

Sex-related Responsiveness to Changes in Tactile Stimulation in Hooded Rats

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Hooded rats were allowed to choose between a Y-maze arm in which the floor had tactually changed, and an unchanged arm. This change was from either two rough (or smooth) arms to one smooth and one rough, or the reverse sequence, following 6- or 12-min acquisition trials. All rats were able to distinguish between the changed and the unchanged arms irrespective of the type of change. Males were less responsive to the novel arm after 12-min (possibly aversive) trials. They later emerged more slowly from a darkened chamber into a brightly lit arena, than equivalent females. For all rats, responsiveness to tactile change was positively correlated with emergence latencies. Fewer first entries of the more novel of two brightly illuminated Y-maze arms suggested disruption of responsiveness to change by an aversive experience.

For nearly 50 years, it has been known that rats are able to recognise which arm of a T maze has changed in brightness from what it was on a previous occasion. In the first study to demonstrate this, a rat was allowed to see into but not enter the black or white arms, through the presence of transparent barriers across each arm entrance (Kivy, Earl, and Walker, 1956). Then, it was taken out of the maze while an arm was exchanged for one of the opposite brightness, and the barriers removed. The rat was returned to the apparatus and, more often than not, was seen to enter the changed arm first. This procedure was repeated by Dember (1956) with one important difference namely, the brightness characteristics of the arms over the two trials were reversed. Thus, on the first exposure trial with the transparent barriers in place, one arm was white and the other black, and on the second choice trial both arms were either black or white. Although the rats experienced greater demands on memory by being faced with two arms of the same brightness, they still chose the arm that had changed. The procedure adopted by Kivy et al. (1956) provided a cue for which arm had changed, in that it was a different brightness from one of the two arms experienced earlier. But Dember's rats had to remember the previous location of the changed arm on the basis of information other than a brightness difference between the two arms.

Dember's report of responsiveness to a noncued brightness change was confirmed by several other investigators in rats (Fowler, 1958; Walk, 1960; Woods & Jennings, 1959) and some other species such as ferrets, *Mustela putorius* (Hughes, 1965) and adult opossums, *Didelphis virginiana* (Platt & James, 1967). It was also later applied to the study of drug and brain lesion effects in the belief that it comprised a test of visual recognition memory (Becker, et al., 1992; Łukaszevska, 1993; Markowska & Łukaszevska, 1981; Poucet & Buhot, 1989). However, as the response depended on memory for the former position as well as brightness of the changed arm, it clearly involved more than visual recognition

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alone.

Recognition of a noncued brightness change has been further developed to include, as well as the arm first entered, the measurement of longer-term responsiveness in the form of repeated entries of and time spent in the changed arm during a 1-min observation period (Hughes, 2002, 2003), after which time interest in the change dissipates (Hughes, 2001). For both economic and ethical reasons, repeated measures designs have also been adopted to avoid using the excessively large numbers of subjects that have typified some earlier research. This modified procedure may render the phenomenon useful for evaluating short term memory changes in the absence of effects of independent variables, such as drugs and other chemical agents, which could interfere with the power of conventional reinforcers and thus influence performance, rather than cognition.

A notable feature of more recent work has been the prevalence of sex differences in responsiveness to brightness change and its modification by the memory-enhancing agents, *d*-glucose and D-cycloserine. Amongst Long-Evans hooded rats that were not treated with any pharmacologically active compounds, females were significantly less inclined to repeatedly enter and spend time in a changed arm than males (Hughes, 2001). Although responsiveness to change was increased by pre-acquisition treatment with glucose in females only (Hughes, 2002), the dose-response relationship for effects of pre- and postacquisition administration of cycloserine on the phenomenon was linear for females, but curvilinear for males (Hughes, 2004). With the exception of the first author's own work, virtually all published research on responsiveness to brightness change has involved male rats only.

Success in detecting a brightness change depends on the length of acquisition trials. Kivy et al. (1956) showed that, in a T maze, male rats required trial lengths of at least 15 min to achieve significant responsiveness to change. Later researchers have shown that further increases are followed by the loss of significant responsiveness (Łukaszewska, 1978). Although trials of 3 min in a Y maze are sufficient for male rats to respond to change (Dember & Millbrook, 1956), there is some evidence that, as with the T maze, longer acquisition trial lengths can lead to chance responding (Levine, Staats, & Frommer, 1958). It has been accordingly suggested that the additional time of confinement to the maze increases the rats' emotionality (Dember, 1958) thereby reducing their tendency to approach the novel arm.

