

Applied Animal Behaviour Science (2000) Volume 67: 241-254

2

doi:10.1016/S0168-1591(99)00120-3

4 **Final Revision – NOT EDITED by the journal**

6

8

SHORT-TERM SOCIAL MEMORY IN THE LABORATORY RAT:

10 **ITS SUSCEPTIBILITY TO DISTURBANCE**

12

OLIVER BURMAN & MICHAEL MENDEL

14

Department of Clinical Veterinary Science, University of Bristol, Bristol, BS40 5DU

16

18

20

22 Corresponding author: Oliver Burman

24 Abstract

26 Adult rats presented with a juvenile conspecific for five minutes on two occasions,
separated by a 15-min inter-exposure interval (IEI), investigated the reintroduced
28 juvenile significantly less in the second encounter. It is suggested that this was
because the adult rats remembered the identity of the juvenile, because when a novel
30 juvenile was introduced for the second encounter, no such reduction in investigation
was observed. When the rats were either handled, placed in a smaller, novel, cage, or
32 introduced to a new juvenile midway through the IEI, investigation of the
reintroduced juvenile did not decrease. This indicated that memory of that juvenile
34 had been disrupted. However, a simple change of cage during the IEI had no
disruptive effect on memory. These results suggest that routine husbandry procedures
36 can disrupt short-term social memory, which may lead to an increase in aggression
due to a failure of recognition. This has implications for the welfare of captive social
38 animals.

40 Keywords: Social memory; Rat; Retroactive interference; Social recognition

Introduction

42

Social memory, the ability of an animal to encode, retain, and refer to information
44 concerning the identity of a conspecific over time, is likely to be crucial for the
determination and maintenance of social structure in many animal species,
46 particularly those living in small, stable social groups (e.g. Caldwell, 1985; Pagel and
Dawkins, 1997). Yet, in contrast to the large amount of research on the abilities of
48 non-human animals to discriminate between conspecifics (e.g. monkeys: Dasser,
1988; chickens: Bradshaw, 1991; rodents: Gheusi et al., 1994a; sheep: Kendrick et al.,
50 1996; invertebrates: Karavanich and Atema, 1998), less attention has been directed
towards social memory itself.

52

The disruption of cognitive function by stressful elements from both housing
54 and husbandry systems could have potentially serious implications for the welfare of
domesticates and captive wild animals (Mendl, in press). For example, if social
56 memory is disrupted by husbandry procedures such as the removal and subsequent
reintroduction of individuals from previously stable social groups, then the
58 subsequent recognition failure may underlie the observed increase in aggression, and
decline in welfare due to injury, which occurs when previously familiar animals are
60 reintroduced (e.g. Ewbank and Meese, 1971). This raises questions about the potential
stability of social memory in the face of interference resulting from environmental
62 disturbances. Recent work on pigs has demonstrated that elements of common
husbandry procedures can have a disruptive effect on the retention of a spatial
64 learning task (Mendl et al., 1997; Laughlin et al., 1999). Here, we extend this work to
investigate whether such procedures can interfere with social memory in rats.

66

Research investigating the effect of retroactive interference, the way in which
68 an event introduced after an initial task can reduce subsequent performance of that
task (e.g. Rodriguez et al., 1993), has revealed that spatial memory in rats appears
70 resistant to disruption when the interpolated ('between-tests') event is different to the
original learned task (e.g. Maki et al., 1979). However, if there is a large amount of
72 interpolated experience, or if the interpolated event is very similar to the original task,
it does appear that interference can occur (Roberts, 1981). Social memory studies
74 have also found that interference can be induced by an interpolated event very similar
to the original task. For example, when a new individual is introduced in the period
76 during which another individual has to be remembered (e.g. Thor and Holloway,
1982; Dantzer et al., 1987).

78

In this study we therefore investigated whether social memory, like spatial
80 memory, appears resistant to interference when the interpolated event is different to
the original learned task. This information would thus allow us to compare between
82 properties of the spatial and social memory systems. It would also allow us to
investigate whether environmental disturbances, such as those commonly involved as
84 part of husbandry or experimental procedures, can interfere with the social memory of
laboratory rats. This study therefore has direct implications for the welfare of
86 laboratory rats, and, if the rat is considered as a model species, may also have
implications for the welfare of other captive social animals.

88

General methods

90

Subjects, housing and care

92

The subjects were unrelated male Lister Hooded rats (Harlan UK Limited), 12
94 at three months of age, and 10 at two months of age. We used two different ages of
adult rats so that all the adults could undergo pre-experimental training
96 simultaneously, but at testing all the rats would be the same age (3-months-old).

Thirty two juvenile male Lister Hooded rats, 21 days old at the start of the
98 experiment, were used as social stimuli. The time schedule was designed to ensure
that the experiments were completed before the juveniles reached sexual maturation at
100 around 50 days old (Wolfensohn and Lloyd, 1994). All the rats were housed
individually in standard laboratory cages (33 X 50 X 21cm) with sawdust bedding and
102 an enrichment toy. Food (Harlan Teklad Laboratory Diet) and water were provided ad
libitum. The temperature of the experimental room was controlled ($19^{\circ}\text{c} \pm 1$), and
104 maintained on a reverse dark-light cycle (light on from 1900-0700 hours), with
observations carried out in the dark phase of the cycle. Red light (60 Watt) allowed
106 the observer to see the rats. The rats were all handled for approximately 15 seconds
each day, for one week prior to the start of the experiment. This was intended to
108 familiarise the subjects to short bouts of handling, in order that transfer of animals
between cages during experiments had minimal effect on behaviour. We used
110 disposable gloves when handling the rats during the experiment, in order to reduce the
chance of odour transfer.

