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Recognition of conspecific odours by laboratory rats (*Rattus norvegicus*) does not show context specificity.

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Abstract

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

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

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

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

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

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

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

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

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

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

Method

Subjects

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

Apparatus

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

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

Treatments

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

Prior experience

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

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

Figure 1

Procedure

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

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

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

Behavioural observations and odour samples

Investigation of the two odour samples by the subjects was recorded directly using an event recorder (Psion Organiser II) with Noldus Observer software (Noldus Information Technology 1993). Investigation included sniffing, licking, and/or the subject’s nose being held within one cm of an odour container, with the majority of non-stimulus investigation directed towards exploration of the environmental context. Each subject rat was used once as a subject, and twice as an odour donor. Odour cues consisted of 10cm^3 of four-day old soiled bedding from the home cage of donor rats presented in spherical wire mesh containers (total volume 20 cm^3) secured to the cage wall. These containers allowed the rats to investigate the odour stimulus without disturbing it.

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

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

Data analysis

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

Results

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

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

Encounters 1-5

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

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

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

Figure 2 (a-c)

Encounter 6

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

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

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

Encounter 7

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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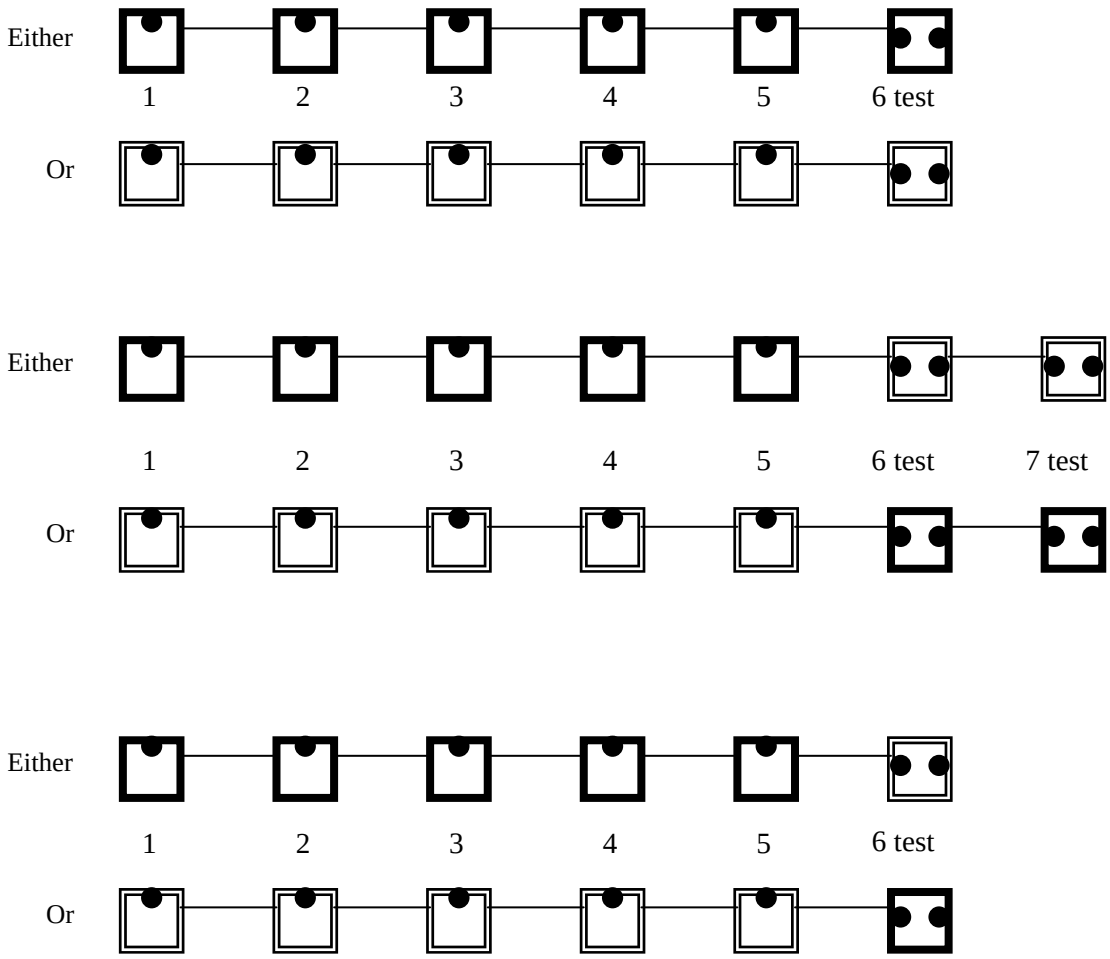
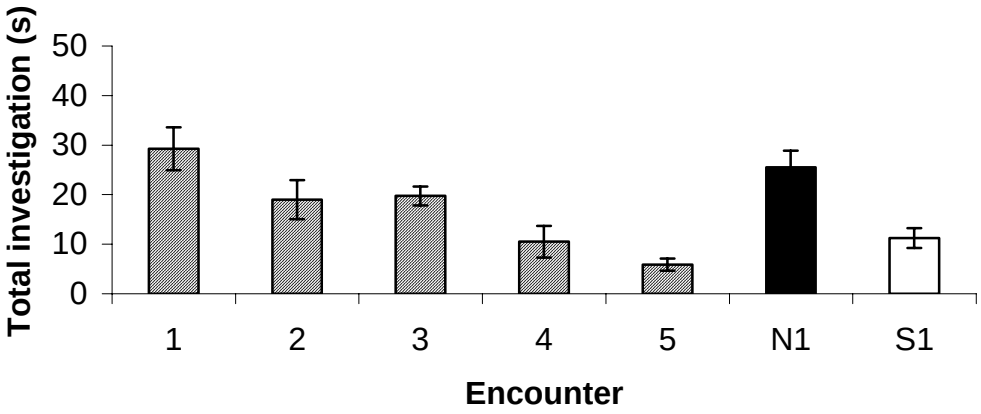