While at least male rats' ability to recognise a brightness change is widely accepted, there have been no assessments of either sex's ability to recognise changes in stimulation involving other sensory modalities. The present study was therefore designed to determine whether or not both males and females were able to recognize a change in tactile stimulation that was experienced when walking on substrates with distinctive tactile properties. It has long been known that rats demonstrate good sensitivity to tactile stimuli, even during fetal development (Raney & Carmichael, 1934), and are able to discriminate between tactually different substrates via cutaneous tactile receptors in their feet and snout (Douglas, 1966; Smith, 1939). The study also investigated whether or not increasing the length of acquisition trials beyond the 6-min duration adopted in previous studies of responsiveness to brightness change in a Y maze (Hughes, 2002, 2003, 2004; Hughes & Neeson, 2003) had any effect on the ability to detect a tactile change.

Experiment 1

Method

Subjects. The subjects were 20 male and 20 female Long-Evans hooded rats, *Rattus norvegicus*, approximately 5 months old at the beginning of testing, that had been bred in the Animal Facility of the Department of Psychology, University of Canterbury. They were caged in groups of 3 or 4 same-sexed animals, with ad libitum food and water in 12 h light/dark reversed lighting, at an ambient temperature of 20 ± 1 °C.

Apparatus. The apparatus was a clear-varnished wooden Y maze comprising two 45-cm long arms, and a 30-cm stem that were all 14 cm high and 10 cm wide. The walls of each arm were lined with black painted aluminum sheeting and contained removable wooden floor inserts onto which had been glued coarse sand paper (grade 40 grit) that was either uncovered (“rough”) or covered with clear Perspex (“smooth”) so that, while tactually different, the two textures were as visually similar as possible. Each type of insert was constructed to ensure that the thickness of both was the same, namely 6 mm. The maze was covered by hinged clear Perspex lids except for the south start end of the stem over which a 15 x 12 cm wooden lid enabled individual rats to be placed into the apparatus. It sat on a 1-m high table which was positioned beneath fluorescent tubes attached to the ceiling of the room that ensured even illumination (approximately 45 lx) of both maze arms. All data were visually recorded by an observer with the use of a PC computer and keyboard. The observer stood behind the start end of the stem.

Procedure. Every testing session for each rat consisted of an acquisition phase followed by a choice trial. The sequence involved placing the animal into the apparatus and allowing it to freely explore both arms for either 6 or 12 min after which it was returned to a holding cage while both of the floor inserts were replaced with clean substitutes, one of which was a different texture from what it had been previously. (Changing both inserts ensured that the rat’s choice behavior was not guided by the presence in one arm and absence in the other of its own earlier-deposited odor cues.) The subject was then reintroduced into the stem for its choice trial, and the first arm entered by all four legs was noted. This entry was then followed by observations for exactly 1 min of the total number of repeated entries of and time spent in both the changed (or novel) and the unchanged (or familiar) arms. All parts of the apparatus were thoroughly washed and dried before the next rat’s acquisition trial.

Every rat experienced two choice trials following a cued change from both arms being rough (or smooth) during the acquisition phase, to one arm rough, and the other smooth. It also experienced two choice trials consisting of the reverse sequence, namely a noncued change from one arm rough and the other smooth to both arms rough (or smooth). Preliminary testing had failed to reveal any preferences for one texture or the other in the absence of changes. The novel arm was on the left for one of the two choice trials in each change condition, and on the right for the other. Each choice trial was separated by an interval of one or two days, and the length of the acquisition trials was 6 min for half of each sex, and 12 min for the other half.

Results

The data from one male that experienced 6- and two males that experienced 12-min acquisition trials were excluded from further analyses because they subsequently failed to enter an arm after 10 min of any choice trial in either change condition. For all remaining subjects, the arm first entered and the total number of repeated entries of and time spent respectively in both arms were recorded. From the latter two measures it was possible to calculate entries of and time spent in the tactually novel maze arm as percentages of the total entries of and time spent in both arms. All resulting data were then subjected to separate Acquisition Trial Duration (6, 12 min) x Sex x Type of Change (cued, noncued) ANOVAs. Mean results for

each group and condition and *F*-test results for all main effects are outlined in Table 1.

Table 1

Mean (± SEM) Values of Total Repeated Entries/Day of and Time Spent/Day in Both Arms, and Percent First Entries of, Repeated Entries of, and Time Spent in the Novel Arm for Each Acquisition Trial Duration Time, Sex, and Type of Change, and Results of F-Tests for Main Effects.