112

The social recognition test

114

This test, developed by Thor and Holloway (1982), is based on the natural

116 investigative behaviour of a rat, in which a rat shows a preference for investigating a
novel conspecific over a familiar one (e.g. Carr et al., 1976). Social discrimination in
118 rats is regulated by the presence of olfactory cues (e.g. Sawyer et al., 1984), and
investigation therefore takes the form of sniffing of the social stimulus, particularly
120 focusing on the ano-genital region (Carr et al., 1976). The test is based upon a
comparison of behaviour, particularly investigation, between two exposures of the
122 same individual to a subject animal, separated by an inter-exposure interval (IEI). A
decrease in investigation in the second exposure implies recognition of the individual.
124 No decrease suggests that the subject's social memory for that individual has decayed
over the IEI, and is the response seen when a novel individual is introduced in the
126 second exposure. This demonstrates that any reduction in investigation is due to
recognition of, and habituation to, a reintroduced stimulus, rather than a non-specific
128 decrease in the motivation to investigate a conspecific per se.

130 A benefit of this test is that it relies on spontaneous behaviour of the rat, but
this also results in a less controlled experimental environment than those tests using
132 operant techniques (e.g. Gheusi et al., 1997). It is also unclear what cues the rats are
remembering and using for the discrimination. In addition to olfactory cues, rats could
134 be discriminating on the basis of visual and auditory, especially ultrasonic, cues (e.g.
Lore and Flannelly, 1977; Sales, 1991). Studies have indicated that it is unlikely,
136 however, that odour deposition, either by the adults on the juveniles, or by the
juveniles in the home cages of the adults, influences the outcome of the social
138 recognition test (e.g. Sawyer et al., 1984; Perio et al., 1989).

140 Although this study was not designed to provoke aggression between animals,

there was a risk of aggression occurring during the social recognition test. To
142 minimise this risk, juveniles were used as stimuli because previous studies had
indicated that immature juveniles elicit little or no aggressive behaviour from adult
144 rats (e.g. Thor, 1979). Other researchers state that although juveniles can be
intimidated by adults, physical injury is rare (Lore and Flannelly, 1977). We found
146 that aggression did occur, but at no point in this study was injury caused by mild
aggression, defined as rolling and standing over the juvenile and/or pushing it away.
148 A researcher was always present to ensure that if overt aggression occurred, e.g.
biting, the encounter was abandoned immediately, with individuals separated before
150 any injury was possible. Those juveniles who experienced overt aggression appeared
to show no subsequent long-term effects, with normal behaviour and food/water
152 consumption observed.

154 Behavioural observations

156 During each exposure of a juvenile to an adult subject rat, the total amount of
investigation and mild aggression, in seconds, expressed by the subject during the
158 course of the test period was continuously recorded by video camera and hand held
event recorder (Psion Organiser II), using Noldus Observer software (Noldus
160 Information Technology 1993). Investigation of the juvenile by the adult was defined
as when the adult was nosing, grooming, sniffing, or following within one centimetre
162 of the juvenile (Thor and Holloway, 1982). Mild aggression consisted of rolling and
standing over the juvenile, and/or pushing it away.

164

Pre-experimental training

166

The fact that, following a 5-min initial exposure, a male adult rat typically
168 recognises a juvenile after an IEI of 30min, but fails to recognise a juvenile after
120min, is often taken as a standard measure of social recognition (e.g. Dantzer et al.,
170 1987; Gheusi et al., 1994b). But there are instances where recognition does not appear
to occur after a 30-min IEI, notably in sexually inexperienced, young (3-months-old)
172 adult males (e.g. Hlinak and Krejci, 1991; Engelmann et al., 1995). For this reason we
made preliminary observations during pre-experimental training, to ensure that the
174 initial exposure and IEI length selected for the disturbance experiments allowed
successful recognition.

176

This also allowed us to remove not only any overtly aggressive rats, but those
178 which failed to investigate the juveniles reliably. The pre-experimental training
session consisted of an exposure to the same juvenile, once a day for four consecutive
180 days. Half the adults received exposures of 5-min duration, the remainder received
exposures of 15min. We introduced a novel juvenile on the fifth day, followed by re-
182 exposure to the original juvenile on the sixth day. A second exposure on the sixth day
of the same original juvenile to the adults, after a short inter-exposure interval of
184 either 15 or 25 minutes, was designed to reveal which combination of initial exposure
and inter-exposure interval lengths was most suitable for use in the main experiments
186 reported here.

188 Experiment one

190 This experiment was designed to investigate the effect of introducing different
potentially disturbing environmental stimuli, (see Table 1), on the social memory of
192 laboratory rats.

