inadequately controlled (e.g. Hall & Honey 1989; Gordon & Klein 1994). A lack of context specificity might have arisen only because the subject has failed to discriminate between the two contexts, whilst any apparent context specificity could just be due to generalization decrement, with the perception of the stimulus being altered by the change in context (Hall & Honey 1989). More recent and controlled studies (e.g. Hall & Channell 1985; Hall & Honey 1989; Honey et al. 1992) have concluded that habituation does not show context specificity. These studies of habituation have focused on unconditioned responses such as orientation towards light (Hall & Channell 1985), consumption of a novel flavour (Honey et al. 1992) and disruption of an appetitively rewarded response by stimulus (either light or tone) presentation (Hall & Honey 1989).

The aim of this experiment was to produce further evidence on whether habituation shows context specificity, and to extend previous work by focusing on the social behaviour of the laboratory rat, particularly the habituation of investigative behaviour after repeated presentations of a conspecific. We also aimed to separate the effects of environmental context per se, from the potentially confounding influence of context novelty. The results of this experiment can therefore be applied directly to situations in which environmental context may be having an influence on an animal's social learning and memory.

METHODS

Subjects, Housing and Care

We used 36 adult (3 months old at start of study) and 24 juvenile (28 days old at start of study) male lister hooded rats (Harlan UK Ltd.). All the rats were housed individually in standard laboratory cages (33 x 50 x 21cm) with sawdust litter and an enrichment toy. Food (Harlan Teklad Laboratory Diet) and water were freely available. All the rats were housed in the same room in which they were tested, with the juveniles and adults kept at opposite ends. The room was temperature controlled (20°c ± 1) and maintained on a reverse lighting schedule (lights on 1900-0700 hours), with red light (60 Watt) providing visibility for the researcher. Dim 'white' light (10 Watt) was provided during testing.

Experimental Design

We used the social recognition test (Thor & Holloway 1982), which is based upon a comparison of behaviour, particularly investigation, between two exposures of the same individual to a subject animal. A reduction in investigation in the second exposure implies recognition of the individual, whereas no change suggests that the subject's social memory of that individual has decayed over the interval between exposures. This latter response is the same as that seen when a novel individual is introduced in the second exposure. We also used elements of the habituation-discrimination technique (e.g. Halpin 1986; Johnston 1993; Johnston & Jernigan 1994), in which a subject animal is repeatedly presented with the odour from one individual, which should lead to habituation, before being presented with the odour of a novel individual, which may or may not result in dishabituation.

As an index of habituation, we used the decline in investigation of a juvenile by an adult. Previous research has demonstrated habituation for multiple short term exposures, such as six bouts of 5 min, separated by short IEIs of 10 min (Sekiguchi et al. 1991). Social memory after short term exposures appears to be relatively brief, with no apparent recognition by a male adult rat of a juvenile previously introduced for 5 min, after an interval of 120 min (e.g. Thor & Holloway 1982; Dantzer et al. 1987). We exposed juveniles to adults for four consecutive 5-min exposures each separated by a 15-min interval, during which the juveniles were returned to their home cages. The fourth 'test' exposure allowed us to determine if habituation to the stimulus remained, or if the treatment, such as a change in context, resulted in dishabituation.

All the adults were introduced to juveniles in a pre test training experiment in order that any overtly aggressive adults could be excluded from the experiment. This training took the form of two exposures of 15 min to the same adult by a particular juvenile, separated by 48 hrs. Observations were made of the total amount of investigation and mildly aggressive behaviour during the introductions. Investigation of the juvenile included sniffing, grooming and following within a distance of 1cm (Thor & Holloway 1982), and mild aggression consisted of rolling/standing over the juvenile, and/or pushing it away. Any overtly aggressive behaviour, such as biting, resulted in the session being abandoned immediately. We recorded these categories of observations continuously throughout the experiment, collecting them using a hand held event recorder (Psion Organiser II) with Noldus Observer software, and also by video camera.

We used 8 of the juveniles as social stimuli in the pre-experimental training, and these individuals were not used again. The remaining 16 juveniles were used only in the actual experiment itself. Four of the adult rats were excluded from the experiment owing to overt aggression during pre test training. We randomly divided the remaining adults into three treatment groups (six sub treatment groups, see Table 1), with 10 rats each in treatments D1 and D2, and 12 rats in treatment S1 (although seven were later excluded from the analysis: See Results). Four adults were tested per day for 8 days, with treatment order balanced over time.

Table One

These different treatments allowed us to observe whether: (1) habituation occurs over the first three exposures to the same stimulus; (2) whether there was any difference in the amounts of behaviour displayed by the rats in those treatments with experience, compared with those without; (3) whether the behaviour of the rats changed in those treatments that changed context for the fourth 'test' exposure; and if so, (4) whether previous experience of both contexts affected this result.

