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Research report

Brief light as a practical aversive stimulus for the albino rat

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ABSTRACT

Bright light was an effective aversive stimulus for Wistar rats in punishment, escape, and avoidance paradigms. Contingent punishment of lever pressing maintained by concurrent schedules of food delivery shifted presses to an alternate lever, and depressed overall response rates. Periodic non-contingent presentation of the light prompted escape responding (head entry into a hole). Unsignaled avoidance contingencies were not effective, but pre-pulse signaling of light supported avoidance behavior. These results demonstrate a possible alternative to foot-shock, one with greater ecological validity, and one that might avoid some of the physiological effects that accompany electric shock.

1. Introduction

Electric footshock has served as the prototypical aversive stimulus in experimental preparations using rats [34,30]. Footshock is popular for its reliability, utility at a wide range of current, and the feasibility of titrating shock levels for individual subjects. But electric shock has its downsides: It often induces secondary effects such as long-term sleep disruption [41], altered social behavior [27], reduction in locomotion, rearing, and grooming behaviors, as well as an increase in immobility and defecation [44]. Footshock has also received criticism when used to model conditions such as depression or anxiety disorder that are produced by stressors that lack a comparable component of pain [28]. Finally, the nature of footshock stimulation precludes its full inclusion in some modern experimental techniques, such as electrophysiology.

As neural, behavioral, and genetic research strives to create better animal models of human disorders, the availability of options other than footshock as aversive stimuli becomes increasingly important. Reed and Yoshino [39] recently noted the utility of a broader range of aversive stimuli, including some that might replace shock and avoid some of the drawbacks that accompany its use. For instance, they demonstrated that response suppression could be effected by a loud, short tone presented with long inter-trial intervals.

The present study aims to systematically test whether bright light is an effective aversive stimulus for rats. Early experiments demonstrated that rats will press a lever to terminate a light stimulus, and that rate of lever pressing increases with light intensity [19]. The rate of escape lever presses is also sensitive to the schedule of negative reinforcement [16–18]. When allowed to control their own daily exposure to light by lever pressing, albino rats decrease their exposure to light intensities greater than 1.25 lux over days, and maintain their exposure to light below this threshold [22–25]. Further examination led Campbell and Messing [6] to suggest that light is likely aversive even at the lowest levels of illumination in rats. However, a considerable number of studies have proposed that light – at some levels – may not be aversive [36], and might even act as a reinforcer [2,14,40].

The following experiments provide a systematic test of light's efficacy as an aversive stimulus. Experiment 1 examined the aversiveness of bright light in a choice situation by adding a light contingency onto one of two otherwise identical alternatives. Experiments 2 and 3 examined escape from and avoidance of light, respectively. It has long been suggested that defensive responses are more efficiently learned when they are consistent with the natural repertoire of the animal [4]. Burrowing is a commonly observed defensive behavior in *Rattus norvegicus* [3,20,33,35]. It

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was thus expected that entering a short tunnel would be an effective escape/avoidance response to light.

2. Experiment 1: punishment

It has been shown that rats prefer dark or dim areas over those that are brightly lit, in both Pavlovian (e.g. [42]) and operant paradigms (e.g. [22–25]). However, lights have also been used as effective reinforcers during operant conditioning [2,27,14]. Experiment 1 aimed to determine whether a brief bright light serves as a punisher. If it does, making the light contingent on pressing one of two levers for food should reduce preference for that lever.

2.1. Methods

2.1.1. Subjects

Six experimentally naive male Wistar rats were housed individually in a room with a 12 h:12 h light:dark cycle, with dusk at 0600 h; experiments were conducted only during the dark cycle. Water was always available in home cages. Supplementary chow was provided to maintain rats at 85% of their free feeding weight, as estimated using growth curves from the provider (Charles River Laboratories, Hollister, CA, USA). Upon starting the experiment the animals were approximately 46 days old and had been food restricted for five days. All conditions were maintained in accordance with the Institutional Animal Care and Use Committee (IACUC) guidelines and regulations at Arizona State University.