194 *Table One*

196 These treatments, excluding the control treatment (treatment A), were selected
as being representative of elements of commonly occurring husbandry/experimental
198 procedures. If these treatments were found to have a disruptive effect on the social
memory of laboratory rats, then this could have important implications for the welfare
200 of these animals, and the accuracy of some experimental research (see Introduction).

202 Method

204 Two of the 12 potential subjects (3-months-old) for this experiment were
excluded due to inappropriate behaviour during pre-experimental training. One was
206 too aggressive, and the other investigated the juvenile stimulus unreliably, displaying
apparently submissive behaviour. We therefore used 10 rats in two replicates (N=5
208 per replicate).

210 The results obtained from pre-experimental training suggested the chosen
timing regime. The experimental procedure consisted of an initial 5-min exposure of a
212 particular juvenile to a resident adult e.g. “A1”, followed by a 15-min IEI before
reintroduction of the same juvenile, “A2”, (see Fig. 1). After 5min of the IEI, each
214 adult was exposed to its particular treatment for a 5-min period. Each adult

experienced the procedure once on each experimental day. The effect of treatment
216 order on the behaviour of the subject animals was taken into account by using a Latin
square design (5 X 5). This experimental design also ensured that the number of
218 animals used was minimised (Still, 1982). The two replicates were tested on alternate
days such that each rat received all five of the treatments, one every other day, the
220 order determined by the Latin square. All exposures to the juvenile stimuli took place
in the home cage of the subjects. Sixteen juveniles were required in total, with adults
222 encountering a different juvenile on all five test days, and no juvenile used more than
once for the same treatment. All the juvenile stimuli were entirely novel to the
224 subjects.

226 *Figure One*

228 Investigation and mildly aggressive behaviour were recorded for analysis (see
earlier). The novel environments (treatments D & E) were wiped down with a mild
230 disinfectant before the introduction of the adult rats in order to reduce the possible
influence of lingering odours.

232

Data analysis

234

Data ($N=10$) were assessed for normality and homogeneity of variance, and
236 those that failed to meet these criteria underwent logarithmic transformation. Pre-
treatment behaviour was analysed first, to ensure that there were no pre-treatment
238 differences between the treatment groups. The difference between pre-treatment and
post-treatment behaviour was then calculated (first - second exposure) and analysed.

240 The difference in the total amount of behaviour displayed during each of the two
exposures to the juvenile was used as a measure of behavioural change, because other
242 measures, such as ratios (e.g. Perio et al., 1989), can fail to uncover differences in the
absolute size of response. The data were analysed initially using a GLM for repeated
244 measures, with treatment (1-5) and pre-experimental training experience (5 or 15min)
as factors. Paired t-tests were used to investigate specific differences within individual
246 treatments. The statistical package used was Minitab (Minitab Inc. 1996).

248 Results

250 There was no difference between the five treatments in the amount of either
investigation ($F_{4,32}=1.39$, N.S.) or mild aggression ($F_{4,32}=1.11$, N.S.) expressed pre-
252 treatment. There was also no effect of previous experience, or any interaction between
experience and treatment, for either investigation or mild aggression. When the
254 difference in behaviour between the two exposures was analysed, a significant effect
of treatment on investigation was found ($F_{4,32}=2.75$, $P<0.05$), but no effect on mild
256 aggression ($F_{4,32}=1.42$, N.S.). Again, there was no effect of previous experience, or
interaction between experience and treatment, for either investigation of mild
258 aggression.

260 *Figure Two*

262 Paired t-tests were used in order to ascertain in what way each of the
treatments were influencing the change in investigative behaviour between the first
264 and second exposures (see Fig. 2). No significant change in investigation was

observed between exposures for treatments B (handling), C (novel conspecific) or D
266 (small novel environment). But a significant decrease in investigation was seen for
both treatment A (control) ($T=2.98$, $N=9$, $P<0.05$) and treatment E (novel
268 environment) ($T=4.19$, $N=9$, $P<0.001$). It therefore seems that the treatments had
different effects on the investigative behaviour of the subject rats.

270

Discussion

272

These results suggest that during both the control and novel environment
274 treatments the rats retained a memory of the juvenile conspecific over the 15-min
inter-exposure interval. The introduction of the rats to a novel environment of similar
276 size to their home cage did not appear, therefore, to disrupt their social memory. The
remaining treatments, however, did appear to disrupt social memory. The apparent
278 interference effect of a novel conspecific confirmed the results of previous studies
(Thor and Holloway, 1982; Dantzer et al., 1987). There appeared to be no effect of
280 different pre-experimental training experience on the subsequent behaviour of the
adult subjects.

282

The introduction of a novel conspecific is the treatment most closely linked
284 with the 'learning task' itself, and may directly compete with information stored about
the original juvenile. Differences in the effect on behaviour between the two novel
286 environment treatments suggest that the increased confinement of the smaller
environment was likely to have been the cause of the observed disruption of social
288 memory. The subject rats had experienced only brief bouts of handling prior to the
implementation of the handling treatment. It is therefore possible that an increase in

290 stress caused by this treatment resulted in a disruption of social memory. It should be
noted that because each treatment was implemented half way through the IEI, they
292 might have affected either memory consolidation or recall (see Mendl, in press).

