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10 Recognition of conspecific odours by laboratory rats (*Rattus norvegicus*)

11 does not show context specificity.

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13

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15

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17

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19

20

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Abstract

22

23 This experiment investigated the effect of contextual cues on the recognition of
24 conspecific odours by laboratory rats. Subjects received five encounters with the same
25 odour stimulus in the same context. For the sixth 'test' encounter all rats received a
26 simultaneous presentation of the original and a novel odour. We tested one group of
27 rats, 'context-same', in the same context as before. For the remaining two groups the
28 test encounter was in a different context which one group 'context-different' had
29 experienced, whilst the other group 'context-novel' had not. We observed successful
30 recognition – based on a significant preference for investigating the novel over the
31 original odour – for 'context-same' and 'context-different' rats, but not for 'context-
32 novel' rats. These results suggest that odour recognition can occur following transfer
33 to a different, but familiar, test context, indicating a lack of context specificity.

34 Contextual cues, both external (e.g. Rodriguez et al. 1993) and internal (e.g.
35 Holloway & Wansley 1973), appear to play an important role in animal learning and
36 memory (e.g. Spear 1973; Bouton & Peck 1989; Bouton & Swartzentruber 1989). For
37 example, social memory, the ability to encode, retain and refer to information related
38 to a conspecific over time, can appear to be influenced by contextual cues such as
39 location. Peeke and Veno (1973) demonstrated in stickleback fish that following
40 habituation of aggressive behaviour to a conspecific, dishabituation was observed
41 when a novel conspecific was introduced. However, the aggressive response was
42 significantly higher when the intruder was presented in a novel location than when
43 presented in the same location as the original conspecific. Such a result suggests that
44 aspects of the environmental context can affect the social recognition of conspecifics.

45

46 Wild rats live in large colonies consisting of numerous small social units
47 (Barnett 1963) centred on areas of reliable food availability, i.e. rubbish dumps (e.g.
48 Lore & Flannelly 1977). Recognition of conspecifics, particularly those of an
49 immediate social group, may remove the need for continued reassessment of
50 repeatedly encountered individuals (e.g. Pagel & Dawkins 1997). However, for other,
51 less frequently encountered members of a colony, unnecessary memories for
52 individuals may prove costly (e.g. Dukas 1998). For such individuals, identification
53 may instead be reinforced by the incorporation of contextual 'aides memoires' – with
54 identity closely linked with contextual cues such as location and surroundings.
55 Indeed, it may be difficult to determine whether a subject is recognising an individual
56 conspecific independently of the context in which that individual has been introduced
57 (e.g. birds: Falls & Brooks 1975, Langmore 1998; mammals: Snowdon & Cleveland
58 1979; fish: Waas & Colgan 1994).

59

60 In our previous experiment looking at the effect of contextual change on social
61 recognition in laboratory rats (Burman & Mendl 1999), we found that following a
62 switch to a different, but familiar, test context, subject rats appeared to successfully
63 recognise a familiar juvenile conspecific. Recognition was inferred from a continued
64 habituation of investigative responses to the juvenile, despite the change in context.
65 However, the omission of animals that behaved aggressively in this previous study
66 resulted in a decreased sample size, so we decided to evaluate this result in the current
67 study. In order to avoid aggression, we extended the previous study by using
68 conspecific odours as stimuli, rather than the conspecifics themselves.

69

70 Olfactory cues play a major role in the social behaviour of rodents (Brown &
71 MacDonald 1985). Odours are used both to discriminate between individual
72 conspecifics (e.g. hamsters: Petrulis et al. 1999; rats: Gheusi et al., 1997; guinea pigs:
73 Beauchamp & Wellington 1984; ground squirrels: Mateo & Johnston 2000) and to
74 communicate information about social relationships (e.g. dominance) to fellow
75 conspecifics (e.g. mice: Hurst et al., 1994; Humphries et al., 1999). Evidence that
76 such olfactory cues represent the identity of individual animals is demonstrated by the
77 substitutability of urine or soiled bedding for live animals as social stimuli in
78 recognition tests (e.g. Sawyer et al. 1984). Olfactory secretions have also been used to
79 demonstrate apparent multi-factor representations of individual identity (Johnston &
80 Jernigan 1994, Johnston & Bullock 2001).