2.1.2. Apparatus

Experimental sessions were conducted in a MED Associates (St. Albans, VT) modular test chamber (305 mm long, 241 mm wide, and 292 mm high), enclosed in a sound- and light-attenuating box equipped with a ventilating fan. The front and rear walls and the ceiling of the experimental chambers were made of clear plastic, and the front wall was hinged and functioned as a door to the chamber. In the center of the transparent ceiling a 64-mm diameter hole allowed direct entry of 1650 lumens of light (8180 lux at the chamber floor), generated by a 150-W indoor/outdoor *Ace* brand Par 38 floodlight lamp (model 3019759). Light measurements (light meter model 401027, Extech Instruments, Watham, MA, USA) were taken from just above the chamber floor, which consisted of thin metal bars above a catch pan. One of the two aluminum side panels served as a test panel. A square opening (51 mm sides) located 15 mm above the floor and centered on the test panel provided access to the hopper (MED Associates, ENV-200-R2M) for 45 mg food pellets (Noyes Precision pellets, Improved Formula A/I, Research Diets, Inc., New Brunswick, NJ, USA). A single pellet was provided with each activation of a dispenser (ENV-203). Two retractable levers (ENV-112CM) flanked the food hopper. The center of each lever was 80 mm from the center of the food hopper, and 21 mm from the floor. Lever presses were recorded when a force of approximately 0.2 N was applied to the end of the lever. The ventilation fan mounted on the rear wall of the sound-attenuating chamber provided masking noise of approximately 60 dB. There was no ambient illumination of the test chambers during experimental sessions. Experimental events were arranged via a Med-PC® interface connected to a PC controlled by Med-PC IV® software.

2.1.3. Procedure

2.1.3.1. Hopper and lever training. Subjects were first hopper-trained for two days. During this time, food was presented non-contingently for 1 h each day on a random schedule. Subsequently, rats were trained to press on the right lever for pellets by progressively increasing the response requirements.

2.1.3.2. Baseline. The rats were then trained on two independent concurrent variable-interval 60 s (VI 60 s VI 60 s) schedules of food reinforcement. On these schedules, after a random interval elapsed, the next response on the appropriate lever delivered a pellet. Intervals were selected from two independent 12-item Fleshler–Hoffman distributions [10], each with a mean duration of 60 s. This condition was effective for approximately 10 sessions, 5 days per week. The *preferred lever* was defined for each rat as the one with more responses during the last five sessions. *Baseline preference* was computed as the proportion of lever presses made on the preferred lever. Sessions lasted for either 1 h or 120 trials, whichever happened first.

2.1.3.3. Choice with light on VI 60 s. 5 s activations of the floodlight contingent on lever pressing were superimposed on baseline experimental conditions. For each rat, the preferred lever was selected to activate the floodlight. Light activations on the preferred lever were delivered according to a VI 60 s schedule, independent of food reward. This condition was in effect for 15 sessions.

2.1.3.4. Choice with light on VI 30 s. The rate of floodlight activation was increased by reducing the mean interval between activations to 30 s (VI 30 s). The schedule of food reinforcement remained unchanged. This condition was in effect for 12 sessions.

2.1.3.5. Reversal of light-activating assignment. The position of the lever activating the floodlight was reversed, with the schedule of light-activation remaining VI 30 s. The lever that previously delivered light activations now delivered only food. Nine sessions were conducted under these conditions.

2.1.4. Data analysis

The data collected for each of the following experiments created a hierarchical, or nested, dataset with multiple observations collected from each subject [38,43]. The nesting of data violates the assumption of independence for inferential testing in ANOVA/regression models, which in turn can lead to an excessively high Type I error rate [43]. In order to take into account the nested structure of the dataset, a mixed ANOVA model with both fixed and random effects was used [15]. The variable that is responsible for the nesting (i.e., subjects) was incorporated into the ANOVA model as a random effect in which each individual subject was specified as a level of the random effect [15]. The standard errors and variance estimators used for significance testing were then adjusted by the mixed ANOVA model for the presence of a nesting variable [38,15]. The experimental condition was specified as a fixed effect. Data from the last three sessions of each of the four conditions were analyzed in order to compare stable data between each subsequent condition, and omitting the learning curve associated with changes between conditions. Because the dependent variable was not normally distributed, robust standard errors were used, which are a distribution-free estimator, and therefore less sensitive to departures from normality [8,38]. Tukey–Kramer post hoc tests were conducted to examine all possible comparisons between conditions; all reported p values are Tukey–Kramer adjusted. Data analysis was conducted using SAS PROC MIXED (SAS Institute, Inc. Version 9.2).