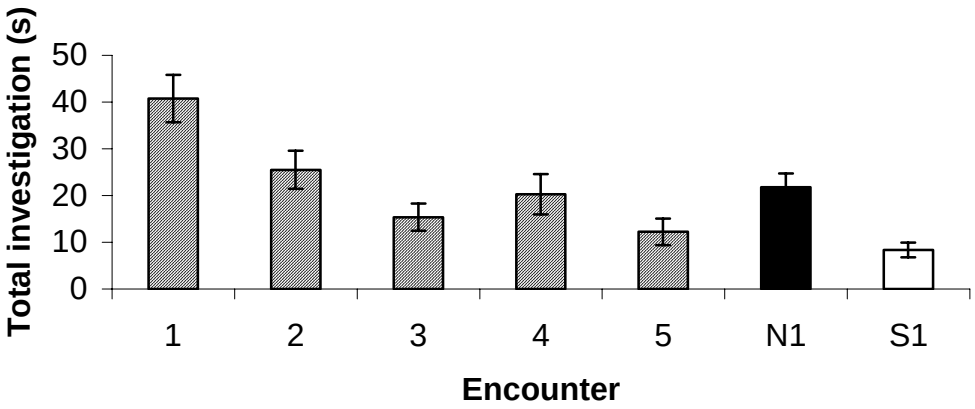
Figure 1. Description of treatments. Each box represents a 5-min encounter (white box: context A; black box: context B) with the odour stimulus, which is represented by one black circle for the first five encounters. In the test encounters 6 & 7, two odour stimuli (black circles) are presented. Each encounter is separated by a 15-min inter-exposure interval, represented by a line. The top two rows show the 'context same' treatment win 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 ± 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).

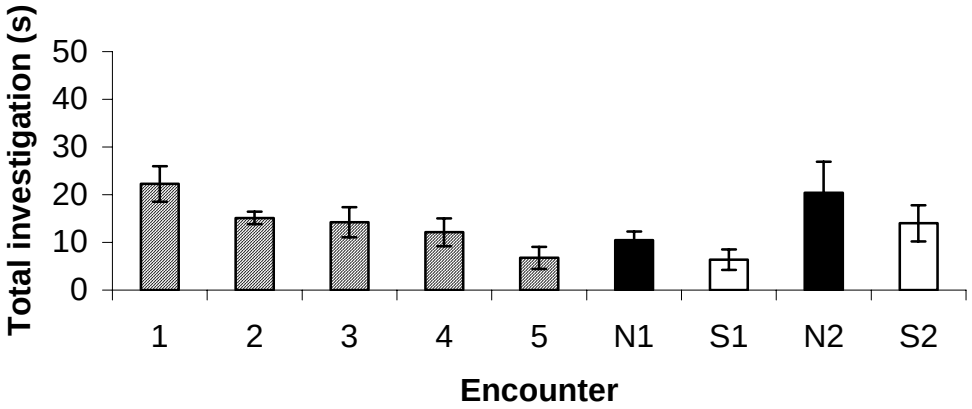
(a)


Total investigation (s)
50
40
30
20
10
0
1
2
3
4
5
N1
S1
Encounter

(b)


Total investigation (s)
50
40
30
20
10
0
1
2
3
4
5
N1
S1
Encounter

(c)


Total investigation (s)
50
40
30
20
10
0
1
2
3
4
5
N1
S1
N2
S2
Encounter

(c)