81

82 The results of our previous study (Burman & Mendl, 1999) also suggested that
83 recognition persisted in a completely novel context, as demonstrated by a continued

84 habituation of stimulus investigation. However, this apparent habituation might
85 actually have been due to increased investigation of the novel context, because an
86 increase in environmental investigation would result in less time available for
87 investigating the stimulus, thereby giving an impression of continued habituation to
88 the stimulus. We addressed this latter issue here by using a different test of
89 recognition memory.

90

91 We used a variation of the habituation-discrimination technique (e.g. Halpin
92 1986; Johnston 1993; Johnston & Jernigan 1994). Following habituation (in terms of
93 a reduction in investigation) to the repeated introduction of the same conspecific-
94 derived odour stimulus (see later), we then presented that stimulus, and one from a
95 novel individual, simultaneously in a test encounter. A significant preference to
96 investigate the odour of the novel individual rather than that of the familiar
97 (habituated) conspecific was taken as an indication of successful recognition of the
98 familiar odour, whereas no such preference suggested recognition failure. In this test,
99 therefore, even if there is a general change, for whatever reason, in overall levels of
100 investigation, we still expect differences in the relative investigation of novel and
101 familiar odours to reveal whether recognition has occurred. This was not possible in
102 the test used in a previous study (Burman & Mendl 1999) and by others (e.g. Thor &
103 Holloway 1982) where only one stimulus was presented.

104

105 This study also contributes to research on the effects of contextual cues on
106 habituation. Previous studies (e.g. Marlin & Miller 1981; Hall & Channell 1985; Hall
107 & Honey 1989; Honey et al. 1992) have concluded that, unlike phenomena such as
108 latent inhibition (e.g. Kaye et al. 1987) and possibly even conditioning itself (Hall &

109 Honey 1989), habituation does appear to transfer successfully to a different test
110 context (i.e. it is not context specific) – provided that the test context is familiar to the
111 subject animal.

112

113 Method

114

115 *Subjects*

116

117 We used 24 female (3 months old at start of study) Lister hooded rats (Harlan
118 UK Ltd, Bicester, U.K.). These animals were selected because, at this age, female rats
119 are able to remember the identity of a juvenile conspecific for at least two hours after
120 an initial 5-min encounter (e.g. Bluthé & Dantzer 1990), and have yet to show the
121 reduction in social recognition abilities apparent in older rats (e.g. Taylor et al.,
122 1999). The rats were housed individually during the experiment in standard laboratory
123 cages (33 x 50 cm and 23 cm high), with sawdust litter and an enrichment toy (a
124 plastic tunnel that was used both as a shelter and a perch). Food (Harlan Teklad
125 Laboratory Diet) and water were freely available. The rats were housed in the same
126 room in which they were tested, in a controlled environment ($20 \pm 1^\circ\text{C}$), on a reversed
127 lighting schedule (lights off 08:30-20:30) with dim light (10 W) allowing visibility for
128 the researcher.

129

130 *Apparatus*

131

132 Two different environmental contexts, A and B, (33cm x 50 x 23, lit by 10W
133 bulbs) were created with contrasting characteristics. They differed in orientation

134 (context A: east/west; context B: north/south), floor type (context A: plastic; context
135 B: wire mesh), and floor/wall colour (context A: white; context B: black). In order to
136 ensure that the subjects were able to move equally freely and see cues equally clearly
137 in both contexts, we kept cage size and lighting the same.

138

139 *Treatments*

140

141 Rats were allocated at random to the three different treatment groups
142 ('context-same', 'context-different', 'context-novel') (see Figure 1), with N=8
143 animals in each group. We tested three rats each day, one from each treatment, with
144 treatment order determined randomly. Half of the rats in each treatment began the
145 experiment in context A, the other half began the experiment in context B. This
146 design allowed for differences between the two contexts to be detected.