2.2. Results and discussion

The mixed ANOVA revealed a significant effect of experimental condition [$F(3,63) = 45.06$, $p < .001$]. During the baseline condition, three rats pressed the left lever more often, and three rats pressed the right lever more often. After extensive training, an average 56 ± 1% of lever presses were made on the preferred lever. Fig. 1

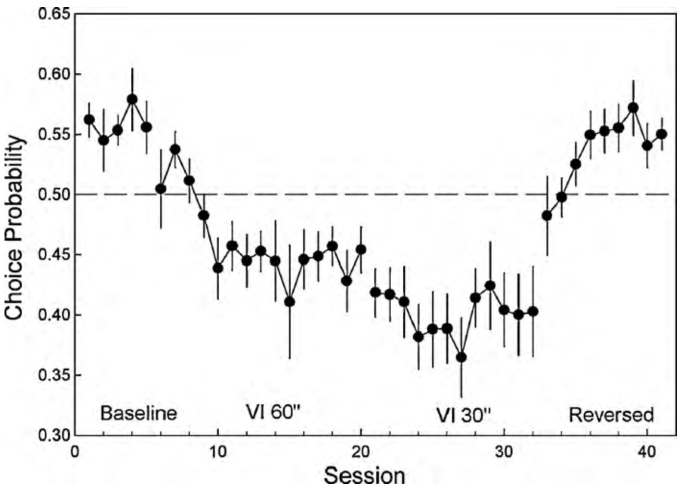

Fig. 1. Mean (±SEM) proportion of presses on the lever that was preferred during baseline. The dashed line indicates indifference between levers. *Baseline* shows the initial proportion of presses on the preferred lever. When bright light was added on a *VI 60* schedule, the proportion of responding shifted toward the originally non-preferred lever. When the rate of bright light presentation was increased to a *VI 30* schedule a slight further decrease in preference was observed. When the bright light was *Reversed* onto the originally non-preferred lever, the proportion of responses on the preferred lever again increased. These data show that lever presses were less frequent on the lever that produced light. Results from the Mixed ANOVA are presented in Section 2.2.

shows the average choice of the preferred lever over baseline and experimental conditions.

Tukey–Kramer post hoc tests revealed that relative rates of responding on the preferred lever decreased following the introduction of the light [$t(63) = 3.63$, $p < .01$], as seen in Fig. 1, to an average of 44.6 ± 1.2% over the last three days of the VI-60 s light condition. Changing the punishment schedule to a shorter interval (VI 30 s) increased the rate of contingent light activations and caused a further reduction of responding to 40 ± 2% [$t(63) = 2.07$, $p = .17$, N.S.]. Switching the light to the originally un-preferred lever quickly drove the relative rates of responding back in favor of the originally preferred lever (54.8 ± 1.3%). This increase was significantly different from the preceding condition [$t(63) = -7.55$, $p < .001$] but not significantly different from baseline [$t(63) = .60$, $p = .93$, N.S.].

The introduction of the response-activated floodlight produced an overall decrease in responding. Prior to the experimental condition, responses averaged 1248 ± 60 per session. Introduction of the light stimulus reduced this average to 800 ± 36 responses/session within five experimental sessions. That average was maintained for the duration of the experiment. This depression in overall responding and the differential depression of the contingent response are consistent with the hypothesis that light punished lever pressing, and that most response suppression occurred on the punished lever.

3. Experiment 2: escape/avoidance

Experiment 2 examined escape responses of albino rats using the operant burrow apparatus. The rates of head entries into the burrow were examined when a bright light was presented at various rates and durations, with entry terminating the light, and also when burrowing did not terminate the light. Given that each successful escape response produced an extended ITI, the present experiment also has a Sidman avoidance component.

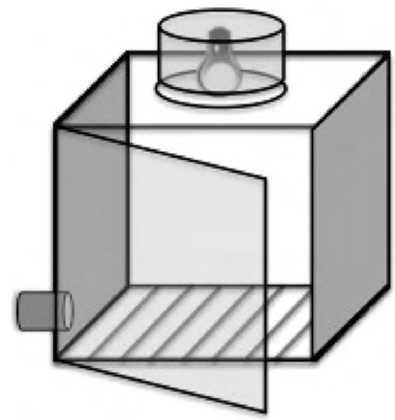

Fig. 2. A diagram of the experimental chamber used in Experiments 2 and 3. The operant burrow apparatus, located in the front lower left quadrant of the chamber measures 60 mm deep and 50 mm in diameter, and contains an infrared photo beam at 21 mm for measuring head entries.