Measure	6 min (<i>N</i> = 19)	12 min (<i>N</i> = 18)	<i>F</i> (1,33)	<i>p</i>
Total repeated entries/day	9.26 (± 0.80)	5.11 (± 0.82)	21.64	0.000
Total time spent/day (s)	21.81 (± 1.29)	14.24 (± 1.84)	18.06	0.000
Per cent first entries	51.46 (± 4.04)	36.11 (± 5.97)	9.98	0.003
Per cent repeated entries*	55.49 (± 1.88)	47.78 (± 5.69)	2.34	0.135
Per cent time spent*	58.79 (± 1.97)	47.72 (± 6.23)	4.89	0.340
Measure	Males (<i>N</i> = 17)	Females (<i>N</i> = 20)	<i>F</i> (1,33)	<i>p</i>
Total repeated entries/day	5.18 (± 0.82)	9.00 (± 0.84)	18.02	0.000
Total time spent/day (s)	14.69 (± 2.14)	21.05 (± 1.18)	12.44	0.001
Per cent first entries	29.43 (± 4.28)	56.25 (± 4.30)	24.17	0.000
Per cent repeated entries*	47.86 (± 5.95)	55.03 (± 2.02)	1.96	0.171
Per cent time spent*	48.18 (± 6.27)	57.84 (± 2.72)	3.36	0.076
Measure	Cued change (<i>n</i> = 37)	Noncued change (<i>n</i> = 37)	<i>F</i> (1,33)	<i>p</i>
Total repeated entries/day	7.14 (± 0.71)	7.35 (± 0.67)	0.55	0.464
Total time spent/day (s)	17.53 (± 1.38)	18.73 (± 1.45)	0.85	0.362
Per cent first entries	45.95 (± 4.92)	42.57 (± 4.19)	0.42	0.521
Per cent repeated entries	52.69 (± 3.95)	50.79 (± 2.90)	0.14	0.710
Per cent time spent	55.39 (± 4.38)	51.42 (± 3.48)	0.59	0.447

Note. * Exposure Time x Sex interaction significant (see text and Figure 1)

Repeated entries of and time spent in both arms were significantly lower amongst rats that had experienced 12-min rather than 6-min acquisition trials. While females achieved higher levels of both these measures than males, all rats combined were unaffected by the type of tactile change encountered.

First entries of the novel arm were significantly lower in the 12-min acquisition group, and in males. As shown by one-sample *t*-tests, rats in the 12-min (but not 6-min) acquisition group entered the unchanged arm first significantly more often than expected by chance, $t(17) = 2.33$, $p < 0.05$. Likewise, males (but not females) entered the unchanged arm first significantly more often than a chance expectancy, $t(16) = 4.81$, $p < 0.0005$. Whether the change was cued or noncued made no difference to this measure. However, while no main effects were significant for the two longer-term measures of responsiveness to change, there were significant Acquisition Duration x Sex interactions for both portrayed in Figure 1: percent repeated entries, $F(1, 33) = 4.41$, $p < 0.05$, percent time, $F(1, 33) = 8.02$, $p < 0.008$.

As shown by Scheffé tests, $p < 0.05$, the interaction for repeated entries arose from significantly fewer entries of the novel arm for males in the 12-min acquisition condition than for their same-sexed equivalents in the 6-min condition. These latter (but not former) rats also entered the novel arm significantly more of-

ten than expected by chance, $t(8) = 2.42, p < 0.05$. The difference between the acquisition conditions was not significant for females.

The difference between the acquisition conditions in the amount of time spent in the novel arm was again significant for males only. However, while such time exceeded chance expectations for males in the 6-min condition only, $t(8) = 3.72, p < 0.006$, it was significant in both conditions for females, 6 min, $t(9) = 2.73, p < 0.025$, 12 min, $t(9) = 2.26, p < 0.05$.

As for responses directed towards both arms, none of the three novelty choice measures were affected by the type of tactile change experienced.

