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Habit Formation in Active Avoidance

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by

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Abstract

Two studies explored feedback value in avoidance learning using rats. We show that limited, but not extended trained rats were sensitive to feedback devaluation via counterconditioning. Identical effects on motivational transfer were obtained. These results suggest that maladaptive avoidance may be established in a similar way to habits of consumption.

Key Words; Negative reinforcement, Avoidance, Outcome Devaluation, Counter Conditioning, Shuttling, Rat, Habit

Introduction

Instrumental conditioning is a learning process in which different kinds of reinforcement (e.g., positive or negative reinforcement) increase or decrease the likelihood of some target behavior occurring again. One of the first people to study operant processes, E.L. Thorndike, observed how the process of reinforcement influences behavior using different preparations. For example, in Thorndike's puzzle box studies, the learning process was referred to as "trial and error" where a hungry cat had to learn how to escape the puzzle box in order to obtain food placed outside of the cage. The experiment showed that the cat eventually stopped performing ineffective escaping behaviors (e.g., scratching and digging) and adapted more successful responses that achieved freedom from the box (e.g., pushing and pulling), and thus, reinforcement. Thorndike referred to this as the Law of Effect where the strength of a behavioral response increased when it is quickly met by a reinforcer. Thus, every time the cat escaped the box, the behavior that led to freeing itself was reinforced by food, which is referred to as positive reinforcement (Thorndike, 1898). Scientists like Skinner have adapted the study of instrumental conditioning to work with rodents. This preparation utilized the popular skinner box paradigm. Many since have used this model to study multiple kinds of reinforcement, including both positive and negative reinforcement.

The model of positive reinforcement is useful for studies of impulsivity and consumption because it evaluates the likelihood of recurring behaviors based on beneficial outcomes such as pleasure and reward. The role of the outcome or consequence of a specific behavior has been empirically shown to influence the chance of that behavior's recurrence. For example, Killcross & Coutureau (2003) used food-reinforced lever-press methods to study how outcome value controls instrumental behavior. These studies compared animals with limited versus extended training and found that rats were sensitive to the value of food outcomes following limited but not extended training. This was interpreted by the authors as suggesting that the subjects who received extended training transitioned from goal directed to habitual behaviors over time. Preliminary responding was goal-directed (e.g., stimulus-outcome) and performed under voluntary control with outcome value as a substrate of motivation. Whereas, extended training of the same behavior led to the development of habitual responding because outcome value was no longer a component of the motivational substrate (e.g., stimulus-response; Killcross, et al., 2003).

Since positive reinforcement involves the consumption of an appealing substance, the psychological mechanisms involved in this form of learning are readily examinable using outcome devaluation procedures. Conversely, much less has been studied about aversive instrumental learning (i.e., avoidance), which depends on negative reinforcement, or the removal of a noxious outcome. For example, in avoidance studies that use a response to prevent a shock, the removal of this aversive stimulus increases the frequency of the preceding behavior. Unlike in positive reinforcement where the food itself is known to be the necessary event, the source of control in negative reinforcement is much less understood (Kamin, 1968; Rescorla, 1969). Thus, when behavioral responses are acquired through negative reinforcement, the psychological mechanisms underlying these behaviors are more ambiguous and this has contributed to less empirical analysis towards this dimension of reinforcement learning (LeDoux et al., 2017; Jean-Richard-Dit-Bressel, Killcross & McNally 2018). A closer analysis of this literature may offer more insight into this mechanism, and a brief background is provided below.

Avoidance Learning

In a standard signaled avoidance study, a researcher pairs an auditory stimulus (i.e., buzzer/tone) with an aversive outcome (i.e., electric shock) on trials where the subject fails to implement some target response during the auditory stimulus. However, if a response is made, the behavior is reinforced by the removal of the auditory stimulus and the omission of the aversive stimulus (i.e., shock). Following some time, the buzzer or tone will sound again, initiating a new trial. Over time, this leads to acquisition of avoidance behavior, in which the subject learns to make appropriate shuttle responses in order to avoid the aversive stimulus.

While in classic signaled studies, the offset of the warning cue is understood as serving a similar function (Kamin, 1968). This classic procedure, however, can be modified by taking away the warning signal before the shock, "leaving the avoidance contingency and the temporal specifications unchanged" (Sidman, 1962). The subject learns to avoid the aversive stimulus only by performing an appropriate behavioral response during a specific period of time, which, in a classic avoidance study, would have been otherwise indicated by a warning signal. In this kind of an unsignaled Sidman active avoidance (USAA) procedure, the noxious stimulus is not marked by a warning signal or exteroceptive event (Sidman, 1962), response feedback is normally provided in the form of a brief cue. Whether this serves the same function as the termination of the warning signal in a classic avoidance preparation is unclear (Rescorla 1969; Kamin, 1968). Studies have shown that the feedback cue comes to acquire conditioned inhibitory properties against shock over avoidance learning (Rescorla & Lolordo, 1965). The studies reported below evaluated whether changes to the status of this 'safety signal' at different points during training influenced avoidance behavior itself as well as the transfer of motivation.