3.1. Methods

3.1.1. Subjects

Five male Wistar rats were housed individually in a room with a 12 h:12 h light:dark cycle, with dusk at 0600 h; experiments were conducted only during the dark cycle. The rats received food and water *ad libitum*. Upon starting the experiment the animals were approximately 270 days old. All five rats had prior experience in two pilot experiments with light stimuli including stroboscopic light and 40 W bulbs prior to their use in the present experiment. All conditions were maintained in accordance with the Institutional Animal Care and Use Committee (IACUC) guidelines and regulations at Arizona State University.

3.1.2. Apparatus

A round opening 50 mm in diameter was made in one of the panels of the box used in Experiment 1, which allowed the animal to enter an aluminum cylinder 60 mm deep, closed at the distal end (the *burrow*, Fig. 2). The center of the opening was located 85 mm from the medial line of the center panel, toward the chamber door. An infrared beam (Med Associates, ENV-254) located 21 mm into the cylinder recorded head entries. The same flood lamp described in Experiment 1 was used; it caused a temperature increase of no more than 4.5 °C, over the course of the session. Chamber temperatures varied below this level depending on escape proficiency.

3.1.3. Procedure

3.1.3.1. Terms and basic conditions. The Light–Light (LL) interval was the interval between the response-independent termination of the light and its subsequent presentation. The Response–Light (RL) interval was the interval between the response-dependent termination of the light and its subsequent presentation. The light duration (D) represents the duration of light stimulus presentation in the absence of a successful escape response. The RL, LL, and D intervals for each of the experimental conditions is indicated below as "(RL:LL:D)". Escapes were defined as head entries into the burrow during the light that caused a break in the infrared beam. A head removal of 2 s (during light or darkness) was required to accept subsequent escape responses. This contingency prevented subjects from avoiding the light by remaining lodged in the burrow.

3.1.3.2. Experimental conditions. Baseline 1 (20:5:10): Subjects were exposed to D = 10 s of light following each LL interval. Head entries during the light terminated it for 20 s (the RL interval). This condition lasted for an average of 22 sessions. If no head entry occurred within the 10-s light period, the light terminated and the LL interval began.

No light (0:0:0): The light was discontinued. Responses during the extinction period were measured in the same way as in the previous condition, with trials defined by the 10 s interval when the light would have been presented. Subjects remained in the no-light condition for an average of six sessions.

Baseline 2 (20:5:5): It was determined that all successful escape responses in baseline 1 occurred within 5 s of the stimulus presentation. Therefore, the light duration (D) was reduced to 5 s. This condition was in effect for 13 sessions.

Inescapable light (0:5:5): The light was made inescapable. Measurement of head-entry responses continued, but entries had no effect in changing the 5 s LL interval or 5 s light duration. Ten sessions were conducted.

Baseline 3: Subjects were returned to baseline 2 parameters (RL = 20 s, LL = 5 s, D = 5 s) for 10 sessions.

Sidman avoidance contingencies (5:5:5): The RL interval was reduced to 5 s. Head entries to the burrow terminated the light. Ten sessions were conducted.

3.1.4. Data analysis

The data for Experiment 2 were analyzed as described above for Experiment 1. Subjects were incorporated into the ANOVA model as a random effect and the experimental condition was specified as a fixed effect. Again, only data from the last three sessions of each of the conditions were used for the analysis.

3.2. Results and discussion

The mixed ANOVA revealed a significant effect of condition on escape probability [$F(4,20) = 261.66$, $p < .001$]. Fig. 3 shows the average proportion of trials in which escape responses were emitted across experimental conditions. Subjects showed an immediate sensitivity to the light, escaping 64 ± 5.0% of the first five sessions and increasing to 84 ± 3.1% during the last three sessions of baseline 1. The mean escape latency was 2.1 s, with all successful escape responses occurring within 5 s of the stimulus presentation. Given the short latency of escapes in the firstcondition, the light duration for subsequent baseline conditions (baseline 2, 3) was reduced to 5 s. This may have caused a slight but non-significant decrease in the frequency of escape responses in subsequent recoveries of baseline (baseline 1 vs. 2, $t(20) = 2.75$, $p = .11$ N.S.; baseline 1 vs. 3, $t(20) = 2.72$, $p = .12$, N.S.). During the no-light condition, responding dropped significantly [$t(20) = 15.64$, $p < .001$], with an average escape rate of 1 ± .4%. The rats did not use the burrow unless driven there by the light.

