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CER to discrete and contextual stimuli: effects of stimulus modality depend on strain of rat

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Abstract

Strain differences in perception, cognition and affect have been found to interact with the effect of experimental treatments on learning. The present study tested Dark Agouti (DA) and Wistar rats in conditioning to discrete and contextual stimuli, for strain differences in conditioned emotional response (CER) and effects of stimulus modality. A Pavlovian trace-conditioning procedure was used in which a discrete target stimulus (flashing light or tone, counterbalanced across groups) was paired either contiguously or at a 30-s trace with footshock. Contextual conditioning was assessed using a background (continuously presented) experimental stimulus (alternate to that used as target). Experiment 1 used 5×0.5 mA, 0.5-s footshock and Experiment 2 used 2×0.5 mA, 1-s footshock. In both experiments, conditioning to the discrete (target) and background stimuli interacted with strain of rat and stimulus modality. For conditioning to the target stimulus, the trace-conditioning effect (of relatively greater suppression in contiguously conditioned than trace-conditioned groups) differed by stimulus and strain. It was greater for the Wistar strain with the flashing light stimulus and for the DA strain with the click stimulus (although the latter was not significant in Experiment 1). In addition, suppression to the background stimulus was affected by stimulus modality for the DA but not Wistar strain in both experiments. DAs conditioned more to the click than the light as background, whereas there was no difference by stimulus modality for Wistars, although the exact pattern of how this stimulus modality effect was mediated differed between experiments. These results demonstrate that stimulus modality can be an issue when considering apparent strain differences in conditioning.

Keywords: Strain differences; CER; Dark Agouti; Wistar; Stimulus modality; Discrete and contextual conditioning

1. Introduction

Behavioural differences in learning tasks have been documented between commonly used strains of laboratory rat (e.g., Refs. [1–3]). These differences may account for some of the inconsistencies in response to psychoactive drugs and affect the choice of strain for animal models of psychiatric disorders. When interpreting behavioural variation, it is important to consider such strain differences. There have been few direct comparisons of the two strains evaluated here (DAs and Wistars) but there is evidence of variation between other strains in sensory processing [4], emotionality [3,5,6] and cognition [7] and their interaction with experimental treatments [8,9].

With respect to modality-specific differences in conditioning, there has been relatively little documented, despite the evidence that rat strains vary in basic visual acuity [10] and this has an impact on their ability to learn visual tasks (e.g., Ref. [11]). Thus, it would seem likely that the use of visual stimuli might underestimate rats' abilities in conditioning task, in at least some strains. Comparison of DA and Wistar strains shows evidence of greater visual acuity in the DA than Wistar strain [10,12], but no differences in auditory sensitivity have been documented (that the authors are aware of). Strain differences in sensory

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abilities may contribute to observed learning differences, e.g., where a light but not a tone stimulus produced latent inhibition (LI; in which the associability of a stimulus is weakened by prior presentation without consequence) in DA rats whereas Wistars demonstrated LI to both stimuli [13].

Recently, there has been a particular interest in the neural basis of selective learning tasks in which the reliability with which a stimulus predicts an event (such as food or footshock) is manipulated, not least because of evidence that such cognitive functions are impaired in schizophrenia [14–17]. For example, LI procedures have been used to investigate the neural substrates of selective learning [16–18]. The trace-conditioning procedures used in the present study can similarly be used to test the effects of experimental treatments on conditioning to relatively uninformative predictors, in this case, provided by the trace-conditioned discrete CS and the contextual background stimuli. Typically, where learning about the discrete CS is weakened by the introduction of the trace interval, increased conditioning to the context has been observed [19,20], although these inverse levels of conditioning have not always been observed [21,22].

Previously, we have used a conditioned emotional response (CER) procedure to measure conditioning to discrete and contextual stimuli that predict shock, for example, using Dark Agouti (DA) rats to test the effects of serotonergic depletion [22] and Wistars to test effects of systemic amphetamine, on fear conditioning [23]. Wistars are a more typical strain for selective learning tasks [24–26]. Therefore, the present study tests for differences between DA and Wistar rats, both in terms of aversive conditioning and how this is moderated by the modality of the target versus background stimulus. Such strain differences have been reported in another selective learning task, LI [13], in that DA rats demonstrated LI to visual but not auditory stimuli, whereas LI was seen to both modalities of stimuli in Wistar rats.

