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The effects of environmental context on laboratory rat social recognition

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OLIVER BURMAN¹ & MICHAEL MENDEL

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

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¹*Corresponding Author*

20

Abstract

22 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
24 the effect of switching environmental contexts on the ability of adult laboratory rats,
Rattus norvegicus, to recognize and habituate to repeated presentations of juvenile
26 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
28 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
30 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
32 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
34 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
36 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
38 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
40 minor role in the short-term social memory of laboratory rats.

There is increasing evidence that the environmental context in which an experiment
44 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
46 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
48 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,
50 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
52 & 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
54 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
56 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
58 a failure of social recognition, and subsequent inappropriate aggression. It is,
therefore, of both fundamental and applied interest to investigate the influence of
60 context specificity on animal learning and memory.

62 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
64 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
66 conspecific independently of the context in which that individual has been introduced

(e.g. Falls & Brooks 1975; Snowdon & Cleveland 1979; Waas & Colgan 1994). To
68 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
70 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
72 as an indication that the conspecific is recognized, because dishabituation occurs
when a novel conspecific is presented.

74
Previous investigations of whether habituation shows context specificity, have
76 revealed conflicting results. Some researchers have found that habituation does
successfully transfer across contexts (e.g. Marlin & Miller 1981); others have
78 observed dishabituation following context change (e.g. Evans & Hammond 1983).
Such studies have been criticized, however, for being inadequately controlled (e.g.
80 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,
82 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 &
84 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
86 context specificity. These studies of habituation have focused on unconditioned
responses such as orientation towards light (Hall & Channell 1985), consumption of a
88 novel flavour (Honey et al. 1992) and disruption of an appetitively rewarded response
by stimulus (either light or tone) presentation (Hall & Honey 1989).

90

The aim of this experiment was to produce further evidence on whether
92 habituation shows context specificity, and to extend previous work by focusing on the
social behaviour of the laboratory rat, particularly the habituation of investigative
94 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
96 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
98 social learning and memory.

100 METHODS

102 Subjects, Housing and Care

104 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
106 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
108 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
110 ($20^{\circ}\text{c} \pm 1$) 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
112 Watt) was provided during testing.

114 Experimental Design

116 We used the social recognition test (Thor & Holloway 1982), which is based
upon a comparison of behaviour, particularly investigation, between two exposures of
118 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
120 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
122 introduced in the second exposure. We also used elements of the habituation-
discrimination technique (e.g. Halpin 1986; Johnston 1993; Johnston & Jernigan
124 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
126 a novel individual, which may or may not result in dishabituation.

128 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
130 exposures, such as six bouts of 5 min, separated by short IEs of 10 min (Sekiguchi et
al. 1991). Social memory after short term exposures appears to be relatively brief,
132 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.
134 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
136 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
138 dishabituation.

140 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
142 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
144 investigation and mildly aggressive behaviour during the introductions. Investigation
of the juvenile included sniffing, grooming and following within a distance of 1cm
146 (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,
148 resulted in the session being abandoned immediately. We recorded these categories of
observations continuously throughout the experiment, collecting them using a hand
150 held event recorder (Psion Organiser II) with Noldus Observer software, and also by
video camera.

152

We used 8 of the juveniles as social stimuli in the pre-experimental training,
154 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
156 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
158 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
160 day for 8 days, with treatment order balanced over time.

162 *Table One*

164 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
166 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
168 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.

170

 A frequent criticism of context experiments is that, depending on the
172 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
174 this experiment the two different contextual environments, context A (white) and
context B (black), were designed to take into account the potential confounding
176 effects that any physical modifications, such as differences in overall surface area,
might have on subject behaviour (see Table 2).

178

Table Two

180

 Rats in treatment D2, which required experience of both contexts before the
182 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
184 session of context familiarization being completed 24 h before the first exposure of
the experiment itself.

186

 All exposures of the juvenile to the adult rat lasted for 5 min, with both the
188 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
190 effect of olfactory cues. All the rats had been given previous experience of handling
to reduce any possible effects on behaviour.