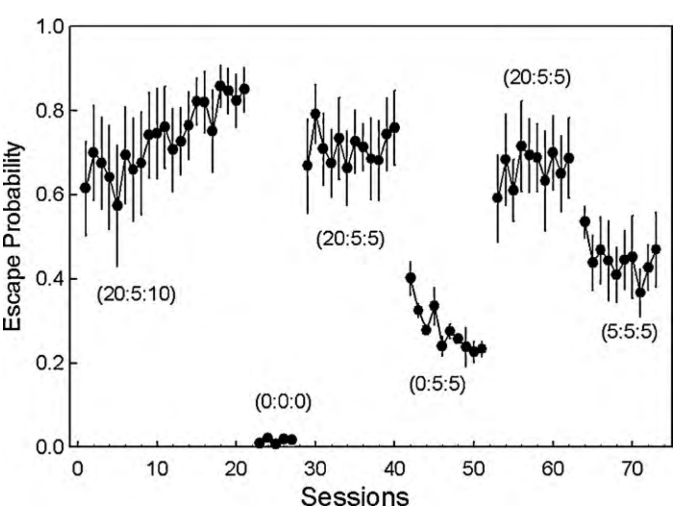

Fig. 3. Mean (±SEM) proportion of trials in which escape responses were emitted. Escape contingencies are described in parentheses using the format RL:LL:D, where RL is the Response–Light interval, LL is the Light–Light interval, and D is the duration of the light. The three baseline [*(20:5:10)*, *(20:5:5)* and *(20:5:5)*] conditions were intermittently followed by conditions in which no light *(0:0:0)* was presented, bright light was made inescapable *(0:5:5)* and in which the Sidman avoidance contingency was debased *(5:5:5)*. Results from the Mixed ANOVA are presented in Section 3.2.

During 10 sessions of inescapable light, animals attempted to escape on 23 ± 1.8% of the light presentations, significantly less than baseline [$t(20) = 12.03$, $p < .001$]. Escape responses during this condition were not fully extinguished, perhaps because the escape cylinder provided some shade. Following this condition, baseline escape responding was again re-established. The last condition decreased the response contingent dark-time to 5 s, which decreased the probability of escape to 42 ± 3.8%, a significant decrement from baseline [$t(20) = 6.20$, $p < .001$].

Overall, the sensitivity of escape responses to contingency manipulations confirms that light was aversive to Wistar rats. When given the opportunity, rats escaped most presentations of the light. The burrow was used substantially less when no light was presented and when the burrow was ineffective. Furthermore, escape responses were sensitive to the duration of the darkness period they produced: shorter periods supported a lower probability of escaping.

4. Experiment 3: escape and avoidance

The escape paradigm used in Experiment 2 was replicated, with additional measures taken to eliminate temperature as a factor. The ability of bright light to support an avoidance response was then tested using the burrow apparatus.

4.1. Methods

4.1.1. Subjects

Six male Wistar rats were housed individually in a room with a 12 h:12 h light:dark cycle, dusk at 0600 h; experiments were conducted during the dark cycle. The rats received food and water *ad libitum*. Upon starting the experiment proper, the rats were approximately 155 days old. All six rats were tested in Experiment 1 prior to their use in the present experiment and therefore had experience with that apparatus: The bright light was identical and the dimensions and floors of the chamber were similar. All conditions were maintained in accordance with the Institutional Animal Care and Use Committee (IACUC) guidelines and regulations at Arizona State University.

4.1.2. Apparatus

The apparatus was similar to that used in Experiment 2. To maintain a consistent temperature, two ventilation fans were added, increasing the masking noise to 72 dB. A tone generator (MED Associates ENV-223), which could produce a tone of 3.5 kHz at 77 dB through a speaker (ENV 224AM) was also added.

4.1.3. Procedure

4.1.3.1. Escape only. Bright light was presented on a random basis every 10 s, but with a 5 s minimum interval and a maximum duration of 8 s. The interval between light presentations constituted the inter-trial interval (ITI). Responses within 8 s of light onset were followed by a 15 s dark period. If no response occurred within the 8 s period, the light was terminated. Either outcome was followed by an ITI. As in the previous experiment, successful escape responses required a preceding 2 s head removal from the operant burrow. This condition was in effect for 10 sessions.

4.1.3.2. Unsignaled avoidance and escape. The light presentation contingencies from the previous condition remained. Head entries during the ITI constituted avoidance responses and were followed by 20 s of darkness. Escape responses during the light were followed by a shorter, 5 s dark period. This condition was in effect for 10 sessions.

4.1.3.3. Signaled avoidance and escape. In addition to the preceding escape/avoidance contingencies, a tone signaled the 5-s period preceding the light onset. This condition lasted for 16 sessions.