A frequent criticism of context experiments is that, depending on the particular results, the chosen contexts are either insufficiently distinguishable or so different that they interfere with the subjects' ability to carry out the learning task. For this experiment the two different contextual environments, context A (white) and context B (black), were designed to take into account the potential confounding effects that any physical modifications, such as differences in overall surface area, might have on subject behaviour (see Table 2).

*****Table Two*****

Rats in treatment D2, which required experience of both contexts before the first exposure to a juvenile, were given a total of 80-min experience of both contexts. This involved a 20-min session in both contexts every day for 4 days, with the final session of context familiarization being completed 24 h before the first exposure of the experiment itself.

All exposures of the juvenile to the adult rat lasted for 5 min, with both the juvenile and the adult removed to their home cages during the 15-min intervals. We cleaned both contexts with a mild disinfectant before each encounter to limit the effect of olfactory cues. All the rats had been given previous experience of handling to reduce any possible effects on behaviour.

Ethical Note

Although this study was not designed to promote aggression between animals, there was a risk of aggression occurring in the social recognition test. To minimize this risk, juveniles were used as stimuli because they elicit little or no aggressive behaviour from adult rats (Thor 1979). Although juveniles can be intimidated by adults, physical injury is rare (Lore & Flannelly 1977). At no point in this study was injury caused by mild aggression. If there was any overt aggression we stopped the encounter immediately, and separated the individuals before any injury could occur. Those juveniles who had experienced overt aggression appeared to show no subsequent long term effects, with normal behaviour and food/water consumption observed.

The rats were individually housed to prevent the formation of group odours (e.g. Barnett 1963) and to try to standardize pre experimental experience. All the rats were therefore individually housed for 1 week prior to the start of the experiment to allow familiarization, and they remained individually housed for the duration of the experiment. Research has indicated that social isolation can reduce social tolerance (Brain et al. 1980; Niesink & Van Ree 1982), but this effect can be ameliorated by allowing some degree of contact with neighbouring rats (Hurst et al. 1997), and this was the case for these experiments in which some olfactory and visual contact was always possible between neighbouring cages, in addition to interactions during test sessions. A researcher was always present during the direct introduction of one rat to another so that any overtly aggressive encounters could be terminated immediately. Initial pre test ‘training’ also provided the opportunity to remove any overtly aggressive rats from the experiment.

RESULTS

All the subjects in treatment D1 (*N*=10 tested, *N*=10 analysed) successfully completed the four separate exposures, and in treatment S1 only two subjects were removed from the experiment because of aggression (*N*=12 tested, *N*=10 analysed). For treatment D2 (*N*=10 tested, *N*=5 analysed), in which the rats had undergone familiarization training in both contexts prior to testing, five rats were overtly aggressive and the encounters were abandoned. Thus of 32 rats tested, the data from 25 were analysed. The data consisted of the total duration (s) of investigation and mild aggression directed towards the juveniles by the adult subjects, recorded during each of the 5-min exposures. Data from the different contexts were analysed together for each treatment, and the effects of context taken into account. The statistical package used was Minitab (version 11).

We compared the three treatments for differences in the total amount of investigative and mildly aggressive behaviour exhibited during the first exposure. The mild aggression data were transformed logarithmically to meet requirements for normality and homogeneity of variance. Analysis of investigation was performed on the raw data. For both investigative behaviour (one-way ANOVA: $F_{2,22}$=9.47, *P*=0.001) and mild aggression ($F_{2,22}$=5.45, P<0.05) there was a significant effect of treatment. A Tukey's pairwise comparison revealed that this difference between treatments was due to rats in treatment D2 showing more investigation (*T*=12.3, *P*=0.05) and mild aggression (*T*=0.25 (transformed), *P*=0.05) than those in the other treatments.

To determine whether habituation to the introduction of the juvenile stimulus had occurred, we compared the duration of behaviour in the initial three exposures in the three treatments. The problems with aggression in treatment D2 meant that there were insufficient data to include context into the analysis. For this reason, we analysed treatment D2 separately using a balanced ANOVA for repeated measures, with only exposure (1-3) as a factor. For both investigation and mild aggression we analysed the raw data. This analysis revealed a significant reduction in investigation ($F_{2,8}$=13.28, P<0.01) over the three exposures, but no significant change in mild aggression (see Fig. 1). Post hoc analysis (Tukey's pairwise comparison) of this result revealed that, although the treatment means for investigation decreased across exposures one, two and three (means: 94; 55; 47.2 respectively), only the decreases between exposures one and two, and exposures one and three were significant (*T*=27.8, *P*=0.05).