In the first study, the USAA method was used to establish steady avoidance responding and we treated the feedback cue as analogous to the reinforcer in studies of appetitive instrumental behavior. Half of the subjects in Experiment 1 were given limited training (i.e., a 10-day USAA training phase) in which a feedback cue was presented after performing a shuttle response. The second half of the subjects were assigned to an extended training group and received the same treatment during a 15-day USAA training phase. If the subjects made a shuttle response and avoided the foot shock, the feedback cue (i.e., tone) was presented. The subsequent shock was then delayed by 30 seconds. Upon the completion of the training phase, groups limited and extended were split into subgroups for further treatment. During this next phase, the tone that was used for the feedback cue during USAA was counter conditioned, by pairing it with a shock or, just simply presented in an unpaired arrangement for control subjects. Following this outcome devaluation training, all subjects experienced a USAA test in which shuttling responses were recorded. In a follow-up study, the effects of these treatments were evaluated in an aversive Pavlovian-Instrumental Transfer (PIT) task that measures conditioned motivation more effectively. The findings from these studies show that devaluation impaired avoidance behavior with limited, but not extended, training. These findings could be interpreted similarly to work by Killcross & Coutureau (2003), in that they might also reflect a transition from outcome dependence to habitual behavior, but in aversive motivation. However, an alternative explanation of these findings is based in conditioned inhibitory processes and how they can control avoidance (Rescorla & Lolordo, 1965).

Experiment 1: The effect of outcome devaluation on USAA Testing

Introduction

Based on findings from appetitive studies using reinforcer devaluation to show that extended but not limited training results in habitual behavior rather than goal-directed behaviors

(Thraikill & Bouton, 2015) we anticipated similar effects in avoidance. Therefore, in the first study, we predicted that extended training would result in insensitivity to outcome devaluation but that limited training should not. Specifically, it was hypothesized that subjects of the limited, unpaired treatment during devaluation would emit higher response rates during USAA testing in comparison to subjects who experienced paired treatment. Furthermore, based on previous research, we predicted that subjects in the extended group would be insensitive to devaluation procedures and fail to produce the same response rates as the limited unpaired group.

Methods

Subjects

Subjects consisted of 48 male Sprague Dawley rats, all of which endured no prior training experience to experiments and weighed nearly 250g upon arrival from Hill Top Lab Animals (Scottsdale, PA, USA). Subjects were individually housed in ventilated Plexiglas cages, in a room maintained on a 12-12 light-dark cycle, with free access to food and water. This study was conducted in accordance with guidelines of the Guide to the Care of the Use of Laboratory Animals, of the National Institutes of Mental Health. Additionally, the protocol was approved by the New York University Animal Welfare Committee.

Apparatus

Eight standard two-way avoidance chambers (Coulbourn model: H10-11R-SC; Allentown, PA) were used to conduct USAA training. Each side of the chamber contained a house light stationed at the center ceiling, blinking on and off when the subject would shuttle from either side. The chamber included Plexiglas walls and stainless steel grid floors. A

Coulbourn Precision Animal Shocker (model H13-15-220; Allentown, PA) delivered a .6-mA shock to the grid floors lasting 1 second in duration. All chambers were kept in sound-attenuated cubicles equipped with a small fan for ventilation.

Outcome devaluation sessions were conducted in four standard conditioning chambers (Coulbourn, model H10-11R0TC). This set of chambers were kept in light and sound attenuated cubicles with 5 ohm speakers connected to an audio generator (Coulbourn, model A12-33) to deliver the 5kHz tone. The conditioning chambers were equipped with stainless steel grid floors connected to a precision animal shocker (Coulbourn, model H13-15-220).

Procedure

The experiment consisted of four general phases that are described in more detail below: 1) USAA training 2) Outcome devaluation 3) Test for USAA performance 4) Test for freezing to the presumed safety signal. See Figure 1F for an example of USAA parameters.