4.1.3.4. Pre-pulse avoidance and escape. A brief (200 ms) flash of light was added at the beginning of the 5-s warning-tone period for 14 sessions. We call this light the *cue-light*, to distinguish it from the 8-s light it cued.

4.1.3.5. Avoidance only. The subsequent 20 sessions allowed subjects to avoid the light stimulus only through the completion of valid responses in the dark; when the light was on, it was inescapable. The warning tone from the previous condition was removed, though the cue-light remained present.

4.1.3.6. Brief light. The duration of the light was reduced from 8 s to 500 ms. Fourteen sessions were recorded. The cue-light remained active during this condition.

4.1.3.7. Unsignaled brief light. Ten sessions were conducted where the cue-light was removed, leaving only the brief flash of light, which was presented every 5 s if no avoidance responses were made, and was delayed by 20 s when an avoidance response was made.

4.1.4. Data analysis

The data for Experiment 2 were analyzed as described above for Experiment 1; however, responses in the light (escape) and those in the dark (avoidance) were analyzed using two separate mixed models. Subjects were incorporated into each of the ANOVAs as a random effect and the experimental condition was specified as a fixed effect. As in the previous experiments, only data from the last three sessions of each of the conditions were used for the analysis.

4.2. Results and discussion

The mixed ANOVA revealed a significant omnibus effect of experimental condition on responses both in the light [$F(5,114) = 570.75$, $p < .001$] and in the dark [$F(4,114) = 88.05$, $p < .001$]. Figs. 4 and 5 show rates of head entry in the light (escape) and in the dark (avoidance), respectively. Escape behavior is not shown for the last two experimental conditions, because the brief light used in those conditions was inescapable. Subjects finished the escape-only condition with an average of 1.1 ± 0.1 escape responses/min, which cancelled the light on $47 \pm 5.1\%$ of trials. These were lower than baseline rates demonstrated in Experiment 2. High rates of responding in the dark, which had no programmed consequences, occurred during the first session of the escape-only condition (0.69 ± 0.1 responses/min), declining to an asymptote of $0.25 \pm .1$ responses/min during the last three sessions.

Permitting avoidance in the second condition (Fig. 5, "Uns Av + Esc") did not increase avoidance responding [0.24 ± 0.02 responses/min; $t(114) = -2.00$, $p = .42$ N.S.]. The addition of a warning tone in the signaled avoidance condition (Fig. 5, "Sig Av + Esc") also caused no increase in avoidance responding (0.24 ± 0.02 responses/min), but continued the unbroken increase in escape proficiency (Fig. 4, "Sig Av + Esc") to levels greater than those observed in the baseline condition [1.53 ± 0.07 responses/min; $t(114) = -5.30$, $p < .0001$]. The addition of a brief cue-light (Figs. 4 and 5, "pre-pulse") to the warning tone significantly increased avoidance responding [0.66 ± 0.08 responses/min; $t(114) = -3.51$ $p < .05$], and significantly decreased escape responding [1.16 ± 0.07 responses/min; $t(114) = 4.57$, $p < .001$] from the previous condition, suggesting