Here, Experiment 1 compared DA with Wistar rats using five shock pairings of conditioned stimulus with a 0.5-mA, 0.5-s footshock. These parameters produced some strain differences in conditioning to experimental stimuli but also some persistent differences in the level of suppression shown to box context. Therefore, Experiment 2 used rats that had been given additional preexperimental handling (details given in Methods). In addition, Experiment 2 used a reduced number of conditioning trials (two pairings of 0.5-mA, 1-s footshock) in an attempt to minimize conditioning on the basis of the intertrial interval and so promote conditioning to the experimental background stimulus. These procedural modifications also allowed us to test the generality of effects found in Experiment 1. Each experiment was conducted in two replications with DA rats tested in the first and Wistar rats in the second replication.

2. Methods

2.1. Animals

Experiment 1 used 48 (n=12 per cell) naïve male Wistar rats (Charles Rivers, Margate, UK) of mean weight 309 g (range 220–362 g) in the first replication and 26 (n=6/7 per cell) naïve male DA rats (Harlan, Bicester, UK) of mean weight 261 g (range 239–285 g) in the second replication. Experiment 2 used 24 (n=6 per cell) male Wistar rats (Charles Rivers) of mean weight 361 g (range 352–422 g) in the first replication and 24 (n=6 per cell) male DA rats (Harlan) of mean weight 253 g (range 232–268 g) in the second replication. All rats were between 8 and 12 weeks old. The animals in Experiment 2 had additional exposure to an open field and T maze, but no experimental treatment or food deprivation, 2 weeks prior to the start of experimental procedures.

All animals were caged in pairs on a 12:12-h light/dark cycle and were tested during the light phase. They were water deprived, receiving 1 h of access to water per day following testing. Food was freely available in the home cage throughout. All procedures were carried out in accordance with the United Kingdom Animals Scientific Procedures Act 1986, Project Licence numbers PPL 40/1423 and PPL 40/2019.

2.2. Apparatus

Four identical fully automated conditioning chambers, housed within sound-attenuating cases containing ventilation fans (Cambridge Cognition, Cambridge, UK), were used throughout. Each of the inner conditioning chambers consisted of a plain steel box (25×25×22 cm high) with a Plexiglas door (19×27 cm) at the front. The floor was a shock grid with steel bars 1 cm apart and 1 cm above the lip of a 7-cm-deep sawdust tray. Mounted in one wall were two retracted levers (not used for these experiments), three stimulus lights and a waterspout.

The spout was 5 cm above the floor and connected to a lickometer supplied by a pump. Licks were registered by the breaking of the photo beam within the spout, which also triggered water delivery of 0.05 ml per lick. The waterspout was illuminated only when water was available. A loudspeaker for the presentation of auditory stimuli was set in the roof.

Two stimuli were used in this procedure as target and background (fully counterbalanced); a click set at 2 Hz and 70 dB (including background) with the pulses of sound separated by 0.5-s intervals; and a flashing light provided by the three wall-mounted stimulus lights and the house light flashing both on and off for 0.5 s. Footshock was delivered through the grid floor by a constant current shock generator (MISAC Systems, Newbury, UK). Stimulus control and data collection was by an Acorn Archimedes RISC computer programmed in Basic with additional interfacing using an Arachnid extension (Cambridge Cognition).

3. Procedure

Experiments were run in two replications over 3 weeks each. Rats were handled for approximately 10 min per day for 2 weeks. Additionally, the animals (both Wistars and DAs) in Experiment 2 had been exposed to an open field and T maze. Water deprivation was introduced the day before shaping. The procedure consisted of four stages.

3.1. Preconditioning

Rats were shaped until all drank from the waterspout and were individually assigned to a conditioning box for the duration of the experiment, counterbalanced for behavioural condition.

There then followed 9 days of pretraining, in which rats drank in the experimental chamber for 15 min each day (timed from first lick). The drinking spout was illuminated throughout, but there were no other stimuli presented in this phase. Latency to first lick was measured as an indicator of habituation to the experimental context.

3.2. Conditioning

Conditioning was conducted in one day following the last preconditioning day. No water was available within the chamber and the waterspout was not illuminated. Thus, there were no measures to record.