147

148 *Prior experience*

149

150 Rats in the 'context-different' treatment were given experience of both
151 contexts prior to testing, whilst rats in the 'context-same' and 'context-novel'
152 treatments were given no experience of either context A or context B before testing
153 began. This prior experience was achieved by introducing the subject rats into the two
154 different contexts for 20-minute periods, once a day for four days, with the last day of
155 context familiarisation taking place 24 hours before each particular subject rat was to
156 be tested. This difference in experience was intended to ensure that when 'context-
157 different' rats were switched to a new context, the new context would be different, but

158 familiar, whereas when ‘context-novel’ rats were switched to a new context, it would
159 be completely novel.

160

161 *Figure 1*

162

163 *Procedure*

164

165 The experimental procedure consisted of introducing a subject rat to one of the
166 contexts, either A or B, which contained an odour sample (see below) from a novel
167 rat, for a five-minute period. During this encounter, total investigation (s) of the odour
168 sample by the subject rat was recorded. Following this initial encounter, the subject
169 rat was returned to its home cage for a 15-minute interval before being reintroduced
170 to the same context and the same odour sample for a second encounter. Again,
171 investigation of the odour sample was recorded for five minutes. This procedure was
172 repeated for five consecutive encounters.

173

174 Fifteen minutes after the fifth encounter, a sixth ‘test’ encounter took place in
175 which the subject was exposed, for five minutes, to both the odour sample of the
176 original conspecific and that of a completely novel individual. For ‘context-same’ rats
177 this sixth ‘test’ encounter took place in the same context as for the previous five
178 encounters, whereas rats in the ‘context-different’ and ‘context-novel’ treatments
179 were switched to a new context for the sixth ‘test’ encounter. For ‘context-different’
180 rats this new context was familiar, but for ‘context-novel’ rats it was completely novel
181 (see ‘previous experience’).

182

183 The ‘context-novel’ rats then received an additional seventh five-minute
184 encounter with the same odour cues in the same context as for the sixth encounter,
185 having spent 15 minutes, with no odour cues present, in that same context. We
186 included this additional ‘test’ encounter because, if discrimination was not occurring
187 in the sixth encounter due to the time spent investigating the novel environment, then,
188 by allowing the rats extra time to explore that environment (between the sixth and
189 seventh encounters), it was hoped that the novelty of the environment would be
190 reduced - and subsequent discrimination become possible.

191

192 *Behavioural observations and odour samples*

193

194 Investigation of the two odour samples by the subjects was recorded directly
195 using an event recorder (Psion Organiser II) with Noldus Observer software (Noldus
196 Information Technology 1993). Investigation included sniffing, licking, and/or the
197 subject’s nose being held within one cm of an odour container, with the majority of
198 non-stimulus investigation directed towards exploration of the environmental context.
199 Each subject rat was used once as a subject, and twice as an odour donor. Odour cues
200 consisted of 10cm³ of four-day old soiled bedding from the home cage of donor rats
201 presented in spherical wire mesh containers (total volume 20 cm³) secured to the cage
202 wall. These containers allowed the rats to investigate the odour stimulus without
203 disturbing it.

204

205 All odour cues were collected at the same time immediately prior to testing,
206 with the result that both the familiar odour stimulus and that of the novel individual
207 were the same ‘age’ when introduced for the sixth ‘test’ encounter. The containers

208 containing the odour cues were changed and disinfected (Virkon, Antec International)
209 between each encounter to prevent odour deposition by the subject rats. During the
210 first five encounters, the odour cue was placed centrally at one end of the home cage
211 (16.5cm from either side). For the test encounter, one of the odour cues was placed
212 centrally on the left of the home cage, the other on the right (both 25cm from either
213 end), and this was balanced across treatments to control for possible side preference.

214

215 *Data analysis*

216

217 The different treatments were analysed (Minitab) to examine whether: (1)
218 prior experience of the context affected investigation time during the five exposures
219 to a novel odour stimulus; (2) the two contexts differed in their influence on subject
220 behaviour; (3) rats habituated after five presentations to the same odour stimulus; (4)
221 rats successfully discriminated between the familiar and a novel odour when tested in
222 either the same, a different (familiar), or novel test context; (5) exposure to a novel
223 context resulted in decreased investigation; (6) after 15-mins in the formerly novel
224 context, investigation increased.