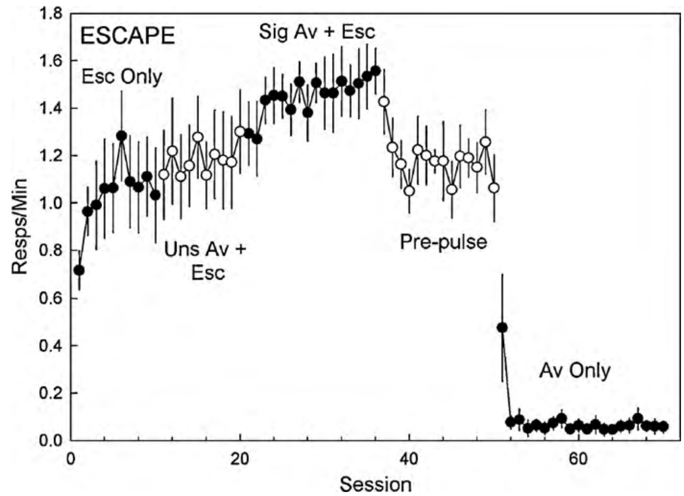

Fig. 4. Mean (±SEM) escape rate (head entries during the light) across five experimental conditions. Filled and empty symbols help identify experimental conditions. In the *Escape only* condition, responses during the light terminated the stimulus and produced a 15 s dark period. The addition of an avoidance contingency during the *Unsignaled avoidance + Escape* condition allowed subjects to delay the light onset for 20 s by producing a head entry prior to light onset. A tone was added 5 s prior to the light onset during the *Signaled avoidance + Escape* condition. A regular increase in response probability was observed across the *Escape only*, and *Unsignaled* and *Signaled avoidance + Escape* conditions. Using a pulse of bright light to signal the avoidance period during the *pre-pulse* condition reduced escape probability. Removal of the escape contingency during the *Avoidance only* condition quickly reduced head entries during the light to near zero levels. Results from the Mixed ANOVA are presented in Section 4.2.

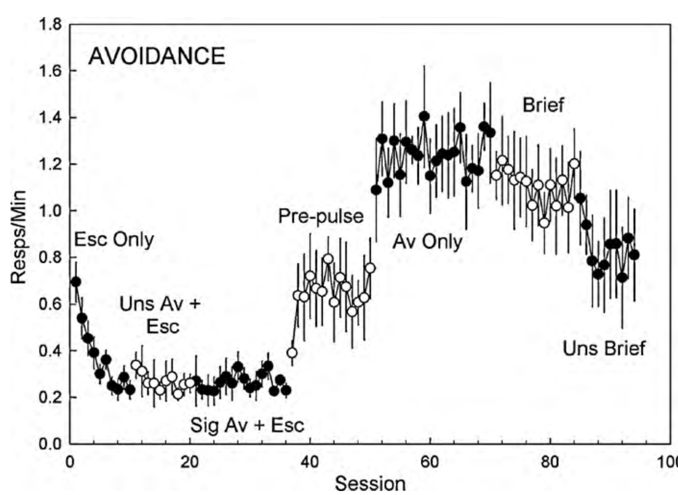

Fig. 5. Mean (±SEM) avoidance response rate (head entries in the dark) across seven experimental conditions. Filled and empty symbols are used to facilitate identification of experimental conditions. During the *Escape only* condition responses in the dark were measured, but had no programmed effect. The addition of either an *Unsignaled* or *Signaled avoidance + Escape* contingency produced no effect on avoidance responses. Using a pulse of bright light (*Pre-pulse*) to signal a 5 s avoidance period before light onset increased rates of avoidance responding. The removal of the escape contingency (*Avoidance only*) further increased rates of avoidance. Reducing the duration of the aversive stimulus to match that of the pre-pulse cue (*Brief*) caused a slight decrease in avoidance responses. Removal of the pre-pulse cue while maintaining the shortened duration of the aversive stimulus further reduced responding. Results from the Mixed ANOVA are presented in Section 4.2.

that the form of the warning stimulus is important for initiating the avoidance response. Maintaining the cue-light while removing the escape contingency during the avoidance-only condition (Figs. 4 and 5, "Av Only") yielded a dramatic increase in avoidance responding compared to the previous condition [1.29 ± 0.09 responses/min; $t(114) = -6.60$, $p < .001$]. Responses in the light (escape) were observed during the first avoidance-only session, but quickly reduced to near zero levels where they stabilized for the remainder of the experiment. Reducing the duration of the light to 500 ms (Fig. 5, "Brief") caused a significant decrease in avoidance responding [1.12 ± 0.09 responses/min; $t(114) = 4.78$, $p < .001$]. Finally, removing the cue-light (Fig. 5, "Uns Brief"), leaving only the 500 ms light, further reduced avoidance responding [0.80 ± 0.11 responses/min; $t(114) = 3.86$, $p < .01$].

Our data analysis shows that Wistar rats both escaped and avoided bright light, and continued to avoid it even when the light was very brief (500 ms). Rats displayed an initial predisposition to produce avoidance responses (enter the burrow during the dark), even when this behavior had no consequences on light presentation. This suggests that avoidance might have been facilitated early in training, had it been reinforced. Still, this predisposition declined as escape contingencies were learned. A warning tone increased rates of escape, but was unable to facilitate avoidance. Avoidance was only acquired when a 200-ms light cued the aversive stimulus. Avoidance rates were further increased when escape contingencies were eliminated. Nearly all escape responses were eliminated within one session. It is of note that the rates of escape (number of responses in the light/total time spent in the light) and avoidance (number of responses in the dark/total time spent in the dark) were mutually exclusive measures. Reducing the duration of the avoidable light and eliminating the cue-light further decreased avoidance behavior, but not to pre-acquisition levels. These results suggest that light avoidance is strengthened if escaping is precluded, that signaled avoidance is much more effective than unsignaled, and that the avoidable light is best cued by visual, not auditory, stimuli.