There was a continuous background stimulus (either flashing light or click) onto which pairings of the 5-s target stimulus (the alternate stimulus to that used as background) and footshock were superimposed. There were five pairings of the target CS with a 0.5-mA, 0.5-s shock. The first pairing was presented 5 min into the session and subsequent pairings were presented at 5-min intervals thereafter, with the final shock delivered 5 min before the end of the session.

Depending on experimental group, the footshock followed either 0 (for the contiguously conditioned groups) or 30 s (for the trace-conditioned groups) after target CS offset. The background stimulus was presented throughout the session, including the 30-s interstimulus interval.

3.3. Reshaping

On the day following conditioning, animals were reshaped following the same procedure as in preconditioning sessions. This was in order to reestablish drinking after conditioning and additionally provided a measure of conditioning to the box context itself (again, latency to first lick).

3.4. Test

There were two test days, one for each of the two experimental stimuli, with the order of testing counterbalanced for experimental condition. The time taken to complete 50 licks prior to any stimulus presentation (the A period) provided a measure of any individual variation in baseline lick responding, to be compared with the time taken to complete 50 licks during stimulus presentation (the B period) in a suppression ratio [measured as A/(A+B), to assess conditioning whilst taking baseline variation into account]. These were extinction tests and the stimulus was presented continuously throughout the session; thus, in each case, the B period was a maximum of 900 s for rats that did not complete 50 licks within the 15-min session (6 DAs).

3.5. Statistics

Analysis of variance (ANOVA) was conducted in a $2\times2\times2$ factorial design. The between-subjects factors were stimulus (i.e., target stimulus type, at levels click and light), trace (at levels contiguous and trace) and strain (at levels Wistar and DA). The dependent variables at test were the A period and suppression ratio. Suppression ratios adjust for variation in the A period on an individual rat basis. At preconditioning and reshape, latency to first lick provided a measure of habituation or conditioning to context (respectively), and was analysed in the same $2\times2\times2$ design, with the repeated-measures factor of days (at 9 levels) for the preconditioning latencies.

Mauchly's test of sphericity was applied to the repeated-measures ANOVAs, and the necessary Huynh–Feldt correc-

Table 1
Mean (±S.E.M.[a]) latency to drink at reshape

Experiment	Strain	0-s Light	30-s Light	0-s Click	30-s Click
1	DA	83 (15)	389 (132)	49 (17)	291 (158)
	Wistar	10 (4)	39 (23)	5 (2)	7 (3)
2	DA	290 (130)	207 (141)	69 (30)	173 (146)
	Wistar	378 (133)	632 (170)	163 (66)	654 (131)

[a] S.E.M.=standard error of the mean.

Table 2
Mean (±S.E.M.[a]) latency to 50 licks (A period) prior to target stimulus presentation at test

Experiment	Strain	0-s Light	30-s Light	0-s Click	30-s Click
1	DA	53 (23)	25 (5)	34 (4)	25 (5)
	Wistar	12 (2)	9 (1)	10 (1)	16 (3)
2	DA	26 (2)	40 (8)	24 (3)	32 (12)
	Wistar	42 (15)	104 (33)	49 (8)	44 (15)

[a] S.E.M.=standard error of the mean.

tions were made where the sphericity assumption was violated. All ANOVAs used an alpha level of .05. Significant main effects and interactions were explored by *t* tests based on the individual error terms (two-tailed). When exploring significant main effects in the absence of interactions, the *t* tests were collapsed across groups.

4. Results

4.1. Experiment 1

Data for three rats were missing due to a technical failure at test. These were all Wistars, one from each of the groups: click 0 s, click 30 s and light 30 s.

4.1.1. Preconditioning

For the latency to drink measure over the 9 days of preconditioning, there was an effect of days, $F(5,299)=18.23$, $P<.001$, with latencies reducing over days (range of means: Day 1=26.48 s to Day 10=5.62 s), as would be expected with habituation to the experimental chamber. There were no interactions of trace, strain or stimulus with days, $F_{max}(5,299)=2.05$. However, there was an overall effect of strain, $F(1,63)=25.28$, $P<.001$, with longer latencies in the DA than Wistar rats (means: DA=15.55 s, Wistar=8.16 s).

4.1.2. Reshape

There was an effect of trace, $F(1,63)=11.73$, $P<.01$, an effect of strain, $F(1,62)=19.79$, $P<.001$ and a Strain×Trace interaction, $F(1,63)=9.32$, $P<.01$.