294 An alternative explanation for the observed results is that the treatments
caused the investigative behaviour of the rats in the second exposure to rise above the
296 expected habituated levels despite an intact social memory, possibly by affecting non-
specific states of arousal or motivation. Attempting to determine whether treatments
298 have disrupted social memory or provoked an increase in motivation or arousal is
problematic. For example, one might expect an aroused adult to investigate a novel
300 juvenile introduced for the second exposure significantly more than if the original
juvenile had been reintroduced. But even if this was the case it may still not prove
302 conclusively that the treatment was having an arousing effect, as significant increases
in investigation can occur upon the introduction of a novel juvenile even when no
304 treatment has occurred (e.g. Sekiguchi et al., 1991). Because of this difficulty, we
focused our attention on treatment E (novel environment), which had not appeared to
306 disrupt social memory.

308 Experiment two

310 This experiment was designed to confirm the findings of experiment one, and
investigate the effect of treatment disturbance on the social memory of the subject rats
312 by comparing behaviour following reintroduction of the original juvenile stimulus
(A²) with that following the introduction of a novel juvenile (B) (see Fig. 3). In the
314 previous experiment we observed that the removal of an adult rat from its home cage

to a large novel environment apparently failed to disrupt the social memory of that rat
316 for a juvenile conspecific, allowing recognition. Alternative explanations for this
result are that the juvenile was not actually recognised, but that investigation was
318 reduced either because of the adult habituating to the experimental procedure, or the
treatment itself acting to suppress behaviour. Both of these explanations also predict a
320 similar reduction in investigative behaviour if a novel juvenile is introduced for the
second exposure, whereas an increase in investigation might be expected if no
322 disruption to social memory is occurring. The same technique has been used to
distinguish between non-specific and specific effects of drug treatments on social
324 memory (e.g. Perio et al., 1989; Gheusi et al., 1994b).

326 *Figure Three*

328 In this experiment, four treatments were used (see Table 2).

330 *Table Two*

332 Method

334 Two of the 10 rats, previously 2-months-old, were excluded because of overt
aggression during pre-experimental training, so eight rats, now three months old, were
336 used. Two replicates (N=4) of a Latin square design (4 X 4) were used to assign
treatment order across time, and 16 juveniles were used in total. As before, all
338 juveniles were introduced only twice a day, were used for different treatments each
day, and were entirely novel to the particular adult to whom they were introduced.

340 The two replicates were tested on alternate days such that each rat received all four of
the treatments, one every other day, with treatment order determined by the Latin
342 square design. The novel environment was cleaned with a mild disinfectant between
uses. Investigation of, and mild aggression directed towards, the juvenile was
344 recorded.

346 Data analysis

348 Data ($N=8$) were treated as before (see experiment one).

350 Results

352 No significant difference between the four treatments types in the relative
amounts of either investigation or mild aggression was observed pre-treatment. There
354 was also no effect of previous experience, or any interaction between experience and
treatment, for either investigation or mild aggression.

356

Figure Four and Figure Five

358

Paired t-tests were used to investigate exactly how the different treatments
360 each affected investigation and mild aggression. Significant changes in the amount of
investigation between the two exposures to the juvenile stimuli were discovered for
362 three out of the four treatments (see Fig. 4). Treatment one (no interference, same
juvenile reintroduced) ($T=4.00$, $N=7$, $P<0.01$) and treatment two (novel environment,
364 same juvenile reintroduced) ($T=2.76$, $N=7$, $P<0.05$) both showed significant

reductions in the amount of investigation between exposures, whereas treatment three
366 (no interference, novel juvenile introduced) displayed a significant increase in
investigative behaviour ($T=-2.83$, $N=7$, $P<0.05$). Investigation also increased in
368 treatment four (novel environment, novel juvenile introduced), and this increase was
nearly significant ($T=-2.24$, $N=7$, $P=0.06$). The only significant change in the amount
370 of mild aggression observed, was an increase in mild aggression following the
implementation of treatment one (no interference, same juvenile reintroduced) ($T=-$
372 2.43 , $N=7$, $P<0.05$) (see Fig.5).

374 Discussion

376 These results confirmed the findings of experiment one in which treatments A
(no interference, same juvenile reintroduced) and E (novel environment, same
378 juvenile reintroduced), showed similar decreases in investigation, suggesting that, for
both those treatments, the adult rats recognised the juveniles reintroduced into their
380 home cages.

382 The results also demonstrate that any observed reduction in the amount of
investigation of the juvenile by the adult rat was due primarily to the habituation of
384 the subject to the stimulus, i.e. recognition, rather than because of any behaviour
suppressing property of the treatment, or general habituation to the experimental
386 procedure. This emphasises the importance of introducing a novel juvenile as a
control to distinguish between specific and non-specific effects of treatment (e.g.
388 Perio et al., 1989; Gheusi et al., 1994b).

390 General discussion

392 The results of experiment one indicate that the implementation of some elements of
common husbandry/experimental procedures appears to be sufficient to disrupt the
394 short-term social memory of an adult laboratory rat, although we are as yet unable to
completely rule out the possible effects of these environmental stimuli on non-specific
396 states of arousal or motivation. Removal to a large novel environment did not appear
to interfere with the social memory of the adult rats, and experiment two confirmed
398 that any reduction in the total amount of observed investigation was unlikely to be
due to behavioural suppression or motivational change.