Treatments S1 and D1 were analysed using a balanced ANOVA for repeated measures (*N*=20): with treatment (S1, D1) and context (A, B) as between factors, and exposure (1-3) as the within factor. The mild aggression data were transformed logarithmically, with analysis of investigation performed on the raw data. No significant difference was found between treatments S1 and D1 for either investigation or mild aggression, and there was also no significant interaction between the factors, but there was a significant effect of exposure on both investigation ($F_{2,32}$=6.3, P<0.01) and mild aggression ($F_{2,32}$=22.13, P<0.001; see Fig. 1). No differences in either investigation or mild aggression were observed between context A and context B. Post hoc analysis (Tukey's pairwise comparison) of the observed behavioural changes revealed that, although the means for investigation of the combined treatments (S1& D1) decreased across exposures one, two and three (means: 56.6; 50.2; 41.95 respectively), only the decrease from exposure one to three was significant (T=10, P=0.05). For mild aggression (means (transformed): 0.25; 0.7; 0.8 respectively), there was a significant increase from exposure one to two, and from exposures one to three (T=0.21, P=0.05).

Figure One

Finally, we investigated whether there was any change in behaviour between the third exposure and the fourth 'test' exposure. This would reveal whether or not rats in treatments D1 and D2, in which the context had been switched for the fourth exposure, showed evidence of the dishabituation which would indicate a failure to recognize the familiar conspecific in a different context. The data failed to attain the requirements of normality and homogeneity of variance after transformation, and were therefore analysed using the non parametric Wilcoxon signed-ranks test (two tailed). No significant changes in either investigation or mildly aggressive behaviour were observed for treatments S1 and D2 between the third and fourth exposures. However, treatment D1 showed significant reductions in the amount of both investigation (T=47, N=10, P<0.05) and mild aggression (T=42.5, N=9, P<0.05) elicited by the juvenile stimuli between the third and the fourth ‘test’ exposure (Fig 1.).

DISCUSSION

Habituation, in terms of declining amounts of investigation, occurred over three separate encounters with the same individual, despite the increasing familiarity with an initially novel environment. This habituation is interpreted as resulting from the recognition of the same conspecific (Thor & Holloway 1982). In direct contrast to this decline was an increase in mild aggression over the three exposures. For the fourth ‘test’ exposure there was no change in the amount of either investigation or mild aggression directed towards the juvenile by the rats in treatment S1, which had not undergone a change in context. This suggests continued recognition of the stimulus juvenile, i.e. no dishabituation was observed, and that after three exposures the adult rats may have already attained a ‘baseline’ level of behaviour, with no further reduction in investigation, or increase in mild aggression, occurring on the subsequent fourth exposure. For treatment D1, in which the rats were switched to novel contexts for the final exposure, a significant drop in both investigation and mildly aggressive behaviour was observed. This suggests that the change of context has not interfered with the memory of the adult rat, as this would have resulted in an increase in investigation and a decline in mild aggression. This decrease in investigation could therefore be interpreted as further habituation towards the juvenile. But, the fact that there was also a significant reduction in mild aggression, which would be expected to rise as the juvenile becomes increasingly familiar, suggests that it is not just further recognition of the conspecific that is affecting the amount of behaviour directed towards the juvenile. This is confirmed by comparing treatment D1 with treatment S1, which showed no further reduction in investigation to the juvenile stimuli after the three initial exposures.

The results from treatment D2, those rats with experience of both contexts, reveal that it was the effect of context novelty that influenced the behaviour of the rats in treatment D1. Thus, if the rat was switched to a familiar context (D2), then the change in context had no effect on behaviour, i.e. it had the same effect as if context had not been changed (treatment S1). This implies continued recognition of the conspecific in a different context and suggests that environmental context, in this experiment, had little influence on short-term social memory in adult male laboratory rats, as long as the contexts were familiar. Because the results suggest that the novelty of the test situation had such a marked effect on behaviour, this emphasizes the importance of disentangling the effect of novelty from that of context per se. Analysis of the first exposure to the juvenile social stimulus provides further evidence of the influence of context novelty on behaviour. The rats in the treatment D2, who had been provided with previous experience of both the different environmental contexts, displayed more investigation and mild aggression than those rats to whom the contexts were novel. It could be that novelty has a suppressive effect on general behaviour, resulting in lower levels of all categories of observed behaviour. But it might also be that the increased time spent exploring a novel environment simply results in less time available for interaction with the juvenile.

These results confirm work by Hall & Channell (1985) and Honey et al. (1992). Honey et al. (1992) found that although consumption of a novel flavour by rats increased in one context and then fell when the context was changed, this dishabituation of a neophobic response only occurred if the context was novel. When the second context was familiar, the context change had no effect on the level of consumption of the flavour by the rats. The assertion that unlike other types of learning, such as classical conditioning, operant conditioning, and latent inhibition, habituation does not appear to show context specificity (e.g. Hall & Channell 1985; Hall & Honey 1989; Honey et al. 1992) is therefore also found to be true for the social recognition of conspecifics, as determined by observed levels of investigation.