Means (see Table 1) show that this interaction arose because although the trace-conditioned groups had longer latencies than the corresponding contiguously conditioned groups for both strains, this difference was significant only in the DA strain, $t(24)=2.53$, $P<.05$. Thus, over and above the unconditioned difference in drink latency seen at preconditioning, the DA rats showed more suppression generally, and in particular in the trace-conditioned group, consistent with an effect on contextual conditioning over and above the unconditioned strain difference.

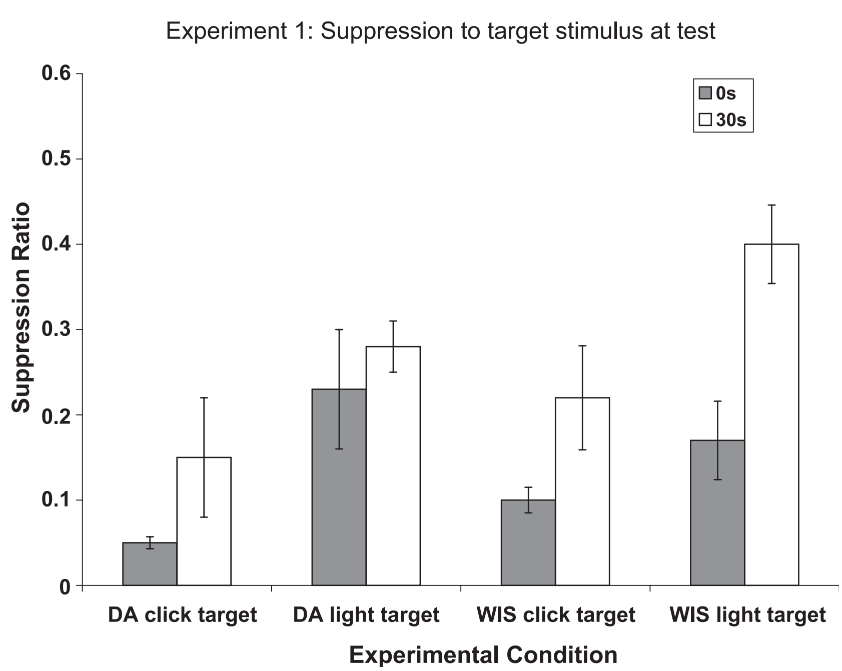

Fig. 1. Experiment 1: Mean suppression ratio for Wistar and DA strains to light or click target CS paired with footshock either contiguously (grey bars) or at a 30-s trace (white bars). Error bars represent two standard errors of the group mean.

Table 3
Mean (±S.E.M.[a]) latency to 50 licks (A period) prior to background stimulus presentation at test

Experiment	Strain	0-s Light	30-s Light	0-s Click	30-s Click
1	DA	28 (4)	21 (2)	60 (17)	23 (3)
	Wistar	12 (2)	11 (2)	13 (3)	13 (2)
2	DA	33 (7)	39 (11)	25 (4)	39 (12)
	Wistar	107 (65)	186 (141)	42 (7)	45 (16)

[a] S.E.M.=standard error of the mean.

4.1.3. Test to target stimulus

A period: As can be seen from the means (Table 2), DA rats again had longer latencies than Wistars, seen as an effect of strain, $F(1,63)=25.33$, $P<.001$. There was also a Strain×Trace interaction, $F(1,63)=4.99$, $P<.05$. However, in contrast to the clear difference in latency seen at reshape, whereby the trace-conditioned rats were slower to drink, on the A periods, there was no significant difference between trace and contiguous groups for either strain, $t_{max}(24)=1.6$, $P=.1$.

As the means show (Table 2), the Strain×Trace interaction must have arisen because the DA 0-s group were more suppressed than any other group, although by t test, that difference did not always reach significance. The DA 0-s group was significantly more suppressed than both 0- and 30-s Wistar groups, $t(33)=3.8$, $P<.01$ and $t(32)=3.43$ $P<.01$, respectively, but as stated above, not significantly more suppressed than the DA 30-s group.

Suppression ratio: As expected, there was an overall effect of trace, $F(1,63)=13.74$, $P<.001$ (means: contiguous=0.13 and trace=0.27) in the absence of an interaction with stimulus or strain, $F_{max}(1,63)=2.67$, $P=.11$. Nor was there any main effect of strain, $F(1,63)=1.26$, $P=.27$. There was, however, a main effect of stimulus, $F(1,63)=17.3$, $P<.001$. This arose because there was greater suppression to the click than to the light. Although there was no significant interaction by strain in the omnibus ANOVA, Fig. 1 suggests that the effect of trace was greatest for the Wistar rats with light as target.