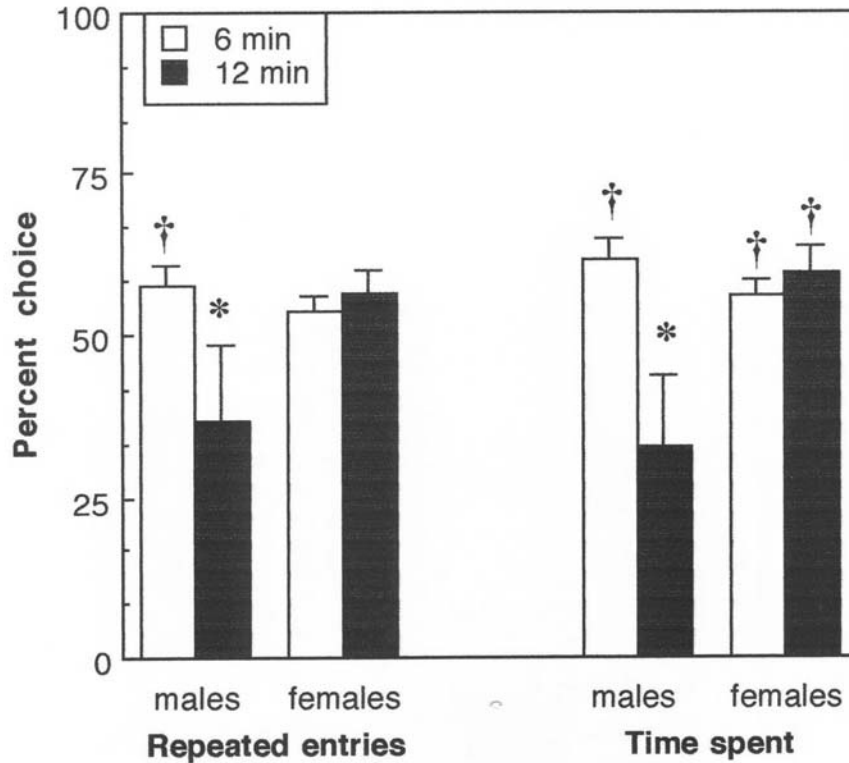


Figure 1. Mean (\pm SEM) percent choice of the novel arm in the form of repeated entries of and time spent in the tactually novel maze arm (expressed as percentages of the total entries of and time spent in both arms) following 6- and 12-min acquisition trials for male and female rats. * Significantly different from 6-min condition. † Significantly higher than a chance frequency of 50%.

Discussion

The most striking finding in this study was the clear indication that all rats were able to distinguish between the tactually novel and familiar arms as determined by their different choices of each. This outcome established that recognition of a change in stimulation is not confined to the visual modality. However, unlike earlier reports of responsiveness to brightness change (Dember, 1956; Hughes, 2001; Kivy et al., 1956), such recognition was not always reflected in preferences for the novel arm, but also appeared as a preference for entering the familiar alternative first. The obvious need for all rats to sample the tactile qualities of each arm before committing themselves to their first full body-length entry was manifested

by varying numbers of unrecorded partial entries that preceded the measure of choice. Then, once committed, the significant first complete entry of the familiar arm following a 12-min acquisition trial, and by all males as well, suggests that the novel arm was initially avoided by rats in these particular groups. However, while male rats showed preferences for repeatedly entering and spending time in the novel arm following 6- but not 12-min acquisition trials subsequent to their first body-length entry, a similar pattern characterised females for time spent in the novel arm after both acquisition trial durations.

From consideration of responsiveness to both arms, irrespective of their novelty value, it seems possible that any sex-related novelty avoidance may have been fear-based. This is because male rats (that are reported to be more fearful than females, Aguilar et al., 2003; Gray, 1971) appeared less active and thus probably more fearful (Archer, 1973) by making fewer entries of both arms and thereby spending less time in them than females. A direct relationship between these latter two measures is supported by a positive Pearson product-moment correlation between them, $r(35) = 0.81$, $p < 0.001$. It has also been shown that fear can reduce responses to brightness change in rats to the extent that a familiar maze arm is preferred (Aitken, 1972; Aitken & Sheldon, 1970) as occurred for the arm first entered by males in the present experiment. So while it is possible to explain overall differences between males and females in this way, when both sexes were combined, it is more difficult to account for fewer repeated entries of and less time spent in both arms, and fewer first entries of the novel arm by greater fear following 12- than after 6-min acquisition trials. However, it is remotely possible that the rats found confinement to the apparatus during acquisition trials aversive. If so, perhaps the longer period of confinement was more aversive than the shorter (as suggested by Dember, 1958), especially for males. But it should be noted there was no evidence of any confinement-related increase in fearfulness following a change in brightness (Hughes, 2001). Nevertheless, some limited support for this possibility is found in an earlier observation that rats made fewer entries of the sections of a symmetrical Y maze and defecated more often when the apparatus was illuminated by an aversive 150-W white light bulb, than by a less aversive 15-W red bulb (Williams, 1971). In addition, contrary to what characterized dim illumination, entries of the maze sections declined during testing sessions with the brighter light. This could suggest an increase in aversiveness of the bright light as the time of exposure became longer, provided one accepts the inverse relationship between fear and activity that is acknowledged by many (Archer, 1973). Although the maze in the present study was not brightly illuminated, its light level and the presence of an observer along with the use of a computer for recording behavior may nevertheless have added to any aversiveness of the 12-min period of confinement. In addition, as the rats had not received any extra handling or adaptation to the apparatus prior to testing, it is likely that the lack of these procedures could have further increased their levels of fear. It is also possible that the strain of the rats was a factor as hooded rats have been shown to have lower preferences for occupying a novel environment than albinos (Hughes, 1973) which might be a reflection of higher fearfulness. Albino rats have been used in most previous investigations of responsiveness to brightness change.