225

226

Results

227

228 The total amount of investigation (seconds) directed towards the odour stimuli for
229 each treatment over the six/seven 5-min encounters is presented in Fig. 2 (a - c).
230 Overall investigation of odour stimuli (mean investigation in encounter one: 30.8s)
231 was lower than that observed for live juvenile conspecifics in previous studies (e.g.
232 70.5s: Burman & Mendl 2000). However, previous research has indicated that both

233 urine and soiled bedding can be used successfully to replace live conspecifics as
234 stimuli in social recognition tests (Sawyer et al., 1984).

235

236 *Encounters 1-5*

237

238 A repeated measures General Linear Model (GLM) with previous experience
239 (yes/no), context (A/B), and encounter (1-5) as factors, was carried out on the
240 investigation data which were both normal and with similar variances. For the first
241 five encounters analysed here 'context-same' and 'context-novel' rats, both without
242 prior experience of either context, were combined because, at this point in the
243 experiment, there was no difference in treatment between these two groups of rats,
244 nor did they differ significantly in levels of investigation ($F_{1,14}=0.98$, NS). This test
245 revealed that those rats with previous experience of both contexts ('context-different')
246 investigated the odour stimuli significantly more than those without experience
247 ('context-same' & 'context-novel') ($F_{1,20}=7.9$, $P<0.05$). No difference in total
248 investigation was observed between contexts A and B. There was a highly significant
249 effect of encounter (1-5) on investigation ($F_{4,80}=23.97$, $P<0.001$), and a significant
250 interaction between experience and encounter ($F_{4,80}=2.7$, $P<0.05$).

251

252 Post-hoc analysis, in which context data were pooled and data for experienced
253 and inexperienced groups analysed separately, revealed that for those rats without
254 experience there was a significant drop (Tukey's Pairwise Comparison, $P<0.05$) in
255 investigation (means \pm SE: 25.8 \pm 2.9, 17.1 \pm 2.1, 17 \pm 1.9, 11.3 \pm 2.1, 6.3 \pm 1.3,
256 respectively) between encounters 1 & 2, 1 & 3, 1 & 4, 1 & 5, 2 & 5, and 3 & 5. For
257 experienced rats ('context-different') (means \pm SE: 40.8 \pm 5.1, 25.5 \pm 4.1, 15.4 \pm 2.9,

258 20.3±4.3, 12.3±2.9, respectively) significant reductions in investigation were
259 observed between encounters 1 & 2, 1 & 3, 1 & 4, and 1 & 5.

260

261 *Figure 2 (a-c)*

262

263 *Encounter 6*

264

265 A repeated measures GLM was used to investigate data from the sixth ‘test’
266 encounter with treatment (‘context-same’/‘context-novel’/‘context-different’), context
267 (A/B) and odour (novel/same) as factors. We found a significant difference between
268 treatments ($F_{2,36}=6.86$, $P<0.01$), and no difference between contexts. Subject rats
269 investigated the novel odour stimulus significantly more than the familiar (original)
270 stimulus ($F_{1,18}=32.16$, $P<0.001$). Post-hoc analysis of the treatment effect, revealed
271 that both ‘context same’ and ‘context different’ rats investigated the odour cues
272 significantly more than ‘context novel’ animals (Tukey’s Pairwise Comparison,
273 $P<0.05$) (means ± SE: 36.5±4.25 (‘context same’), 30.1±3.55 (‘context different’),
274 16.9±3.18 (‘context novel’).