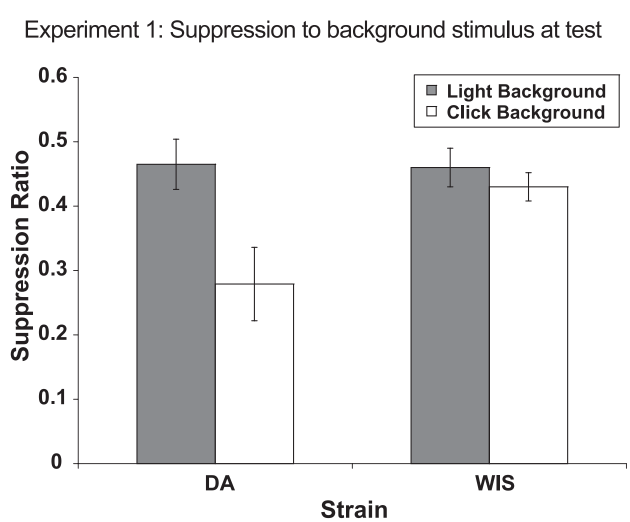

Fig. 2. Experiment 1: Mean suppression ratio for Wistar and DA strains to light (grey bars) or click (white bars) as background CS (alternate to target CS). Error bars represent two standard errors of the group mean.

4.1.4. Test to background stimulus

A period: There was an effect of trace, $F(1,63)=10.42$, $P<.01$; an effect of strain, $F(1,63)=35.5$, $P<.001$; an effect of stimulus, $F(1,63)=6.93$, $P<.01$; a Trace×Stimulus interaction, $F(1,63)=3.94$, $P<.05$; a Trace×Strain interaction, $F(1,63)=9.20$, $P<.01$; a Strain×Stimulus interaction, $F(1,63)=4.66$, $P<.05$, and a three-way interaction of Trace ×Stimulus×Strain, $F(1,63)=4.65$, $P<.05$. Table 3 shows that the three-way interaction arose because the 0-s DA group with click as target (and therefore, light as background) had longer latency to 50 licks than any other experimental group, $t_{min}(11)=2.26$, $P<.05$.

Suppression ratio: On the suppression ratio measure, the level of suppression to the background stimulus did not depend on target trace condition as there was no effect of trace or interactions with trace, $F_{max}(1,63)=2.88$. There was an effect of strain, $F(1,63)=4.88$, $P<.05$, an effect of stimulus, $F(1,63)=11.15$, $P<.001$, and a Strain×Stimulus interaction, $F(1,63)=5.22$, $P<.05$. Fig. 2 shows that the Strain×Stimulus interaction arose because the DA rats with click as background stimulus (and light as target) were more suppressed to the background than all other groups, $t_{min}(24)=2.69$, $P<.05$.

4.2. Experiment 2

4.2.1. Preconditioning

The latency to commence drinking reduced over the 9 days of preconditioning as would be expected with habituation to the experimental chamber (means: Day 1=18.64 to Day 10=7.38 s). This increasing readiness to drink was not affected by strain or by the experimental conditions (to be) of stimulus or trace. This was seen statistically as an effect of days, $F(2,57)=6.21$, $P<.001$, in the absence of any effects of strain, stimulus, trace or their interaction, $F_{max}(1,40)=2.1$.

4.2.2. Reshape

There was an effect of trace, $F(1,40)=4.62$, $P<.001$, an effect of strain, $F(1,40)=9.30$, $P<.01$, and a Trace×Strain interaction, $F(1,40)=4.12$, $P<.05$. This interaction arose because of the longer latency to drink in the trace-conditioned Wistar rats, compared with all other groups (see Table 1), $t_{min}(22)=2.90$, $P<.01$. There was no effect of stimulus, either overall or in interaction, $F_{max}(1,40)=1.56$.

4.2.3. Test to target stimulus

A period: There were no effects of trace, stimulus, strain or interactions, $F_{max}(1,40)=2.85$, in the time taken to 50 licks in the absence of the target stimulus.