It could be argued that the apparent failure of memory to be affected by the change in context was actually because the two contexts were insufficiently distinguishable (e.g. Hall & Honey 1989; Gordon & Klein 1994). However, the fact that behaviour was significantly affected by the context change when the context was novel (treatment D1) argues against this. The contexts must have been sufficiently different to allow recognition of the new surroundings. Another problem with context based experiments is the risk of 'generalization decrement' (e.g. Lovibond et al 1984). This occurs when the two different contexts allow contrasting levels of stimulus recognition. If this discrepancy results in a different response rate between the two contexts, then the results could be misinterpreted as being caused by context specificity. We did not observe any difference in behaviour between context A and context B. There was therefore no one context in which interaction with the juvenile was more frequent, implying that the juvenile was no more difficult to locate in one context than in the other.

The rats in treatment D2, which had been given familiarization training in the two different environmental contexts before exposure to the juveniles, were unexpectedly aggressive. This may have implications for animal welfare if experience of a context prior to the mixing of unfamiliar animals results in an increase in observed aggression. A possible explanation for this aggression is that because the rats in treatment D2 were familiar with the contexts, more of their behaviour could be directed towards the juvenile than into exploration of a novel environment. Increased familiarity with the contexts could also result in territory formation of some kind. Yet research using the social recognition test (e.g. Perio et al. 1989), involving the direct introduction of a juvenile into the home cage of an adult, has reported far lower levels of aggression than observed in this experiment. The finding that environmental context does not appear to influence social recognition, at least in the short term, suggests that mixing previously familiar animals in a novel context may not disrupt recognition. If so, this might help decrease the aggression and related animal welfare problems that sometimes arise when previously familiar animals are reunited (e.g. Ewbank & Meese 1971), and that may be caused by a failure of recognition.

To conclude, we have shown that social recognition, in terms of the declining investigation of a familiar conspecific, does not appear to show context specificity provided that the subject animal is familiar with the context to which it is transferred. More research, however, needs to be undertaken to allow further definition of the role that contextual cues might play in social recognition and memory in non human animals, particularly when this involves long-term memory.

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Table 1. Description of treatments

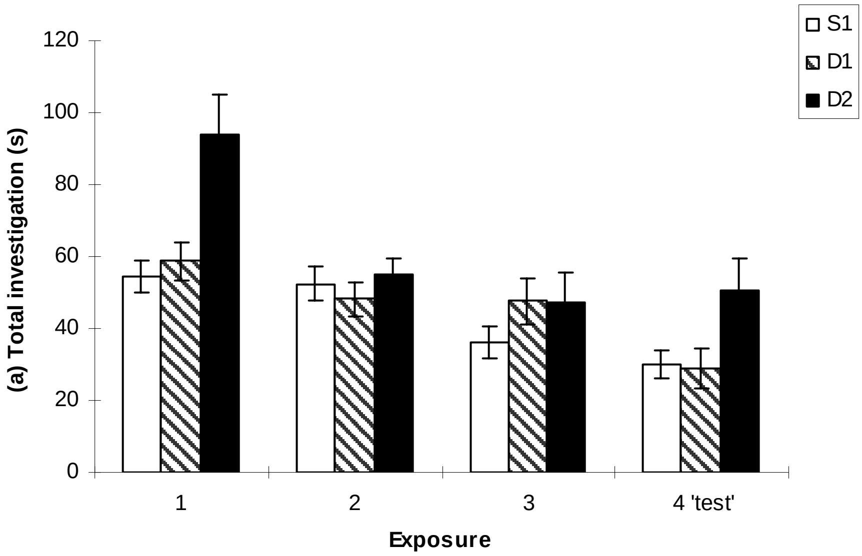
Treatment	Description	Number of rats used in analysis
S1a	All four exposures in context A.	5
S1b	All four exposures in context B.	5
D1a	The first three exposures in context A, the fourth in context B.	5
D1b	The first three exposures in context B, the fourth in context A.	5
D2a	The first three exposures in context A, the fourth in context B, with previous experience of both contexts.	2
D2b	The first three exposures in context B, the fourth in context A, with previous experience of both contexts.	3

Table 2. The contextual environments and their differences in physical modification

	Context A	Context B
Measurements (cm)	33 x 50 x 21	33 x 50 x 23
Light source	10W bulb	10 W bulb
Orientation	North-South	East-West
Floor	Plastic	wire mesh
Colour of floor and walls	White	Black
Roof height (cm)	21	23

Figure 1. Changes in the duration of (a) investigation and (b) mild aggression for treatments S1, D1, and D2 by the adult subjects during four separate exposures to the same juvenile stimuli. Data are expressed as means ± St.error. See Tables 1 & 2 for descriptions of treatments and contexts.

(a)



(b)