400

Other researchers have observed anecdotally that the way animals are handled
402 can be important for minimising variation in baseline investigation times (Dantzer et
al., 1987), and that removal from the home cage between exposures fails to interfere
404 with subsequent recognition (Perio et al., 1989). This paper, in contrast, specifically
investigated the effects of mild environmental stimuli on social memory, and
406 therefore has implications for the use of the social recognition test in research.

Experiments that apparently indicate recognition failure may actually result as a side
408 effect of the experimental technique itself, i.e. excessive handling, rather than because
of the specific treatment. The influence of these external factors should therefore be
410 taken into account. The findings of this experiment also reflect work on the disruption
of spatial memory in pigs (e.g. Mendl et al., 1997; Laughlin et al., 1999) and
412 demonstrate that, at least in the short term, social memory in rats can be disrupted.

The exact way in which the memory has been disturbed is more open to question. The
414 introduction of an environmental stimulus shortly after the learning task may disrupt

memory formation, or, once the social memory for a particular individual has been
416 formed, the introduction of an environmental stimulus may act to block attempts to
retrieve the retained memory (Mendl, in press).

418

When compared to the spatial memory of rats, social memory appears more
420 susceptible to disruption, even by relatively mild environmental stimuli. There may be
species specific reasons for this apparent discrepancy. For a group living animal like
422 the wild rat (Barnett 1963) it is perhaps only worth forming a lasting memory of
another individual if there is a high probability of repeat encounters with the same
424 individual over a short space of time (Caldwell 1985), particularly if this recognition
forms the basis for a dominance hierarchy (Pagel & Dawkins 1997). This may be
426 difficult for a rat to evaluate on a first encounter, so it may not be cost-effective to
keep forming a memory of a new individual on the first meeting, as that same
428 individual may never be encountered again. There is strong biological foundation for
the notion that maintenance of accurate memories requires substantial resource
430 expenditure (Dukas 1998). In direct contrast to social memory, spatial memory needs
to be more immediately resistant to disturbance over the short-term. The location of a
432 food source or a potential nest site, and routes to and away from familiar areas, must
instantly be stored in memory otherwise the animal could starve or become lost. There
434 is therefore potentially a far greater requirement for spatial memory to be remembered
in the short-term because of the greater cost to the animal of memory failure. One
436 could therefore predict that spatial memory is less susceptible to disturbance over
short-term than social memory, as found, but that social memory will become
438 increasingly resistant to disruption after long term formation. One might also predict
that those individuals who ‘mean’ more to a specific individual will be remembered

440 faster and be more resistant to disruption than those with little, or no, meaning, i.e. the
referent of the social stimulus may have a direct effect on the way it is processed.

442

Conclusions

444

These results could have implications for the welfare of both laboratory rats
446 and other captive social animals. The removal of an individual rat from a social group
followed by the inadvertent introduction of a potentially disruptive environmental
448 stimulus, may mean that upon return to its social group the rat is unable to recognise
its former companions, resulting in an increase in aggression and corresponding
450 reduction in welfare. However, this study looked only at the effects of environmental
disturbance on short-term social memory. It is likely that with a longer initial
452 exposure, social memory will become more resistant to disruption. It is therefore
essential that the current work is followed up by investigation into more long-term
454 social memory.

456 Acknowledgements

458 This research was supported by a University of Bristol Postgraduate Scholarship. We
would like to thank Innes Cuthill, Suzanne Held, Christine Nicol and an anonymous
460 referee for comments on the manuscript. With thanks also to A.V. & W. F-C.

462 References

464 Barnett, S.A., 1963. A study in behaviour - principles of ethology and behavioural

physiology, displayed mainly in the rat. The Camelot Press Ltd, London and
466 Southampton.

Bradshaw, R.H., 1991. Discrimination of group members by laying hens Gallus
468 domesticus. Behavioural Processes 24, 143-151.

Caldwell, R.L., 1985. A test of individual recognition in the stomatopod
470 Gonodactylus festae. Animal Behaviour 33, 101-106.

Carr, W.F., Yee, L., Gable, D., Marasco, E., 1976. Olfactory recognition of
472 conspecifics by domestic Norway rats. Journal of Comparative and
Physiological Psychology 90, 821-828.

474 Dantzer, R., Bluthé, R-M., Koob, G.F, Le Moal, M., 1987. Modulation of social
memory in male rats by neurohypophyseal peptides. Psychopharmacology 91,
476 363-368.

Dasser, V., 1988. A social concept in Java monkeys. Animal Behaviour, 36, 225-230.

478 Dukas, R., 1998. Constraints on information processing and their effects on
behaviour. In: Dukas, R. (Ed.), Cognitive Ethology - the evolutionary ecology
480 of information processing and decision making, The University of Chicago
Press, Chicago and London.

482 Engelmann, M., Wotjak, C.T., Landgraf, R., 1995. Social discrimination procedure -
an alternative method to investigate juvenile recognition abilities in rats.
484 Physiology and Behavior 58, 315-321.

Ewbank, R., Meese, G.B., 1971. Aggressive behaviour in groups of domesticated
486 pigs on removal and return of individuals. Animal Production 13, 685-693.