It is notable that, as also typified brightness changes (Hughes, 2001), whether the tactile change was cued or noncued made no difference to any re-

corded measure, even though the latter type was obviously more demanding on memory.

Experiment 2

In view of the possibility that fear may have played an important part in determining the rats' (especially males') responsiveness to change, a brief investigation was designed of relationships between individual reactivity to a mildly stressful situation and their earlier novelty choices in those subjects that had experienced the possibly more aversive 12-min acquisition trials. This study involved the rats' natural aversions to bright light through measuring their emergence latencies from a darkened area into a brightly illuminated arena. The general procedure is a commonly used measure of fearfulness which exploits a conflict between rodents' natural curiosity about a novel environment, and their fear of bright light (Hascoët, Bourin, & Dhonnchadha, 2001; Sanchez, 1996).

Method

Subjects and Apparatus. The subjects were all the rats that, approximately two weeks earlier, had last been tested in the Y maze following 12-min acquisition trials and whose data had been included in the analyses (i.e., 8 males and 10 females). The apparatus comprised a 20 x 15 x 20-cm high darkened start box that could open, by means of a wooden slid, into a 50 x 40 x 20-cm high arena. It was constructed from wood apart from the floor and ceiling of the arena that consisted of translucent white Perspex, and fine wire mesh respectively. The interior of the start box was painted black, and the walls and ceiling of the arena were painted white. The floor of the arena was illuminated from underneath by two 16-lux fluorescent tubes.

Procedure. Each rat was placed in the start box of the emergence apparatus, and 60 s later, the slide obstructing the entry to the arena was withdrawn. The time it took the rat to fully emerge (all four feet) was recorded by a hand-held stopwatch. If it had not emerged after 6 min, the trial was terminated and the rat assigned a score of 360 s. All rats experienced two such trials with an interval of two or three days between each.

Results and Discussion

The average latency of emergence was calculated for each rat. Because of a skewed distribution of the resulting scores, nonparametric statistical analyses were adopted to determine the significance of the difference between the sexes, and correlations between emergence latencies and levels achieved in the Experiment 1 measures.

Median latencies (in s) for males ($N = 8$) and females ($N = 10$) were 96.31 and 62.03 respectively. As shown by a two-tailed Mann-Whitney U -test, this sex difference was significant, $U = 16$, $z(\text{corrected for ties}) = 2.13$, $p = 0.033$. Spearman rank-order correlation coefficients were calculated between emergence latencies and each of the measures recorded in Experiment 1 (see Table 2).

Statistically significant negative correlations were obtained between emergence and first entries and repeated entries of the novel arm. Marginally significant negative correlations were also obtained between emergence latencies and time spent in the novel arm as well as repeated entries of both arms.

These results supported the claim that male rats in Experiment 1 were more fearful than females, and that choices of the novel arm and entries of the two arms

by both sexes combined may have been affected by individual rat's responsiveness to fear-inducing stimuli. However, while this evidence suggests that levels of what might be referred to as "trait fear" could have been a factor in determining their earlier choice behavior, it does not directly support the view that fear arising from an aversive experience, such as longer confinement to the apparatus during acquisition (Dember, 1958; Łukaszewska, 1978) can affect responsiveness to novelty.

Table 2
Separate Spearman Rank-order Correlations Between Emergence Latencies and Each Measure Recorded in Experiment 1.