275

276 There were no significant interaction effects in the model, although the
277 interaction between treatment and odour approached significance ($F_{2,36}=2.97$,
278 $P=0.077$). This seemed to be due to less clear discrimination between the novel and
279 familiar odours in the ‘context novel’ group (see Fig. 2), and therefore necessitated
280 further analysis - in order to avoid any misinterpretation of the apparent overall
281 preference of the rats for investigating the novel odour stimulus. We used either
282 paired t-tests or Wilcoxon signed-ranks test (both two-tailed), depending on whether

283 or not the data met requirements for normality and homogeneity of variance.
284 ‘Context-same’ ($t_8=5.19$, $P=0.001$) and ‘context-different’ ($t_8=4.15$, $P<0.01$) rats both
285 investigated the odour of a novel conspecific significantly more than that of a familiar
286 individual. In contrast, the ‘context-novel’ rats ($T=30$, $N=8$, $P=0.107$) showed no such
287 preference.

288

289 *Encounter 7*

290

291 A final analysis compared the investigation of the novel and familiar odour
292 cues between the sixth ‘test’ encounter and the subsequent seventh encounter for
293 ‘context-novel’ rats. During the 15-min period between these tests the subjects
294 remained in the previously novel environmental context. A GLM with encounter (6/7)
295 and odour (novel/same) as repeated factors revealed that, whilst there was no
296 significant difference in the time spent investigating novel as compared to familiar
297 odour stimuli ($F_{1,7}=1.86$, NS), the rats investigated the stimuli at a significantly higher
298 level in the seventh encounter than in the sixth ‘test’ encounter ($F_{1,7}=6.31$; $P<0.05$).

299

300

Discussion

301

302 Habituation, in terms of declining amounts of investigation, occurred over five
303 separate encounters with an odour stimulus obtained from the same individual, with
304 all treatments showing a reduction of investigation between the first and the fifth
305 encounters. For the sixth ‘test’ encounter, ‘context-same’ and ‘context-different’ rats
306 preferred to investigate the odour of a novel, rather than familiar, individual - which
307 suggests successful recognition of the familiar (habituated) odour (see introduction,

308 cf. Johnston 1993). The switch to a different, but familiar, environmental context did
309 not therefore appear to disrupt social recognition.

310

311 In contrast, the apparent failure to discriminate between the novel and familiar
312 odours in the novel context during the sixth ‘test’ encounter indicates that a switch to
313 a different, and entirely novel, context interfered with stimulus discrimination. In that
314 sixth encounter, the ‘context-novel’ rats investigated the odour stimuli significantly
315 less than those rats that were familiar with the test context. It therefore seems likely
316 that this reduction in investigation was caused, at least in part, by a redirection of
317 behaviour away from investigation and towards the exploration of the novel
318 environment (cf. Burman & Mendl 1999).

319

320 This explanation is supported by the observed increase in investigation of the
321 odour stimuli in the seventh encounter, following a further 15-min experience of the
322 novel test context. After the rats had gained that additional experience of the novel
323 environment between the 6th and 7th encounters, they may have had more time
324 available to investigate the odour stimuli because they were spending less time
325 exploring the environment. Alternatively, exposure to the novel environment may
326 have caused an increase in excitability, resulting in sensitisation to the presence of the
327 odour stimuli (e.g. Thompson & Spencer 1966), and a subsequent increase in stimulus
328 investigation.

329

330 However, despite this increase in overall stimulus investigation in the seventh
331 encounter, the rats still appeared unable to discriminate between the novel and
332 familiar stimuli. This suggests a further effect of the novel context on subject

333 behaviour, in addition to the apparent redirection of behaviour away from the
334 stimulus and to the surrounding environment. A possible explanation could be that
335 any stress caused by switching the rats to an entirely novel context might be sufficient
336 to disrupt the discrimination process. This would reflect the results of a previous
337 study (Burman & Mendl 2000) in which a 5-min exposure to a novel environmental
338 context in between two introductions to the same juvenile conspecific, appeared to
339 interfere with the recognition of that familiar individual.

340

341 It should be noted that there are potential explanations for the observed results
342 based solely on the design of the environmental contexts. For example, each context
343 needs to be sufficiently distinguishable from the other, but without causing a
344 discrepancy in the subjects' perception of the stimuli. However, throughout this
345 experiment no difference in investigative behaviour was recorded between the two
346 contexts, suggesting that it was unlikely that any of the observed changes in
347 behavioural response upon a context switch were due solely to differing stimulus
348 perception between the two different contexts (e.g. Lovibond et al. 1984; Hall &
349 Honey 1989). The change in behaviour when rats were switched to a novel test
350 context also provides some post-hoc evidence that the two different environmental
351 contexts were sufficiently distinguishable from each other in this study (e.g. Gordon
352 & Klein 1994).