Unsignaled Sidman Active Avoidance (USAA)

On days 1-10, all subjects received USAA training. During this phase, across a 25-minute protocol, a .6-mA electric shock was delivered for 0.5 seconds. If a subject responded by shuttling to the other side of the chamber before the shock, the subject would hear a .3 second tone, serving as the feedback cue (514 hz, 80 dB). The subsequent shock would be delayed by 30 seconds. If the subject failed to shuttle, shock would continue to be presented every 5 seconds. This procedure was designed to promote shuttling behavior in subjects as they learned to avoid the shock (Lazaro-Munoz, LeDoux, & Cain, 2010). Avoidance responding was defined as occurring between shocks whereas escapes occurred during shocks. An avoidance response was reinforced with the tone when the subject performed a shuttle response before the shock. If an escape response was made, the subject was able to terminate the shock by shutting to the other side of the chamber, thus signaling the tone. On each USAA training day subjects also received exposure to the non-avoidance chambers used for outcome devaluation in phase 2. These sessions were at least 1 hour after avoidance training and lasted for 15 minutes. On day 11, the cohort was split into two groups of 48 subjects (extended and limited group). The extended group continued USAA training for an additional 5 days. Thus, while the limited group began the devaluation phase following 10 USAA training sessions, the extended group did so after 15 days of USAA training.

Outcome Devaluation

During devaluation, half of the subjects from each group experienced a 30 second tone coterminating with a 1 second foot shock in the non-avoidance context where no escape was possible. The other half were presented with shock and tone using an unpaired arrangement. There were 25 trials over the course of a 67-minute session. The outcome devaluation sessions were repeated for three consecutive days.

USAA Test

The day following the end of outcome devaluation a USAA test was conducted for each group to evaluate whether devaluation influenced avoidance performance. During the USAA test, the subjects did not receive any tone feedback or shock stimuli. Subjects were free to shuttle through the chamber and responses were recorded over 25 minutes. Poor performing subjects were identified based on USAA training using established criteria (Lazaro-Munoz et al., 2010).

Subjects with two or more consecutive avoidance sessions prior to day 10 with more than 20 avoidance responses were classified as good performers. Test data from these subjects were compared to poor performing subjects that did not meet this criterion.

Freezing Test

All subjects were tested for freezing five days after the USAA test in another non-avoidance context. Over a 25-minute session, a tone was presented three times for a duration of thirty seconds with an inter-trial interval of approximately 180 seconds. Freezing was counted in seconds for any amount of time the subject showed a complete absence of movement.

Results

USAA

Data from the training phase were analyzed and are presented in Figures 1A. The figure depicts the average avoidance responses for each group across all training days. A univariate analysis of variance (ANOVA) was conducted for each group (limited vs extended) to observe if subjects from the different US devaluation conditions (paired vs unpaired) performed equally across training days. For the limited group, a significant effect of Day showed that all subjects in the limited group (paired vs unpaired) acquired avoidance behavior normally over training F_{Day} (9, 414) = 12.82, p= .001 The unpaired and paired subgroups performed similarly (Group) F_{Group} (1, 46)= .020, p= .889, $F_{Day\ x\ Group}$ (9,414) = .699, p= .710. The subjects in the extended group also acquired avoidance behavior across training days F_{Day} (14, 644)= 19.23, p= .001. Unpaired and paired subjects in this group acquired similarly F_{Group} (1, 46)= .128, p= .722, $F_{Day\ x\ Group}$ (14, 644)= .446, p=. 959.

Insert Figure 1 Here

USAA Test

The average number of avoidance responses made during USAA testing are shown for all groups in Figure 1B & D. The following analysis includes data from the USAA testing phase for both limited and extended groups (unpaired vs paired). A 2x2 ANOVA was conducted to detect any significant effects involving the factors of Treatment (unpaired v paired) and Performance (good v poor performers) for each group. *Group Limited:* The analysis revealed a significant interaction in the limited training group, $F_{Treatment\ x\ Performance}(1,44) = 5.61$, $p = .022$, CI 95%, [-31.6, 35.6]. The effect on Performance (good vs poor) was significant, $F(1,44) = 12.36$, $p = .001$, meaning that subjects classified as good performers had significantly higher response rates compared to poor performers. Additionally, there was no significant effect on Treatment (paired vs unpaired), $F(1,44) = 1.28$, $p = .264$. *Group Extended:* The analysis revealed that there was no significant interaction in the extended training group, $F_{Treatment\ x\ Performance}(1,44) = 1.28$, $p = .264$. Therefore, the unpaired and paired Treatment assignments had no effect on Performance on the USAA test. The effect on Treatment (paired vs unpaired) was also insignificant, $F(1,44) = .089$, $p = .767$. However, there was a significant effect on Performance (good vs poor), $F(1,44) = 15.78$, $p = .001$. The results from this study confirm our impression of the data.