5. General discussion

Our results demonstrate that light may bring behavior under aversive control within three paradigms: punishment, escape, and signaled avoidance. When rats had a choice between food and food plus light (Experiment 1), they displayed an unambiguous preference for food alone. When light was presented non-contingently (Experiments 2 and 3), rats escaped to an artificial burrow; this response was rarely emitted in the dark. Changes in the frequency (Experiment 1) and duration (Experiments 2 and 3) of the light stimulus and of the efficacy of operant responses to escape and avoid it (Experiments 2 and 3) caused changes in behavior that are consistent with the hypothesis that bright light is aversive. Moreover, exposure to the light stimulus over dozens of sessions did not result in detectable levels of habituation of escape or avoidance behavior. Finally, it has been shown here and by others [1,19] that bright light has a depressive effect upon responding, similar to that observed with shock, tail pinch, and other validated forms of punishment.

It is important to note that when the aversive light was signaled (Experiment 3), rats avoided it if the signal was visual, but not if it was auditory. These results suggest greater efficacy for warning cues that are similar to the sensory properties of the aversive stimulus [11]. While it was of interest in the present study to examine within-subject changes in behavior in order to examine possible habituation effects, it remains evident that the order-effects produced by such a design might have impeded subjects from initially learning the avoidance response in Experiment 3. Still, once produced, the avoidance response in the latter conditions was quite reliable.

It should also be noted that the pairing of the light and burrow apparatus in the present experiments provides a method by which a species-specific avoidance response can be elicited and effectively measured. Still, a number of other factors may influence the reinforcing or aversive properties of light. For instance, the angle of light presentation may be important: Overhead stimuli may be more closely associated with environmental or predatory cues [26], whereas local cues (e.g. those near a response manipulandum) may not. The reinforcing or punishing properties of luminous stimuli might also vary with the experimental apparatus (e.g. closed operant chamber versus open elevated maze) and the ambient level of stimulation in such an environment.

The present study is also limited in that only one level of illumination was tested throughout the experiments. Although bright light seems to follow the typical psychophysical curves of other aversive stimuli [6], these results are subject to interspecies differences and have also yet to be tested in concert with burrowing behavior. Future experiments will be necessary to determine the role of these and other factors in the elicitation of light aversion or approach.

Like other aversive stimuli, bright light appears to affect molecular processes involved in responses to stressors. McQuade et al. demonstrated that exposure to unconditioned light [28] or the conditioned cues that predict it [29] are both able to produce an increased noradrenergic response as measured by *in vivo* microdialysis. Activation of the locus coeruleus – the main source of noradrenaline in the brain – has also been shown to coincide with the administration of footshock [7]. The un-cued presentation of light has also been shown to increase dopamine [32], and 5-HT [31] in the occipital cortex, although only the increase in 5-HT seems to affect upstream processing in the medial prefrontal cortex [37]. Interestingly, these increases in 5-HT mirror those observed in the prefrontal cortex following fear conditioning [46].

Knutson et al. [21] showed that bright light reduces the incidence of positive-affective ultrasonic vocalizations produced in the anticipation of play with concomitants. These results are in line with decrements in positive-affective vocalizations observed when a cue predicting food reward was altered to predict footshock [5]. Unlike results seen for shock [9], however, anxiety responses to bright light as measured by open arm entries, time spent in the open arm, and the total number of arm entries in an elevated plus maze did not seem to be responsive to anxiolytic drugs [45].

It has been demonstrated previously that behavioral responses such as freezing observed in the presence of bright light differ greatly from those observed for footshock and other aversive stimuli [12,13]. This indicates that bright light as a stressor/aversive stimulus is activating different neural and behavioral responses than those produced by footshock. Further research may elucidate the cause of these differences. Certainly, clinical disorders related to fear, stress, and anxiety are not indifferent to the nature of the stressor.

The present study provides systematic evidence that bright light can be used effectively as an aversive stimulus, producing reliable behavioral results over the course of more than 100 daily exposures. Furthermore, bright light and the burrow apparatus provide a method that is easily implemented within most behavioral paradigms, and that could be incorporated into a number of unique behavioral arrangements with little effort. These advantages, along with cost efficiency when compared to grid floors, scramblers, and so forth make bright light a practical, reliable alternative to footshock.

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