192

Ethical Note

194

Although this study was not designed to promote aggression between animals,
196 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
198 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
200 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.
202 Those juveniles who had experienced overt aggression appeared to show no
subsequent long term effects, with normal behaviour and food/water consumption
204 observed.

206 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
208 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
210 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
212 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

214 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
216 another so that any overtly aggressive encounters could be terminated immediately.
Initial pre test 'training' also provided the opportunity to remove any overtly
218 aggressive rats from the experiment.

220 RESULTS

222 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
224 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
226 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
228 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
230 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
232 Minitab (version 11).

234 We compared the three treatments for differences in the total amount of
investigative and mildly aggressive behaviour exhibited during the first exposure. The
236 mild aggression data were transformed logarithmically to meet requirements for
normality and homogeneity of variance. Analysis of investigation was performed on
238 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
240 treatment. A Tukey's pairwise comparison revealed that this difference between
treatments was due to rats in treatment D2 showing more investigation ($T=12.3$,
242 $P=0.05$) and mild aggression ($T=0.25$ (transformed), $P=0.05$) than those in the other
treatments.

244

To determine whether habituation to the introduction of the juvenile stimulus
246 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
248 were insufficient data to include context into the analysis. For this reason, we
analysed treatment D2 separately using a balanced ANOVA for repeated measures,
250 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
252 ($F_{2,8}=13.28$, $P<0.01$) over the three exposures, but no significant change in mild
aggression (see Fig. 1). Post hoc analysis (Tukey's pairwise comparison) of this result
254 revealed that, although the treatment means for investigation decreased across
exposures one, two and three (means: 94; 55; 47.2 respectively), only the decreases
256 between exposures one and two, and exposures one and three were significant
($T=27.8$, $P=0.05$).

258

Treatments S1 and D1 were analysed using a balanced ANOVA for repeated
260 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
262 logarithmically, with analysis of investigation performed on the raw data. No
significant difference was found between treatments S1 and D1 for either

264 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
266 ($F_{2,32}=6.3, P<0.01$) 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
268 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
270 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
272 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
274 exposures one to three ($T=0.21, P=0.05$).

276 *Figure One*

278 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
280 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
282 recognize the familiar conspecific in a different context. The data failed to attain the
requirements of normality and homogeneity of variance after transformation, and
284 were therefore analysed using the non parametric Wilcoxon signed-ranks test (two
tailed). No significant changes in either investigation or mildly aggressive behaviour
286 were observed for treatments S1 and D2 between the third and fourth exposures.
However, treatment D1 showed significant reductions in the amount of both
288 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
290 1.).

292 DISCUSSION

294 Habituation, in terms of declining amounts of investigation, occurred over three
separate encounters with the same individual, despite the increasing familiarity with
296 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
298 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
300 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
302 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
304 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
306 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
308 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
310 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
312 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

314 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
316 three initial exposures.

318 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
320 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
322 had not been changed (treatment S1). This implies continued recognition of the
conspecific in a different context and suggests that environmental context, in this
324 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
326 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
328 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
330 provided with previous experience of both the different environmental contexts,
displayed more investigation and mild aggression than those rats to whom the
332 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
334 might also be that the increased time spent exploring a novel environment simply
results in less time available for interaction with the juvenile.

336

 These results confirm work by Hall & Channell (1985) and Honey et al.
338 (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
340 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
342 consumption of the flavour by the rats. The assertion that unlike other types of
learning, such as classical conditioning, operant conditioning, and latent inhibition,
344 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
346 social recognition of conspecifics, as determined by observed levels of investigation.

348 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
350 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
352 novel (treatment D1) argues against this. The contexts must have been sufficiently
different to allow recognition of the new surroundings. Another problem with context
354 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
356 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
358 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
360 was more frequent, implying that the juvenile was no more difficult to locate in one
context than in the other.