Freezing

Figure 1C & E depict freezing data from experiment 1 for groups limited and extended. Two tailed independent *t*-tests were used to analyze freezing data. Limited (paired vs unpaired) subjects classified as good performers showed a significant difference in freezing between treatment groups, $t(16) = 9.6$ $p < .001$. Good performers in the extended group also showed a significant difference on percent of freezing between groups (unpaired vs paired), $t(20)= 3.5$, p <.001. Additionally, a *t*-test analysis was conducted for poor performing subjects in group limited and extended, $t(28)= 5.5$, $p < .001$; $t(24)= 4.58$, $p < .001$. In summary, the analysis revealed that subjects who were placed in the paired treatment group froze significantly more to the tone compared to unpaired subjects.

Discussion

The results suggest that avoidance behavior is dependent on the value of the feedback stimulus but less so with more training. Outcome devaluation for limited, unpaired subjects resulted in higher rates of responding during USAA testing. During USAA training subjects learned that the tone was a safety signal, indicating that they avoided a foot shock. When subjects were placed in outcome devaluation sessions, those that experienced tone and shock together consequently started to fear the tone. Subjects in the extended-good/paired group outperformed all other subgroups. This may be due to the fact that extended training can lead to habitual responses rather than goal-directed ones.

Experiment 2: The effect of outcome devaluation on aversive Pavlovian-Instrumental Transfer

Introduction

Pavlovian-to-instrumental transfer (PIT) is described as an effect where a conditioned stimulus (CS) facilitates instrumental responding (Campese, McCue, Lázaro-Muños, LeDoux, & Cain, 2013). In PIT studies, an aversive CS enhances the rate that the subject elicits avoidance behaviors in order to avoid and prevent harm. While an aversive CS typically results in freezing, if it is presented when performing a previously trained avoidance response, the CS will instead promote avoidance behavior (Campese, Kim, Rojas, & LeDoux, 2017). There has been extensive research conducted with appetitive conditioning and PIT. However, little research has investigated PIT with aversive conditioning. Aversive PIT is different from appetitive PIT in that it facilitates responding rather than suppressing it. In Experiment 2, the study was designed to address how devaluing a feedback cue following USAA training would influence the PIT effect. In the second experiment, similar to the first study, we predicted that the extended training group would be insensitive to outcome devaluation during PIT testing compared to the limited group. This hypothesis is derived from research that found that extended training lead to a decrease in reinforcer devaluation and decreased Pavlovian instrumental responding (Holland, 2004). PIT tests are a measure of motivation and we can determine if this motivation is dependent on goal-directed behaviors.

Methods

Subjects

Subjects consisted of 96 experimentally naive male Sprague Dawley rats, weighing approximately 250g upon arrival from Hilltop Lab Animals (Scottsdale, PA, USA). Subjects were housed individually in ventilated cages in a room operated on a 12-12 light-dark cycle. All animals had free access to food and water.

Apparatus

Training and testing took place in the same two-way avoidance chambers from experiment 1, manufactured by Coulbourn (H10-11R-SC. Allentown, PA). A Coulbourn

Precision Animal Shocker 220V (model H13-15-220) produced a .6-mA shock for a duration of 1 second. Chambers were housed in sound-attenuating cubicles.

Aversive Pavlovian conditioning and outcome devaluation sessions took place in four standard conditioning chambers (Coulbourn, model H10-11R0TC). The chambers were housed in sound and light attenuated cubicles with 5 ohm speakers connected to an audio generator (Coulbourn, model A12-33) to deliver the 5kHz tone and white noise. The chambers were equipped with stainless steel grid floors, which were connected to a precision animal shocker (Coulbourn, model H13-15-220).

Procedure

Experiment 2 consisted of 5 general phases 1) Pavlovian Threat Conditioning 2) USAA training 3) Outcome devaluation 4) Pavlovian Instrumental Transfer (PIT) tests 5) Test for freezing outside of avoidance arena. See Figure 2E for how outcome devaluation was incorporated in a Pavlovian-instrumental design.

Pavlovian Threat Conditioning

Pavlovian Threat Conditioning (PTC) began the first phase of this experiment and was run over a single session. During this protocol, a tone conditioned stimulus (30s, 5 kHz, 80 dB) co-terminated with an US (1 second .7-mA foot shock). Following a 5-minute baseline period, three CS-US trials occurred over a 15 minute sessions, separated by 180-second intervals.