Suppression ratio: There was an effect of trace, $F(1,40)=17.35$, $P<.001$, an effect of stimulus, $F(1,40)=5.80$, $P<.05$, and a Trace×Stimulus×Strain interaction, $F(1,40)=4.17$, $P<.05$. As can be seen from Fig. 3, the interaction arose because although the contiguously conditioned groups were more suppressed than the trace-conditioned groups, this was only significant for the Wistar light and DA click groups, $t(10)=2.8$, $P<.05$ and $t(10)=2.46$, $P<.05$, respectively.

4.2.4. Test to background stimulus

A period: There were no effects of strain, trace or stimulus, $F_{max}(1,40)=2.43$, on responding prior to background stimulus presentation.

Suppression ratio: On the suppression ratio measure, there was a Stimulus×Strain interaction, $F(1,40)=4.32$, $P<.05$. As Fig. 4 illustrates, this interaction arose because for the DA rats, the group with light as background (therefore, click as target) were significantly less suppressed than those DAs with click as background (and light as target), $t(22)=2.58$, $P<.05$, whereas for the Wistar strain, there was no significant difference, $t<1$ by stimulus modality. There were no other main effects or interactions, $F_{max}(1,40)=2.32$.

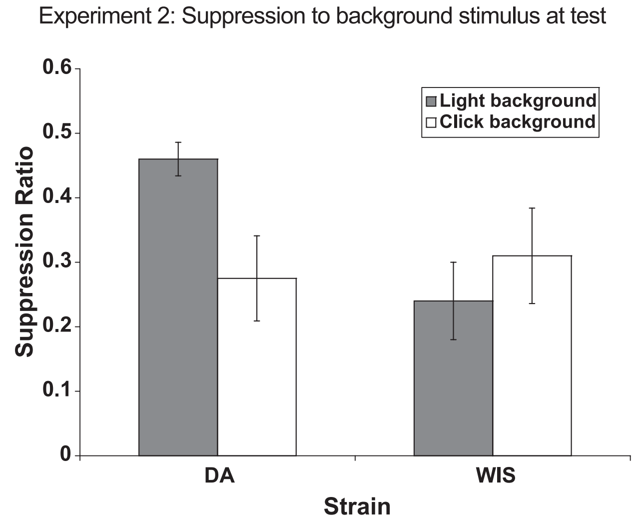

Fig. 4. Experiment 2: Mean suppression ratio for Wistar and DA strains to light (grey bars) or click (white bars) as background CS (alternate to target CS). Error bars represent two standard errors of the group mean.

5. Discussion

At face value, these results suggest that reliable demonstration of a difference between trace and contiguously conditioned groups can depend on both modality of stimulus and strain of rat in use. However, we should also consider effects that may be confounded before reaching a

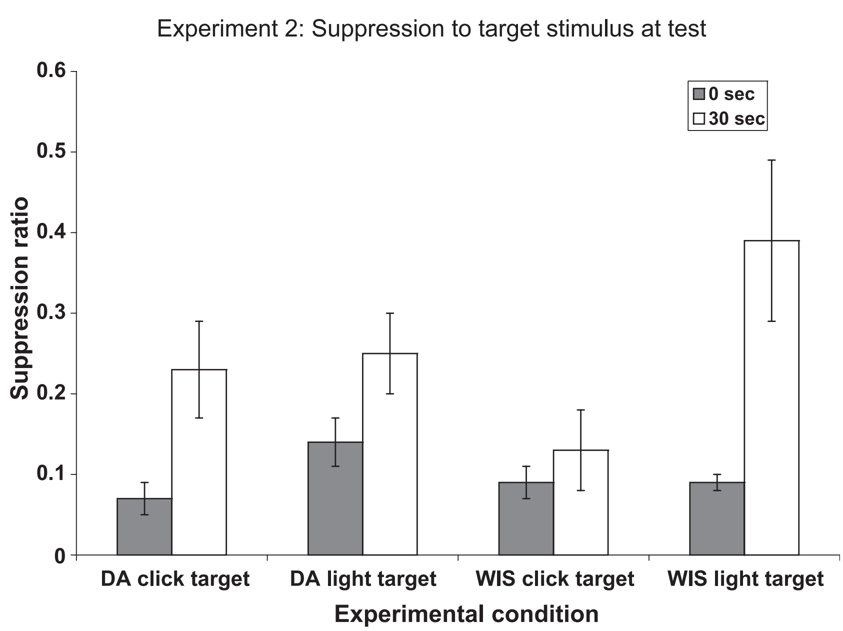

Fig. 3. Experiment 2: Mean suppression ratio for Wistar and DA strains to light or click target CS paired with footshock either contiguously (grey bars) or at a 30-s trace (white bars). Error bars represent two standard errors of the group mean.

firm conclusion with respect to how apparently strain-specific effects were mediated.