Experiment 1 measure	r_s (corrected for tied ranks)	z	P
Per cent first entries	-0.50	2.06	0.039
Per cent repeated entries	-0.61	2.51	0.012
Per cent time spent	-0.46	1.92	0.055
Total repeated entries/day	-0.47	1.94	0.053
Total time spent/day	-0.30	1.22	0.222

Experiment 3

This experiment involved an attempt to more directly relate levels of "state fear" to choices of a tactually novel maze arm in both male and female rats. It was reasoned that, if higher levels of fear inhibit responsiveness to change, then increasing light levels within the apparatus should reduce tendencies to select a tactually novel arm. This was because rats generally find bright light aversive and accordingly show evidence of increased fear in its presence (Broadhurst, 1957; Williams, 1971). They also are less inclined to respond to a brightness change if it involves a change from black to white rather than the reverse (Hughes, 2001). Previous research has demonstrated avoidance of a brightness change following forced exposure to an aversive electric shock (Aitken, 1974; Aitken & Sheldon, 1970).

Method

Subjects and Apparatus. A further 8 male and 8 female previously untested hooded rats, approximately 5 months old, were tested in the same Y maze that was used in Experiment 1.

Procedure. In a nonsystematic fashion, all rats received 4 pairs of acquisition and choice trials when each arm was brightly illuminated by a circular 40-W fluorescent lamp, and another 4 pairs when the lamps were switched off. The light levels in each arm were 240 lx with the lamps on (the bright condition), and 4 lx with them off (the dim condition). In view of the lack of any difference between cued and noncued changes demonstrated in Experiment 1, the rats only experienced cued tactile changes. This meant that, for all acquisition trials, both arms contained two rough or two smooth floor inserts, followed by choice trials with one rough and one smooth insert. Individual animals had equal numbers of acquisition trials with both inserts rough and smooth, and equal numbers of choice trials with the changed arm on the left and on the right. Testing sessions were separated by 2 or 3 days.

Results and Discussion

The results for each measure are described in Table 3 along with outcomes of separate two-way ANOVAs for the effects of sex and light level.

Table 3

Mean (\pm SEM) Values of Total Repeated Entries/Day of and Time Spent/Day in Both Arms, and Percent First Entries of, Repeated Entries of, and Time Spent in the Novel Arm for Each Light Level, and Sex, and Results of F-Tests for Main Effects.

Measure	Bright light ($n = 16$)	Dim light ($n = 16$)	$F(1,14)$	p
Total repeated entries/day	1.58 (\pm 0.20)	2.52 (\pm 0.25)	12.80	0.003
Total time spent/day (s)	17.97 (\pm 2.48)	27.65 (\pm 1.70)	15.62	0.001
Per cent first entries	47.00 (\pm 5.00)	68.75 (\pm 4.75)	6.93	0.020
Per cent repeated entries	63.93 (\pm 4.40)	60.87 (\pm 4.28)	0.43	0.524
Per cent time spent	68.37 (\pm 4.55)	63.33 (\pm 4.70)	0.87	0.368

Measure	Males ($N = 8$)	Females ($N = 8$)	$F(1,14)$	p
Total repeated entries/day	1.62 (\pm 0.24)	2.47 (\pm 0.20)	7.26	0.018
Total time spent/day (s)	21.00 (\pm 2.76)	24.62 (\pm 1.70)	1.24	0.284
Per cent first entries	57.75 (\pm 4.75)	57.75 (\pm 3.25)	0.00	1.000
Per cent repeated entries	69.34 (\pm 6.40)	55.45 (\pm 1.42)	4.50	0.053
Per cent time spent	73.56 (\pm 6.06)	58.14 (\pm 2.29)	5.67	0.032

Repeated entries of and time spent in both arms were greater when the rats were tested in dim light than in bright, thereby suggesting that, in the latter condition, the rats were less inclined to visit either arm. As observed in Experiment 1, females entered both arms more often than males (thereby further supporting their higher levels of activity, Archer, 1973) but in this case did not spend more time in them.

First entries of the novel arm were the only indication that responsiveness to change was significantly affected by the difference in light levels. The rats first entered the novel arm more often in dim light than in bright. In the former but not latter condition, these choices were significantly greater than a chance expectancy of 50%, $t(15) = 3.87$, $p < 0.002$. While repeated entries of and time spent in the novel arm were not significantly modified by the level of illumination, in both bright and dim light the changed alternative was chosen in each condition more often and for longer periods of time than expected by chance; entries: bright, $t(15) = 3.17$, $p < 0.007$, dim, $t(15) = 2.54$, $p < 0.025$; time: bright, $t(15) = 4.04$, $p < 0.002$, dim, $t(15) = 2.84$, $p < 0.013$. Although females achieved significantly lower scores than males for both these measures (but not for first entries of the novel arm), in either case, choices of the novel arm exceeded chance expectations for each sex; entries: males, $t(7) = 3.02$, $p < 0.019$, females, $t(7) = 3.84$, $p < 0.006$; time: males, $t(7) = 3.89$, $p < 0.006$, females, $t(7) = 2.84$, $p < 0.013$. Except for repeated entries by females, significant above-chance frequencies of these two measures were also separately generated by male and female rats given 6-min ac-

quisition trials in Experiment 1 (see Figure 1). However, unlike the present experiment, differences between the sexes were not significant.