USAA

On days 1-10, all subjects received USAA training in two-way avoidance chambers manufactured by Coulbourn (H10-11R-SC. Allentown, PA). Across a 25-minute protocol, a .6-mA electric shock was delivered. If a response was made by the subject by shuttling to the other side of the chamber before the shock, the subject would hear a .3-second noise (514 Hz, 80 dB) (i.e., feedback cue), and the next shock would be delayed by 30-seconds. If the subject did not make a shuttle response, the subsequent shock would be presented every 5 seconds. This protocol was intended to promote shuttling behavior as subjects learned to avoid the shock. Avoidance responses were counted when subjects shuttled between shocks whereas escape responses were defined by responses made during shocks. On each day of USAA training, subjects also received exposure to the chambers used for outcome devaluation occurring in phase 3. Habituation sessions took place at least 1 hour following training and lasted 15 minutes. On day 11, the cohort was split into two equal groups (extended and limited group). The extended group had an additional 5 days of USAA training. Therefore, while the limited group began the devaluation sessions following 10 USAA training sessions, the extended group entered phase 3 after 15 days of USAA training. Following experiment 1, data revealed that poor performing subjects did not offer insight into our results. Therefore, poor performers were excluded from experiment 2 using established criteria (Lazaro-Munoz et al., 2010). Good performers were classified as subjects who performed two or more consecutive avoidance sessions prior to day 10 with 20 or more avoidance responses. These subjects proceeded to complete the rest of the study.

Outcome Devaluation

During outcome devaluation sessions, half of the subjects from each group endured a 30-second noise, simultaneously terminating with a 1 second foot shock (paired group). The other half of the limited group was presented with shock and tone using an unpaired assignment (unpaired group). The protocol included 25 trials over the course of a 67-minute session. The outcome devaluation sessions took place over the course of three consecutive days as was done above in experiment 1.

Pavlovian-Instrumental Transfer (PIT) Testing

Following three days of outcome devaluation sessions, both the extended and limited group were given two consecutive days of PIT testing. During these sessions, there was no unconditioned stimulus (i.e., foot shock) presented to the subject. The conditioned stimulus (i.e., tone) from the Pavlovian Threat Conditioning phase of this study was presented to subjects when shuttle responses were below two responses per minute for approximately two minutes. Because some rats initially freeze when placed into the avoidance chambers, rats were given 15 minutes to shuttle under USAA extinction without a CS present. Once the CS was presented, the tone remained on until 10 shuttle responses were performed by the subject. Following the 10th shuttle response, the CS terminated, thus ending the session. To measure the PIT effect, shuttling rates were compared over the Pre CS and CS periods.

Freezing Test

All good performers were tested for freezing five days following the second PIT test. During the course of a 25-minute session, a tone (510 hz, 80 dB) was presented three times for a duration of thirty seconds with an inter-trial interval of 180 seconds. Freezing behaviors were counted in seconds when there was an absence of movement during the stimulus.

Results

USAA

Data collected from the training phase were analyzed as in experiment 1 and are shown in Figure 2A. The figure reflects the average avoidance responses made by subjects in all groups across all training days. A univariate analysis of variance (ANOVA) was conducted for each group (limited vs extended) to indicate whether subjects from the different US devaluation conditions (paired vs unpaired) acquired training equally throughout training days. Subjects given extended training showed significant effect of Day revealed that all subjects in the extended group (paired vs unpaired) obtained avoidance behavior normally over the course of training F_{Day} (14, 12) = 20.663, *p*= .001. The unpaired and paired subgroups performed similarly, $F_{Day\ x\ Group}$(14, 12) = 1.963, *p*= .124. Subjects in the limited group acquired avoidance behaviors across training days F_{Day} (9, 15)= 10.88, *p*= .001. Subjects in unpaired and paired assignments acquired avoidance behavior similarly, $F_{\mathrm{Day\ x\ Group}}$(9, 15)= .852, *p*=.584.

Insert Figure 2 Here

Pavlovian to Instrumental Transfer

PIT data is shown in Figure 2C and shows the average number of avoidance responses per minute for all subgroups during the Pre CS and CS period. PIT test results were recorded over two days and shuttling responses were measured during the Pre CS and CS period. Analysis of these data were conducted using a mixed repeated measures ANOVA with *Interval* (Pre vs. CS) as the within subjects factor and Treatment (Paired vs. Unpaired) as the between subjects factor. Because initial analyses revealed no differences between test 1 and 2 (F_{Test}(1, 48) =3.052, *p*= .087) or interactions between test and most other factors, (Test x Treatment: *F*(1, 48)= .142, *p*=.708; Test x Interval x Group: *F*(1, 48)= .249, *p*= .620, Test x Group x Treatment: *F*(1,48)=

.014, p= .906; Test x Group: F(1,48)= .024, p= .876) data were then collapsed across both tests and presented as an average. The one exception to this was the significant interaction between Test x Interval F(1, 48)= 6.435, p= .014. Because this did not interact with Group, further analyses were collapsed across this factor and are presented separately for each group.