5.1. Baseline differences in drinking (preconditioning)

In both experiments, the groups were evenly matched for prospective trace and stimulus group allocations prior to conditioning. However, there was a difference between strains in Experiment 1 even before any conditioning had taken place, in that the DAs had longer latencies to drink than Wistars. This strain difference was reduced in Experiment 2, most likely because of the increased amount of handling and exposure to novel environments (in open field and T maze) prior to experimental procedures in the second experiment, although possible contribution of other differences between the two experiments cannot be ruled out. DA rats have shown higher levels of emotionality than other strains in tasks such as open field and plus maze [3,5]. Such differences were reduced by (even quite minimal) handling and restraint stress for injections [3]. Similarly, chronic handling has effectively decreased anxiety in other rat strains [27,28]. Thus, where DAs are appropriate for a learning task (for example, where good visual ability is necessary), present findings support the importance of sufficient handling and/or exposure to novel stimuli to reduce anxiety levels.

5.2. Baseline differences in conditioning to box context

Over and above the unconditioned differences in drinking, there were differences in suppression to box context after conditioning (at reshape). It might be predicted, in line with other findings [19,20], that trace-conditioned rats (without a good predictor of footshock) would condition more to the experimental context than contiguously conditioned rats (with a good predictor). This pattern was seen in DA rats in Experiment 1 and Wistar rats in Experiment 2 (see Table 1). The different baseline levels of conditioning between the two experiments might account for this apparent discrepancy. In Experiment 1, the Wistars demonstrated relatively little suppression and in Experiment 2, the DAs showed less suppression than Wistars, so any difference between trace and contiguous groups may have been obscured by a floor effect.

The A periods (at conditioning test) measure fear of the box context that persists after exposure to box context at reshape. As would be expected, latencies to drink were generally reduced compared with those at reshape (cf. Tables 1, 2 and 3). In Experiment 2, there were no differences between experimental groups, but in Experiment 1 (at both background and target test), there was greater suppression to box context for the DA contiguously conditioned rats. This differential suppression to box context was opposite to that seen at reshape (in that at reshape, DA trace-conditioned rats took longer to lick than their contiguously conditioned counterparts). This difference between the reshape and A-period latencies can only reflect differential extinction but is difficult to explain. In any event, the difference seen in the A period was modest relative to that seen at reshaping, and for the purpose of assessing, conditioning to experimental stimuli was taken into account in suppression ratios.

Again, as with the unconditioned latency to drink measure, the finding that the greater conditioning to box context in DAs compared to Wistars at test (in the A periods) in Experiment 1 was reduced in Experiment 2 may be a result of the increased handling and exposure to novel environments prior to conditioning in Experiment 2. Heightened contextual conditioning in the DA strain is consistent with their reported higher emotionality [3,5] as conditioned freezing to context is an index of anxiety [29] that may have been reduced by the extra handling. Alternatively, the different baseline levels of suppression between the two experiments may have interacted with the strain difference in level of emotionality.

The level of conditioning to the box context varied between experiments with generally more suppression in Experiment 2 (see Tables 1, 2 and 3), particularly for the Wistar strain. This increase in conditioning to context may be accounted for by the reduction in the number of shock pairings in Experiment 2, rendering the intertrial interval less effective as a temporal cue.

In summary, for the most part, there was effective extinction of conditioning to the experimental box over the reshape session allowing unconfounded measurement of conditioning to stimuli at the test presentations. Whether conditioned or unconditioned, individual variation in drinking was in any case accounted for by the suppression ratio.

5.3. Effects of strain or of replication?

Because rats of a single strain were tested together (in each case, one strain per experimental run), effects attributed to strain are in principle confounded with those that could arise as replication effects. However, although experimental parameters varied from experiment to experiment, they were identical within an experiment. More importantly, the modality-specific differences in conditioning that were found between strains were clearly reproducible from one experiment to the next. For the background stimulus, suppression was affected by stimulus modality for the DA but not the Wistar strain in both experiments. For the target stimulus, the trace-conditioning effect was greatest for the Wistars with light in both experiments (although the Trace×Strain interaction was only statistically significant in Experiment 2). The same pattern of stimulus modality effects despite differences in experimental parameters shows that such strain differences are robust.