353

354 The results of this study confirm the findings of our previous project (Burman
355 & Mendl 1999), in which, because of the effect of aggression and reduced sample
356 size, the conclusion that stimulus recognition had occurred following a switch to a
357 different, but familiar test context, required further evaluation. This study also

358 suggests that the continued habituation of investigation observed after a switch to a
359 novel context in our previous study was at least partly due to competing responses
360 restricting the subjects' available time for stimulus investigation. In addition, this
361 study provides further evidence that if odour cues alone are used as social stimuli,
362 rather than conspecifics, then discrimination is still possible by subject rats (e.g. Carr
363 et al. 1976; Sawyer et al. 1984; Gheusi et al. 1997) whilst ensuring that any potential
364 aggression between individuals is avoided. The use of odour cues in the
365 habituation/discrimination procedure (e.g. Johnston 1993; Johnston & Jernigan 1994),
366 is an important alternative to the use of live individuals because it also excludes the
367 possibility that the behaviour of the introduced animal could be influencing the
368 behaviour of the subject.

369

370 It therefore appears that – for this study at least - laboratory rats did not use
371 contextual cues to aid short-term social recognition. This contrasts with the results of
372 research on other species (e.g. birds: Falls & Brooks 1975; marmosets: Snowdon &
373 Cleveland 1979; fish: Waas & Colgan 1994)) that do appear to use contextual cues as
374 an aid for discriminating between individual conspecifics. It is possible that, although
375 individually distinguishable to the rats, the designs of the contexts in this study were
376 not conducive for developing contextual associations. Further manipulations of
377 contextual cues should be the target of future investigations.

378

379 In conclusion, this study confirms previous research (e.g. Hall & Channell
380 1985; Hall & Honey 1989; Honey et al. 1992) in which habituation, unlike other types
381 of learning, does not appear to show context specificity – provided that the test
382 context is familiar to the subject - and extends this finding to the social recognition of

383 conspecific odours, as determined by observed levels of stimulus investigation. In
384 addition, this validation of odour use demonstrates an alternative methodology to the
385 use of live conspecifics as stimuli, thereby avoiding the potentially confounding
386 effects of behavioural interaction and aggression.