Gheusi, G., Bluthé, R-M., Goodall, G., Dantzer, R., 1994a. Social and individual
488 recognition in rodents: methodological aspects and neurobiological bases.
Behavioural Processes 33, 59-88.

490 Gheusei, G., Bluthé, R-M., Goodall, G., Dantzer, R., 1994b. Ethological study of the
effects of Tetrahydroaminoacridine (THA) on social recognition in rats.
492 *Psychopharmacology* 114, 644-650.

Gheusi, G., Goodall, G., Dantzer, R., 1997. Individually distinctive odours represent
494 individual conspecifics in rats. *Animal Behaviour* 53, 935-944.

Hlinak, Z., Krejci, I., 1991. Social recognition in male rats: age differences and
496 modulation by MIF-I and Alaptide. *Physiological Research* 40, 59-67.

Karavanich, C., Atema, J., 1998. Individual recognition and memory in lobster
498 dominance. *Animal Behaviour* 56, 1553-1560.

Kendrick, K.M., Atkins, K., Hinton, M.R., Heavens, P., Keverne, B., 1996. Are
500 faces special for sheep? Evidence from facial and object discrimination
learning test showing effects of inversion and social familiarity. *Behavioural*
502 *Processes* 38, 19-35.

Laughlin, K., Huck, M., Mendl, M., 1999. Disturbance effects of environmental
504 stimuli on pig spatial memory. *Applied Animal Behaviour Science*, 64, 169-
180.

506 Lore, R., Flannelly, K., 1977. Rat societies. *Scientific American* 236, 106-116.

Maki, W.S., Brokofsky, S., Berg, B., 1979. Spatial memory in rats: resistance to
508 retroactive interference. *Animal Learning & Behavior* 7, 25-30.

Mendl, M., In Press. Performing under pressure: stress and cognitive function.
510 *Applied Animal Behaviour Science*.

Mendl, M., Laughlin, K., Hitchcock, D., 1997. Pigs in space: spatial memory and its
512 susceptibility to interference. *Animal Behaviour* 54, 1491-1508.

Minitab Inc. 1996. Reference Manual, Version 11. State College, Philadelphia:
514 Minitab.

- Noldus Information Technology 1993. The Observer Base Package. Reference
516 Manual, Version 3.0. Wageningen, The Netherlands: Noldus Information
Technology.
- 518 Pagel, M., Dawkins, M.S., 1997. Peck orders and group size in laying hens: 'futures
contracts' for non-aggression. *Behavioural Processes* 40, 13-25.
- 520 Perio, A., Terranova, J.P., Worms, P., Bluthé, R-M., Dantzer, R., Biziere, K., 1989.
Specific modulation of social memory in rats by cholinomimetic and nootropic
522 drugs, by benzodiazepine inverse agonists, but not by psychostimulants.
Psychopharmacology 97, 262-268.
- 524 Roberts, W.A., 1981. Retroactive inhibition in rat spatial memory. *Animal Learning
and Behavior* 9, 566-574.
- 526 Rodriguez, W.A., Borbely, L.S., Garcia, R.S., 1993. Attenuation by contextual cues
of retroactive interference of a conditional discrimination in rats. *Animal
528 Learning and Behavior* 21, 101-105.
- Sales, G.D., 1991. The effect of 22 kHz calls and artificial 38 kHz signals on activity
530 in rats. *Behavioural Processes* 24, 83-93.
- Sawyer, T.F., Hengehold, A.K., Perez, W.A., 1984. Chemosensory and hormonal
532 mediation of social memory in male rats. *Behavioural Neurosciences* 98, 908-
913.
- 534 Sekiguchi, R., Wolterink, G., van Ree, J.M., 1991. Short duration of retroactive
facilitation of social recognition in rats. *Physiology & Behavior* 50, 1253-
536 1256.
- Still, A.W., 1982. On the number of subjects used in animal behaviour experiments.
538 *Animal Behaviour* 30, 873-880.
- Thor, D.H., 1979. Olfactory perception and inclusive fitness. *Physiological*

540 Psychology 7, 303-306.

Thor, D.H., Holloway, W.R., 1982. Social memory of the male laboratory rat.

542 Journal of Comparative Physiology & Psychology 96, 1000-1006.

Wolfensohn, S., Lloyd, M., 1994. Handbook of laboratory animal management and

544 welfare. Oxford University Press, Oxford.