The analysis of group limited revealed a significant effect of Interval, F(1, 25)= 20.609, p= .001. The significant effect of Interval reflects that responding was higher during the CS period compared to the Pre CS. Additionally, there was a significant interaction of Interval x Treatment, F(1, 23) = 5.098, p =.034. This result shows that the Limited Paired subjects responded less during the CS compared to the Unpaired subjects. Analysis of the extended group (paired vs unpaired) revealed a significant effect of Interval, F(1, 25)= 20.609, p= .001. Similar to the limited group, significance of Interval indicates higher responding during the CS period. There was no significant interaction of Interval x Treatment, F (1, 25) = 1.073. p =.310. Because there was no interaction effect of Interval x Treatment, this shows that the unpaired v paired treatment on the extended group had no impact on rates of responding during PIT tests.

Freezing data

Data for the freezing data are presented in Figure 2B & D. These figures represent the average percent of time spent freezing to the CS presented. A two-tailed independent t-test was conducted to compared time spent freezing between treatment groups (paired vs unpaired). The t-test for group limited revealed a significant difference on freezing time between treatment groups, t(23)= 3.1, p < .001. The analysis for group extended did not reveal a significant difference in freezing between paired and unpaired subjects, t(10)= .39, p= .70

Discussion

The results of Experiment 2 extended the findings of Experiment 1. The expression of the PIT effect and devaluation insensitivity were differentially affected due to the amount of USAA training. Similar to Experiment 1, it is clear that avoidance behavior is dependent on the value of the feedback cue, for limited, but not extended training groups. Subjects in the Extended group were insensitive to outcome devaluation trials due to extended training. As previously mentioned, this effect is likely due to the gradual change of goal-directed responses to habitual responses. In other words, our results indicate that the extended group (paired vs unpaired) did not exhibit the same effect of outcome devaluation on PIT testing compared to the limited group. This could be due to devaluation insensitivity as a result of extended training.

General Discussion and Future Directions

In Experiment 1 it was shown that avoidance behavior is dependent on the value of the feedback cue as a safety signal. Following outcome devaluation sessions changing the status of this cue impaired avoidance for subjects with limited USAA training. However, the extended group was insensitive to this devaluation procedure. These results are similar to findings we have seen in habit formation from studies of appetitive learning that use outcome devaluation (Killcross & Coutureau, 2003; Corbit, Janak, & Baeilline, 2007). It is possible that we are seeing the emergence of habitual behaviors and that outcome devaluation is an effective tool to study this transition.

Alternatively, these findings might be interpreted more simply. It is possible that animals acquired stronger conditioned inhibition over the course of avoidance training. The additional five days of training gave the subjects more exposure to trials with response-feedback pairings.

Work by Rescorla & Lolordo (1965), suggests that the feedback cue becomes a conditioned inhibitor during avoidance training. Their study showed that the feedback cue was able to suppress avoidance responding. This suggests that the cue acquired inhibitory control over avoidance training.

Both retardation and summation procedures are necessary to evaluate whether a cue has become a conditioned inhibitor (Rescorla & Holland, 1977). For example, in a purely Pavlovian procedure, Rescorla (1969) utilized a summation test that evaluated whether a conditioned inhibitor would reduce the response which would typically be elicited by a separate excitatory conditioned stimulus. Additionally, this study conducted a retardation of acquisition test that showed the inhibitor acquired excitatory responding more slowly than a novel stimulus (Rescorla, 1969). Because Rescorla & Lolordo (1965) did not include these procedures, the question of whether their auditory feedback stimulus became a conditioned inhibitor remains opened.

To address this alternative interpretation, a future experiment will assess 1) whether the avoidance feedback cue does indeed become a conditioned inhibitor by running summation and retardation tests following 15 days of avoidance training; and 2) by training an extended avoidance group with more outcome devaluation trials to overcome deepened conditioned inhibition. If the feedback cue became a stronger conditioned inhibitor in the extended group during avoidance and prevented a devaluation effect on this basis, more trials may establish the cue as an exciter and generate a devaluation effect. Furthermore, in a subgroup, the feedback cue should show inhibition effects in retardation and summation tests. This would suggest that the conditioned inhibition interpretations are correct. If this this does not influence the results, then perhaps the transitional interpretation between goal directed behavior and habit may be a more accurate account of our findings.