362

The rats in treatment D2, which had been given familiarization training in the
364 two different environmental contexts before exposure to the juveniles, were
unexpectedly aggressive. This may have implications for animal welfare if experience
366 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
368 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
370 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
372 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
374 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
376 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.
378 Ewbank & Meese 1971), and that may be caused by a failure of recognition.

380 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
382 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
384 that contextual cues might play in social recognition and memory in non human
animals, particularly when this involves long-term memory.

386

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388

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rivals on the basis of visual cues alone. Animal Behaviour, 47, 7-13.

474 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

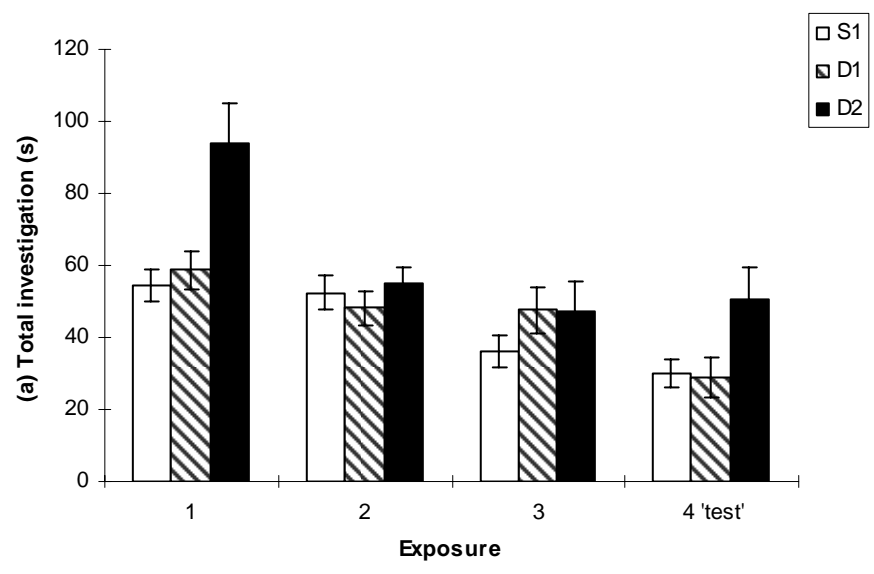
Table 2. The contextual environments and their differences in physical modification

	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

478

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

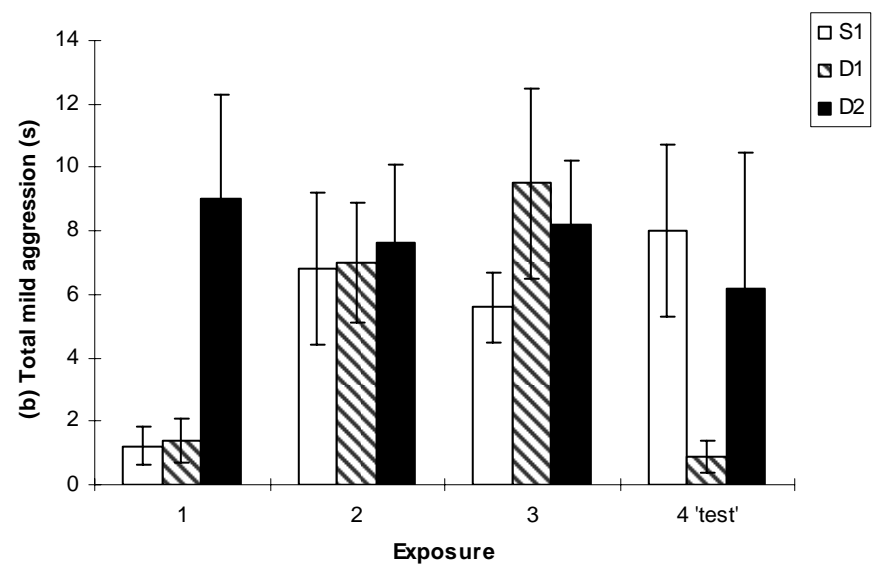
(a)



486

488

(b)



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