As only first entries of the novel arm were affected by the difference in light levels, it seems likely that the rats were more reluctant to initially enter the changed alternative when both arms were brightly lit. This finding along with clear indications that they entered both the novel and familiar arms less often and spent less time in them when they were brightly lit suggests that they found this level of illumination aversive and thus to some extent inhibiting, in terms of initial interest in the arm that had changed. However, after their initial choice, there seems to have been some adjustment to the level of illumination so that eventually the bright light had no effect on longer term responsiveness to the novel arm.

General Discussion

The most significant outcome of this study is the first-time demonstration that rats are capable of recognising a change in environmental stimulation that does not primarily involve the visual modality in the form of brightness characteristics. The results also showed that, unlike a recent report of responsiveness to brightness change (Hughes, 2001), females are indeed able to detect a tactile change and, in this particular respect, differ from males only in magnitude of the ability (Experiment 3) and effects of longer acquisition trials (Experiment 1). But it is not yet possible to determine if these sex-related outcomes were due to sex differences in memory or rate of habituation to novelty. For both possibilities sex differences have been described, namely, better spatial discrimination in males (Einon, 1980) upon which memory for a change could depend, and faster habituation rates in females (Hughes, 1990) that may conceivably give impressions of overall lower reactivity to novelty. Although fear can detract from responsiveness to change (Aitken & Sheldon, 1970), this is unlikely to account for the sex differences observed in the present study because, as shown in Experiment 2, the males seemed more fearful than the females even though they were more responsive to change in Experiment 3.

It is likely that exposure to the brightly lit maze arms led to some degree of fear in both sexes that interfered with at least their inclination to enter the changed arm first, as shown for other aversive experiences (Aitken, 1972; Aitken & Sheldon, 1970). Although no direct evidence is available for a possibly aversive effect of 12-min acquisition trials in Experiment 1, the relationship between "trait" fear and responsiveness to change and the effects of bright light, shown in Experiments 2 and 3, support the view that the phenomenon can be disrupted by aversive experiences, such as longer periods of confinement to the apparatus (Dember, 1958). But precisely why such confinement might be aversive still remains to be determined.

As the ability to detect a tactile change depends on recognising the previous position of the novel maze arm, there must be some reliance on directional cues that enable spatial judgments to be made. Therefore, in future research, it would be valuable to explore what cues are used by both males and females when responding to tactile or other forms of sensory change. It would also be desirable to determine the extent to which species other than the rat are responsive to changes in

stimulation, what directional cues they make use of and whether or not the sexes differ in either of these respects.