On a final note, this study only utilized male subjects. A growing trend in neuroscience research is to study male and female animals side by side. Therefore, this limitation should be addressed by future studies that consider this factor and evaluate any potential gender differences.

Captions

FIGURE 1. Figure 1A reflects the mean avoidance responses made across all USAA training days for each subgroup. Figure 1B shows the mean shuttle responses made for group Limited during the USAA test. Figure 1C represents the percent of time spent freezing for group Limited. Figure 1D shows the mean shuttle responses made during the USAA test for group Extended Figure 1E reflects the percent of time spent freezing for group Extended. Figure 1F presents the unsignaled avoidance procedure (USAA). Distinctions between avoidance and escapes are made clear as well as how the feedback cue occurs in relation to responding.

FIGURE 2. Figure 2A shows the average avoidance responses for all USAA training days from Experiment 2. Figure 2B represents the percent of time spent freezing for unpaired and paired subjects in group Limited. Figure 2C depicts the average rate of responding per minute during the Pre CS and CS period for all subgroups. Figure 2D portrays the percent of time spent freezing for group Extended. Figure 2F is a representation of the procedures in Experiment 2. The pictures show Pavlovian threat conditioning (PTC), USAA training, feedback devaluation (FB DEV), followed by the Pavlovian-instrumental transfer test.

Figure 1.