Thus, although, in principle, the methodological differences between experiments could have contributed to the baseline differences discussed above (e.g., in suppression to box context measured as latency to drink at reshape), the main claim of this paper is that there are conditioning differences between strains that depend on stimulus modality, and these are consistent across experiments. Any argument about confounded methodological variation between experiments only applies to the differences in the prestimulus baseline measures, and these are anyway controlled for within each experiment by the use of suppression ratios (as explained above).

5.4. Conditioning to the target stimulus

The basic trace-conditioning effect (of relatively greater conditioning in contiguously conditioned than in trace-conditioned groups) depended on stimulus modality and strain (see Figs. 1 and 3). Specifically, the target stimulus that produced the greatest trace-conditioning effect for Wistar strain was the light; and for DA strain, it was the click. This effect was clearest (statistically) in Experiment 2, and the pattern of effects was replicated in Experiment 1 (cf. Figs. 1 and 3).

This difference by stimulus modality was consistent across experiments despite differences in footshock parameters and level of handling. It could have arisen because of different levels of suppression supported by these stimuli in the two strains. However, it is not simply the case that more salient stimuli are suitable for learning tasks where weakly and strongly predictive stimuli are to be compared, as such effects emerge only as a difference between groups. In the present study, the trace-conditioning effect was clearest with the stimulus that produced higher suppression (the click) in DA rats and with the stimulus that produced least suppression (light) in Wistars.

The effects of stimulus modality observed in these experiments are consistent with other instances of differential performance in conditioning tasks. These have previously been found to depend on the nature of the stimulus, typically across but also within modalities [4,30] as well as on strain [7] and the interaction between modality and strain [13]. The basis of these differences may be differences in pigmentation. Although direct comparisons of albino and pigmented strains have shown little difference in most learning tasks (e.g., appetitive classical and instrumental conditioning, taste aversion and spatial learning: Refs. [12,31]), in tasks that may tap into the same psychological processes as those here, there have been differences between pigmented and albino rats. For example, hooded Wistars have demonstrated greater LI (a selective learning task) with auditory stimuli than albino Wistars [31].

5.5. Conditioning to the background stimulus

For conditioning to the background stimulus, strain differences in the effects of stimulus modality on learning were the same in the two experiments. For the DA strain, the click background produced greater suppression than the light background (cf. Figs. 2 and 4), whereas for Wistars, there was no difference by stimulus modality.

In the present study, the pattern of this stimulus modality effect in DAs on conditioning to background differed by behavioural condition between experiments, in that in Experiment 1, the difference was mediated by an increase in suppression to click background (compared with barely any suppression in any other group), whereas in Experiment 2, it was mediated by reduced suppression to light compared with the level in all other groups. The interpretation of this difference is not clear-cut, as there were several methodological differences between the two experiments, but it may be explained in terms of the difference in general levels of conditioning to background between the two experiments. Consistent with the hypothesis that five regularly spaced conditioning trials provide temporal cues that might overshadow conditioning to background, when the number of conditioning trials was reduced from 5 to 2, the level of conditioning to the background was increased.

The lack of effect of stimulus modality in Wistar rats was not simply due to a floor in conditioning to background (as might be claimed for Experiment 1) because it also held true at the higher level of conditioning to background observed in Experiment 2. This effect of stimulus modality in DA but not Wistar rats is consistent with findings in an LI study [13] where effects of stimulus modality were also observed in DA but not Wistar rats (although with conditioning to discrete stimuli in LI).

5.6. Conclusions and implications

These results suggest that for a clear trace-conditioning effect (i.e., difference between trace and contiguously conditioned groups), a visual CS is more effective for Wistar rats and an auditory CS for DA rats. Additionally, for DA rats, a click stimulus was more effective in producing relatively greater conditioning to background than a light stimulus.

The differential effect of modality by strain might be mediated directly or through differential overshadowing by the competing background stimulus. Although overshadowing seems a good account of the effect of stimulus modality on conditioning in some experimental groups, it does not fit with the pattern of conditioning between target and background observed in others.

Whatever the best explanation, these results show that stimulus modality can be an issue when considering apparent strain differences in conditioning.

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