References

- Aguilar, R., Gil, L., Gray, J. A., Driscoll, P., Flint, J., Dawson, G. R., Giménez-Llort, L., Escorihuela, R. M., Fernández-Teruel, A., & Tobena, A. (2003). Fearfulness and sex in F2 Roman rats: males display more fear though both sexes share the same fearfulness traits. *Physiology and Behavior*, **78**, 723-32.
- Aitken, P. P. (1972). Aversive stimulation and rats' preference for familiarity. *Psychonomic Science*, **28**, 281-282.
- Aitken, P. P., & Sheldon, M. H. (1970). Electric shock and rats' preference for the familiar arm of a maze. *British Journal of Psychology*, **61**, 95-97.
- Archer, J. (1973). Tests for emotionality in rats and mice: a review. *Animal Behaviour*, **21**, 205-235.
- Becker, A., Grecksch, G., Rüttrich, H-L., Pohle, W., Marx, B., & Matthies, H. (1992). Kindling and its consequences on learning in rats. *Behavioral and Neural Biology*, **57**, 37-43.
- Broadhurst, P. L. (1957). Determinants of emotionality in the rat. *British Journal of Psychology*, **48**, 1-12.
- Dember, W. N. (1956). Response by the rat to environmental change. *Journal of Comparative and Physiological Psychology*, **49**, 93-95.
- Dember, W. N. (1958). A comment on "studies on 'Response by the rat to environmental change' ". *Psychological Reports*, **4**, 242.
- Dember, W. N., & Millbrook, B. A. (1956). Free-choice by the rat of the greater of two brightness changes. *Psychological Reports*, **2**, 465-467.
- Douglas, R.J. (1966). Cues for spontaneous alternation. *Journal of Comparative and Physiological Psychology*, **62**, 171-183.
- Einon, D. (1980). Spatial memory and response strategies in rats: Age, sex and rearing differences in performance. *Quarterly Journal of Experimental Psychology*, **32**, 473-489.
- Fowler, H. (1958). Response to environmental change: a positive replication. *Psychological Reports*, **4**, 506.
- Gray, J. A. (1971). Sex differences in emotional behaviour in mammals including Man: endocrine bases. *Acta Psychologica*, **35**, 29-46.
- Hascoët, M., Bourin, M., & Dhonnchadha, B. A. (2001). The mouse light-dark box paradigm: a review. *Progress in Neuropsychopharmacology and Biological Psychiatry*, **25**, 141-166.
- Hughes, R. N. (1965). Spontaneous alternation and response to stimulus change in the ferret. *Journal of Comparative and Physiological Psychology*, **60**, 149-150.
- Hughes, R. N. (1973). Effects of LSD on exploratory behavior and locomotion in rats. *Behavioral Biology*, **9**, 357-365.
- Hughes, R. N. (1990). Sex-dependent habituation to novelty in rats. *Current Psychology: Research and Reviews*, **9**, 277-284.
- Hughes, R. N. (2001). Responsiveness to brightness change in hooded rats: effects of sex and procedure. *Behavioural Processes*, **55**, 143-155.
- Hughes, R. N. (2002). Sex-related glucose effects on responsiveness to brightness change in middle-aged rats. *Pharmacology, Biochemistry and Behavior*, **73**, 485-490.
- Hughes, R. N. (2003). Effects of glucose on responsiveness to change in young adult and middle-aged rats. *Physiology and Behavior*, **78**, 529-534.
- Hughes, R. N. (2004). Responsiveness to brightness change in male and female rats following treatment with the partial agonist of the N-methyl-D-aspartate receptor, D-cycloserine. *Behavioural Brain Research*, **152**, 199-207.
- Hughes, R. N., & Neeson, L. T. (2003). Prevention of memory loss for a brightness change in adult and middle-aged rats by post-exposure administration of glucose. *Pharmacology, Biochemistry and Behavior*, **76**, 119-123.
- Kivy, P. N., Earl, R. W., & Walker, E. L. (1956). Stimulus context and satiation. *Journal of Comparative and Physiological Psychology*, **49**, 90-92.
- Levine, S., Staats, S. R., & Frommer, G. (1958). Studies on "Response by the rat to environmental change". *Psychological Reports*, **4**, 139-144.

- Lukaszewska, I. (1978). The effects of exposure time and retention interval on response to environmental change in rats. *Acta Neurobiologiae Experimentalis*, **38**, 323-331.
- Lukaszewska, I. (1993). Scopolamine affects response-to-change test involving 20-min retention interval after locomotor exploration in rats. *Physiology and Behavior*, **53**, 763-767.
- Markowska, A., & Lukaszewska, I. (1981). Response to stimulus change following observation or exploration by the rat: differential effects of hippocampal damages. *Acta Neurobiologiae Experimentalis*, **41**, 325-338
- Platt, J. J., & James, W. T. (1967). Response to stimulus change in the opossum. *Journal of Psychology*, **67**, 85-89.
- Poucet, B., & Buhot, M-C. (1989). Scopolamine impairs response-to-change based on distal cues in the rat. *Physiology and Behavior*, **46**, 355-359.
- Raney, E. T., & Carmichael, L. (1934). Localizing responses to tactual stimuli in the fetal rat in relation to the psychological problem of space perception. *Journal of Genetic Psychology*, **45**, 3-21.
- Sanchez, C. (1996). 5-HT1A receptors play an important role in the modulation of behavior of rats in a two-compartment black and white box. *Behavioural Pharmacology*, **129**, 197-205.
- Smith, D. E. (1939). Cerebral localization in somaesthetic discrimination in the rat. *Journal of Comparative Psychology*, **28**, 161-188.
- Walk, R. D. (1960). Response of dark- and light-reared rats to stimulus change. *Journal of Comparative and Physiological Psychology*, **53**, 609-611.
- Williams, D. I. (1971). Maze exploration in the rat under different levels of illumination. *Animal Behaviour*, **19**, 365-367.
- Woods, P. J., & Jennings, S. (1959). Response to environmental change: a further confirmation. *Psychological Reports*, **5**, 560.

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