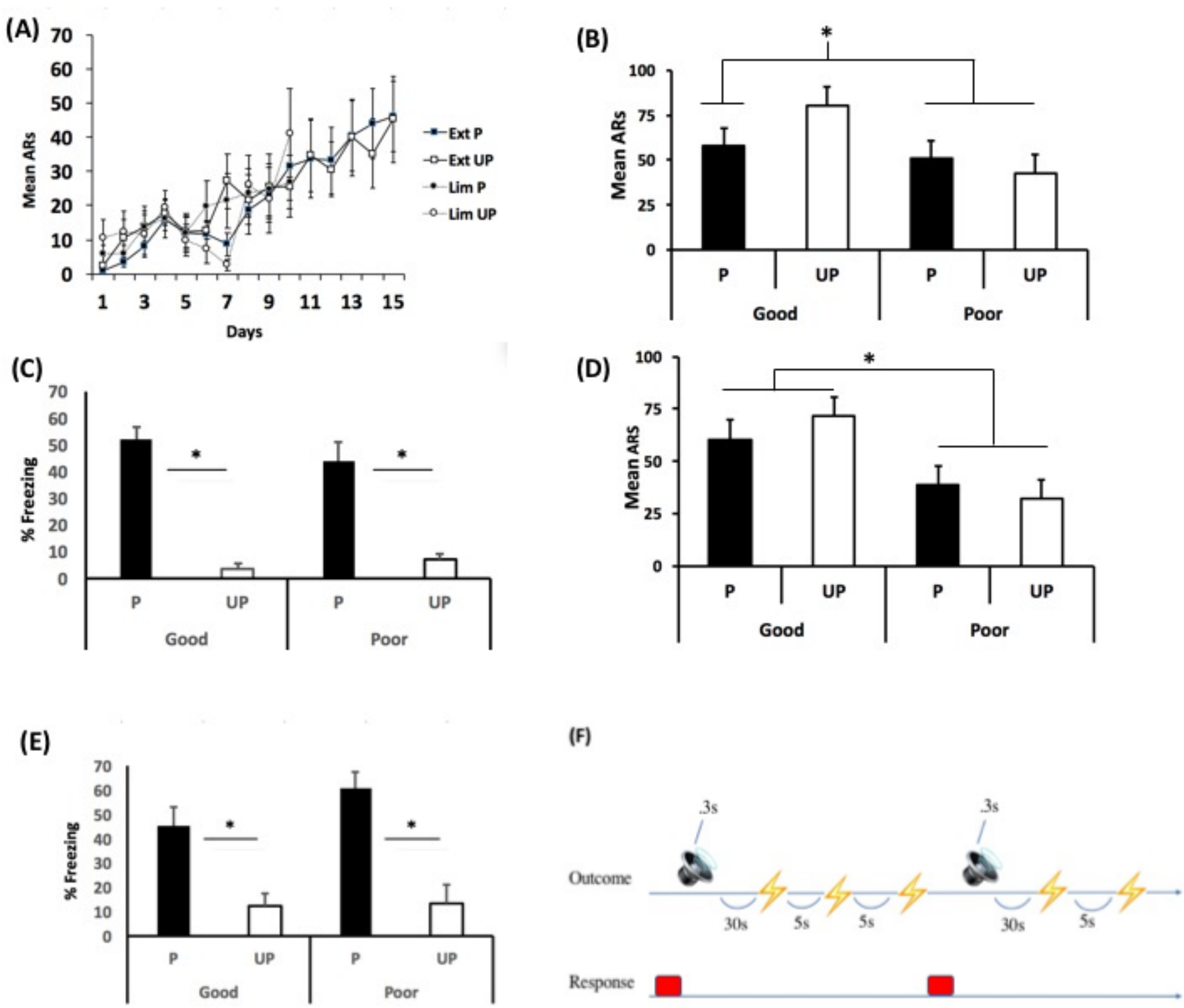
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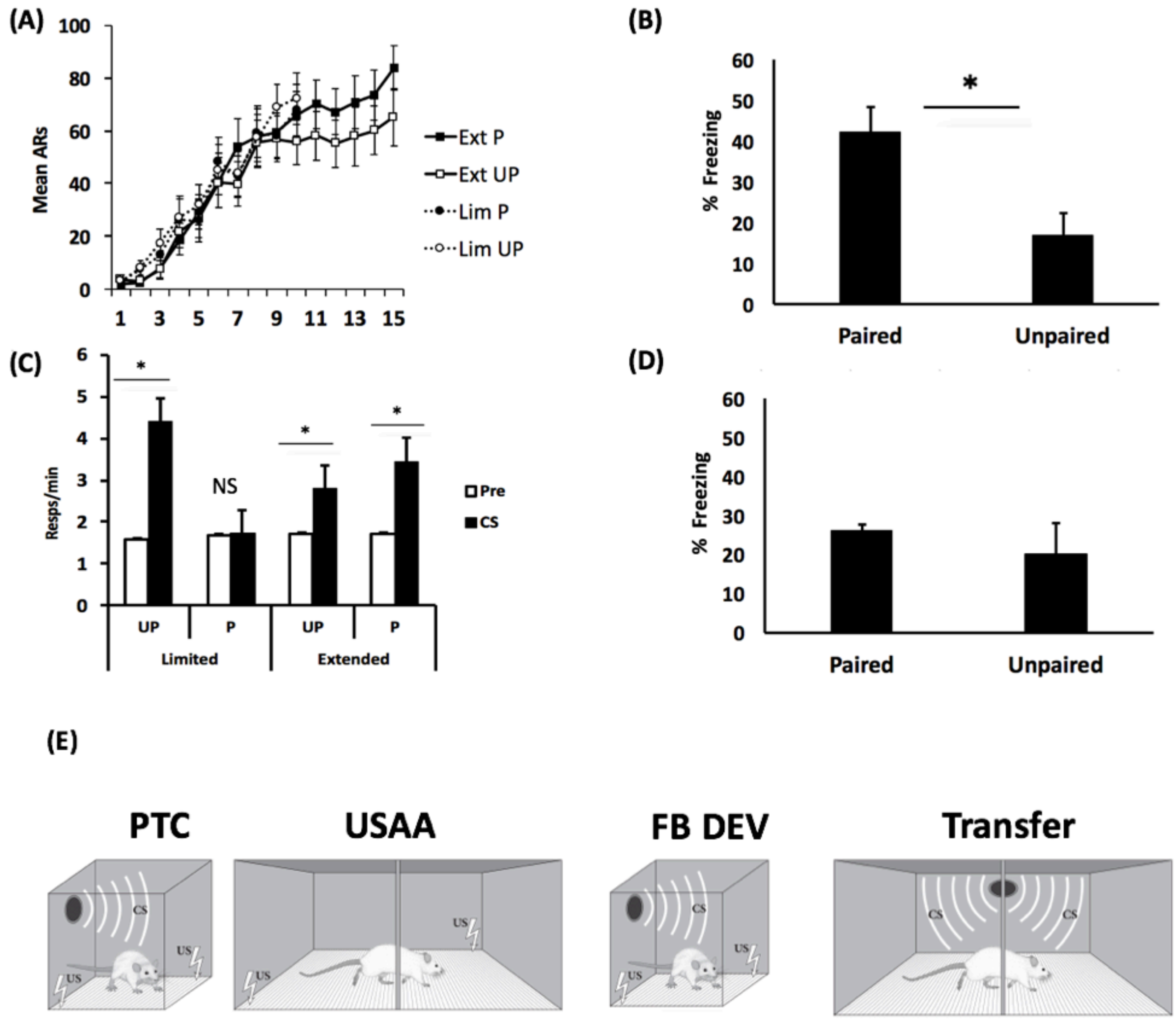
Figure 2.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