387

388

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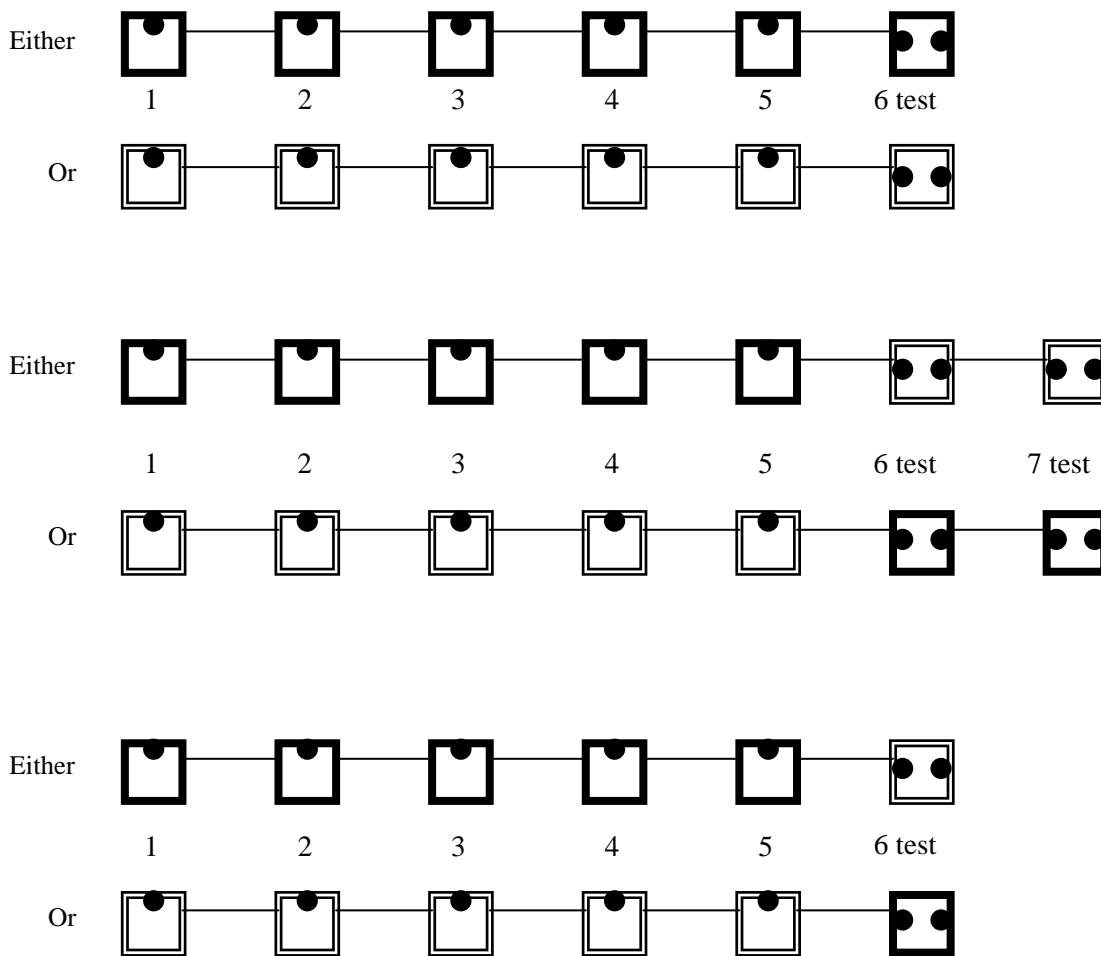
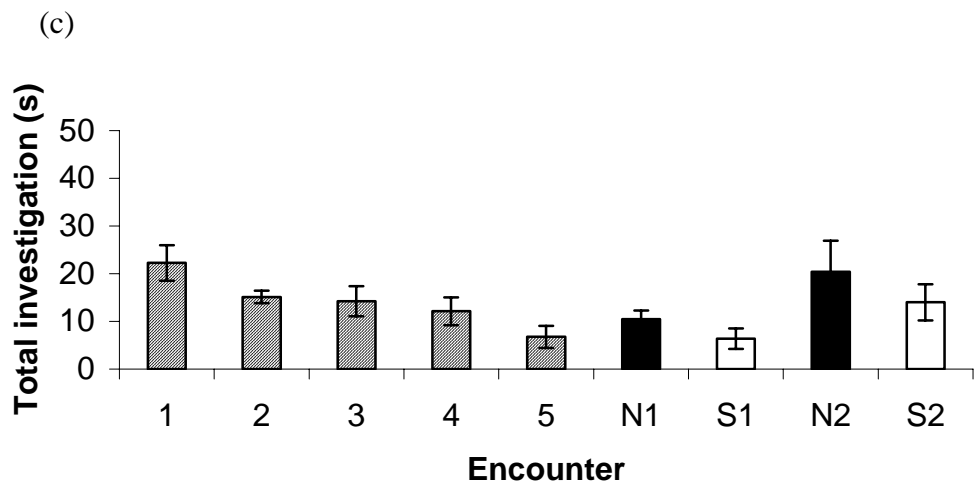
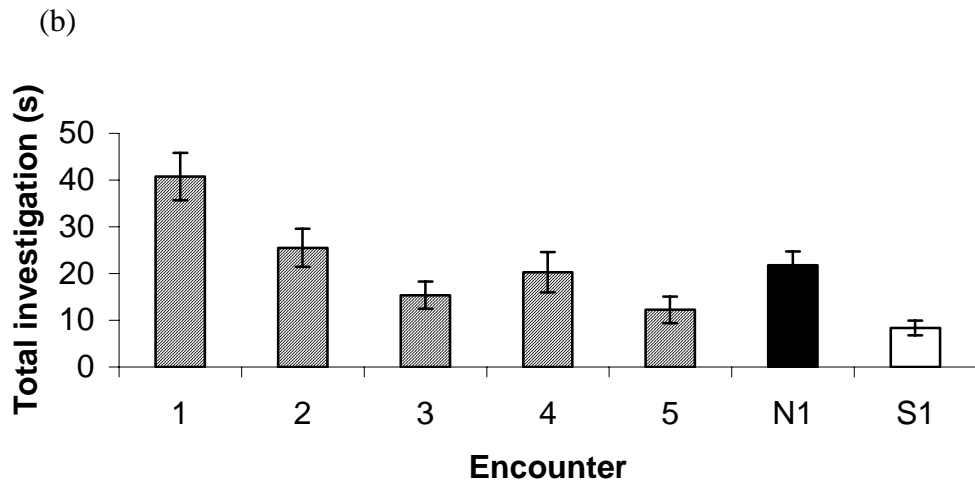
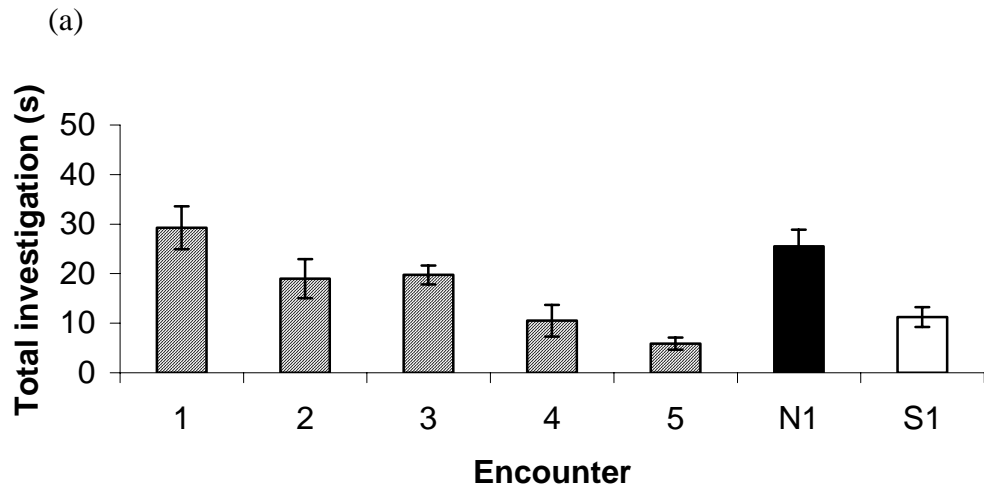


Figure 1. Description of treatments. Each box represents a 5-min encounter (white box: context A; black box: context B) with the odour stimulus, which is represented by one black circle for the first five encounters. In the test encounters 6 & 7, two odour stimuli (black circles) are presented. Each encounter is separated by a 15-min inter-exposure interval, represented by a line. The top two rows show the ‘context same’ treatment in which all six encounters were in one context (either A or B), with no previous experience of either context. The middle two rows show the ‘context novel’ treatment in which the first five encounters were in one context (either A or B), and the sixth and seventh in the other context, with no previous experience of either context. The bottom two rows show the ‘context different’ treatment in which the first five encounters were in one context (either A or B), the sixth in the other context, with previous experience of both contexts.

Figure 2 (a-c). The mean \pm SE investigation of the odour stimulus during each encounter for (a) 'context-same' (b) 'context-different' and (c) 'context-novel' treatments are presented. N1 = investigation of the novel odour in the first discrimination test; S1 = investigation of the same odour, as introduced for the initial 5 encounters, in the first discrimination test; N2 = investigation of the novel odour when reintroduced for a second discrimination test (context novel rats only); S2 = investigation of the same odour, as introduced for the initial five encounters, when reintroduced for a second discrimination test (context-novel rats only).



(c)