546 Table 1: Descriptions of the different treatments received between exposures

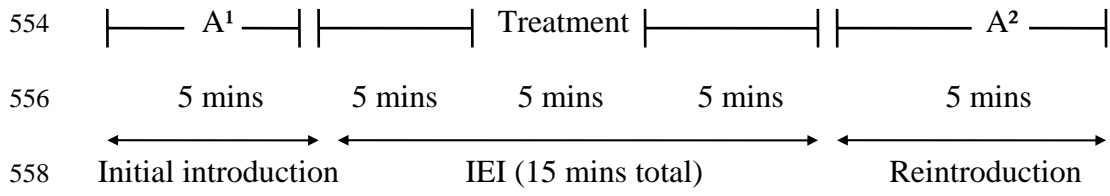
Treatment A	No Interference (control): Subject remains in home cage between introductions of juvenile
Treatment B	Handling: Subject is handled in its home cage for five minutes between juvenile introductions, consisting of being picked up every 15 seconds for five seconds
Treatment C	Novel Juvenile: A novel juvenile is introduced to the home cage of the subject for five minutes between exposures of the original juvenile
Treatment D	Small novel environment: Subject was introduced to a small novel environment measuring 30 X 13 X 11cm with a plastic floor surface for 5 minutes between introductions of the juvenile
Treatment E	Novel Environment: Subject was introduced to a novel environment measuring 33 X 50 X 21cm (same size as the home cage) with a metal wire floor surface for five minutes between introductions of the juvenile

548 Table 2: Descriptions of different treatments received between exposures

Treatment 1	No Interference (Same): Subject remains in home cage between introductions of same juvenile.
Treatment 2	Novel Environment (Same): Subject was introduced to a novel environment measuring 33 X 50 X 21cm with a metal wire floor surface for five minutes between introductions of the same juvenile.
Treatment 3	No Interference (Novel): Subject remains in home cage between introductions of novel juveniles.
Treatment 4	Novel Environment (Novel): Subject was introduced to a novel environment measuring 33 X 50 X 21cm with a metal wire floor surface for five minutes between introductions of the novel juveniles.

550 Figure One

552



560

Figure Three

562

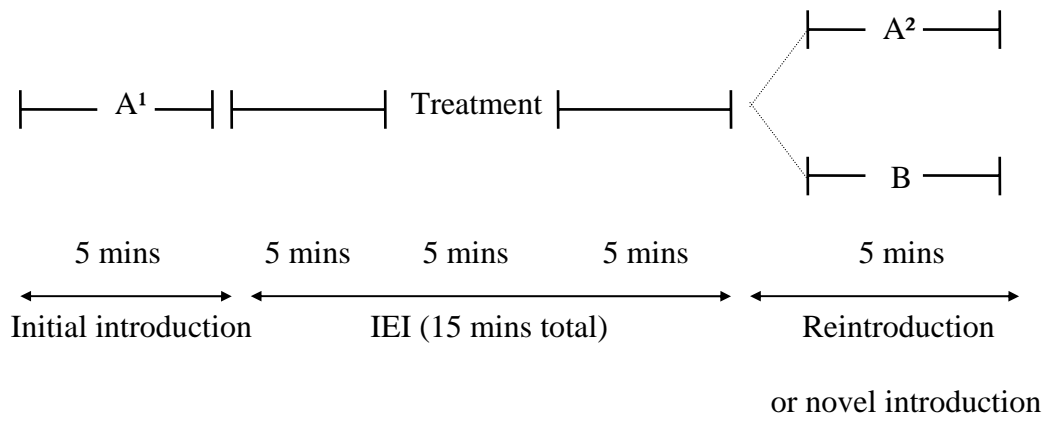
564

566

568

570

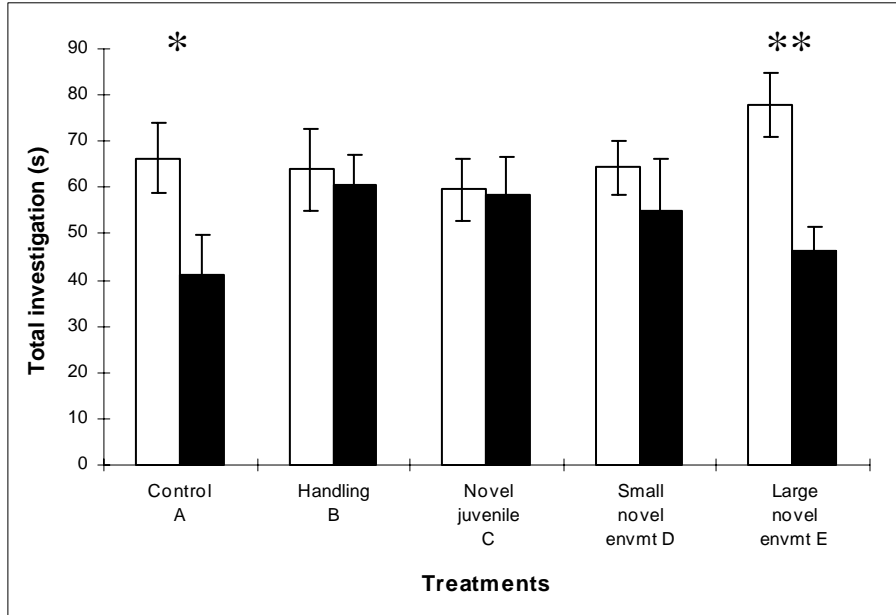
572



574

576

578 Figure Two:

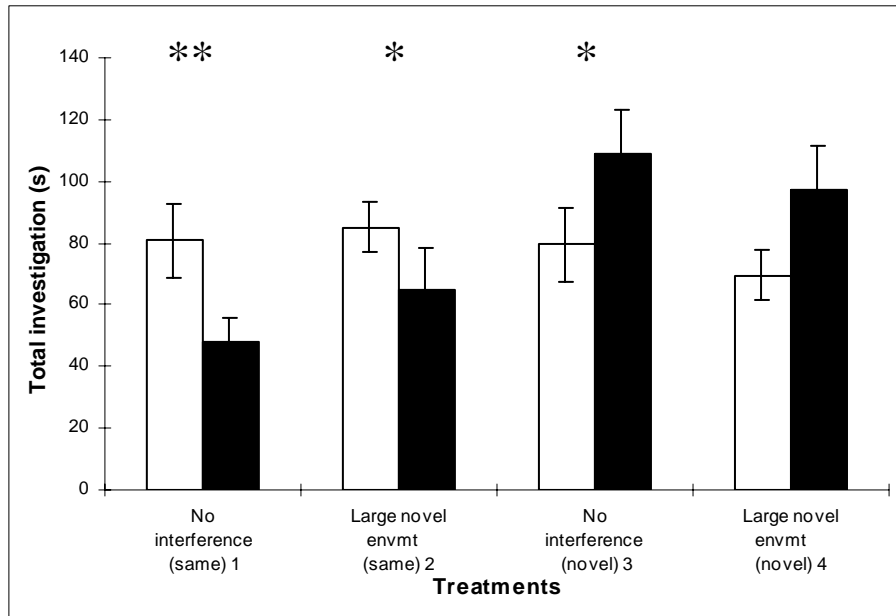


580

582

Figure Four:

584

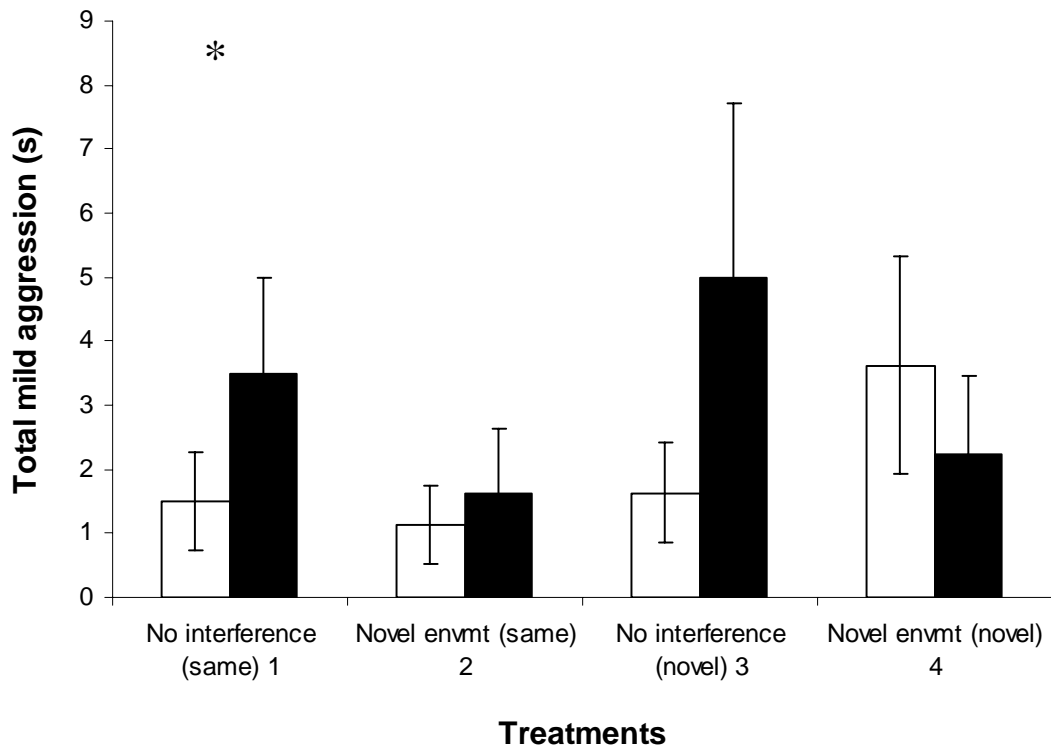


586

588

Figure Five:

590



592

594

596 Figure 1. The protocol for experiment one, with a disturbance treatment introduced
midway through the inter-exposure interval, and the same juvenile stimuli
598 reintroduced for the second exposure.

600 Figure 2. Change in the total amount of investigation of the juvenile stimuli by the
adult subjects between exposures, for five different treatments. The white columns
602 represent mean \pm SE pre-treatment, the black columns represent mean \pm SE post-
treatment. * $P < 0.05$; ** $P < 0.01$

604

Figure 3. The protocol for experiment two, with a disturbance treatment introduced
606 midway through the inter-exposure interval, and either the same juvenile stimuli
reintroduced, or a novel juvenile introduced, for the second exposure.

608

Figure 4. Change in the total amount of investigation of the juvenile stimuli by the
610 adult subjects between exposures, for four different treatments. The white columns
represent mean \pm SE pre-treatment, the black columns represent mean \pm SE post-
612 treatment. * $P < 0.05$; ** $P < 0.01$

614 Figure 5. Change in the total amount of mild aggression directed towards the juvenile
stimuli by the adult subjects between exposures, for four different treatments. The
616 white columns represent mean \pm SE pre-treatment, the black columns represent mean
 \pm SE post-treatment. * $P < 0.05$