

RUNNING HEAD: Posttraining Devaluation and Outcome-Selective PIT

**Cue-elicited food seeking is eliminated with aversive outcomes following outcome
devaluation**

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Abstract

In outcome-selective Pavlovian-to-instrumental transfer (PIT), stimuli that are predictive of specific outcomes prime instrumental responses that are associated with these outcomes. Previous human studies yielded mixed evidence in respect to whether the PIT effect is affected by a posttraining devaluation of an outcome, with the PIT effect being preserved after a devaluation of primary reinforcer (food, drugs) but not following the devaluation of a secondary reinforcer (money). The present research examined whether outcome-selective transfer is eliminated when the devaluation of a primary (liquid) reinforcer is strong and aversive. Experiment 1 confirmed these expectations following a devaluation with bad tasting Tween20. However, outcome-selective transfer was still observed when the earned (devalued) outcome was not consumed immediately after each test (Experiment 2). These results suggest that the capacity of a Pavlovian cue to motivate a specific response is affected by the incentive value of the shared outcome only when the devaluation yields an aversive outcome that is consumed immediately.

Keywords: outcome-selective Pavlovian-to-instrumental transfer; posttraining outcome devaluation; habit; goal-directed action; aversive motivation;

Numerous studies showed that stimuli that are predictive of a specific outcome can augment responses that are related to the same outcome—a phenomenon that was termed *outcome-selective Pavlovian-to-instrumental transfer of control* (specific PIT; for reviews see Holmes, Marchand, & Coutureau, 2010; Urcuioli, 2005). In a typical demonstration of specific PIT, relations between stimuli and differential outcomes (Pavlovian learning: S1-O1,S2-O2) and relations between responses and outcomes (instrumental learning: R1-O1,R2-O2) are established in separate training sessions. In a transfer test, both responses are then made available in extinction and the preference for a specific response is measured in the presence of each conditioned stimulus (i.e., S1: R1 vs. R2; S2: R1 vs. R2). The typical result is a preference for the response whose outcome is signaled by the Pavlovian cue, suggesting that this stimulus has gained control over instrumental responding. It has been argued that specific PIT is involved in a broad range of common behaviors in animals and humans, provoking and invigorating instrumental actions that procure rewards such as food, drinks, and drugs (e.g., Bray, Rangel, Shimojo, Balleine, & O'Doherty, 2008; de Wit, Niry, Wariyar, Aitken, & Dickinson, 2007; Hogarth, Dickinson, Wright, Kouvaraki, & Duka, 2007; Lovibond & Colagiuri, 2013; Ostlund & Balleine, 2008). For instance, a recent rodent study showed that environmental cues paired with intravenous cocaine administration augment responding in an independently trained task in which rats administered cocaine to themselves with lever presses (LeBlanc, Ostlund, & Maidment, 2012). This research shows that drug-paired cues can have a powerful influence on drug-seeking behavior, promoting recurrent and often compulsive consumption of drugs (Everitt & Robinson, 2005; Hogarth, Dickinson, & Duka, 2010).

Researchers have studied the underlying knowledge structures of specific PIT effects with a reinforcer devaluation immediately before a PIT test. Following Pavlovian and instrumental training, one reinforcer is devalued, while the other reinforcer is still intact. Several rat experiments (e.g., Colwill & Rescorla, 1990; Holland, 2004; Rescorla, 1994; Weingarten, 1983) and human studies (e.g., Hogarth & Chase, 2011; Watson, Wiers, Hommel, & de Wit,

2014) observed that outcome-selective PIT is unaffected by a devaluation of a shared outcome. That means, responding for a devalued reinforcer was significantly augmented by the presentation of an associated Pavlovian cue (relative to an unrelated cue), although the devaluation treatment decreased both instrumental baseline responding and consumption of the devalued reinforcer. Furthermore, there is evidence from animal lesion studies (e.g., Corbit & Balleine, 2005) and human brain imaging studies (e.g., Bray, Rangel, Shimojo, Balleine, & O'Doherty, 2008; Talmi, Seymour, Dayan, & Dolan, 2008) that the neural circuits associated with the effects of Pavlovian cues and outcome devaluation on instrumental performance are independent and mediated by anatomically and neurochemically distinct processes. These findings suggest that cue-elicited responses are insensitive to the current incentive value of the associated outcome and therefore habitual.

At least one published study, however, obtained positive evidence for an influence of posttraining reinforcer devaluation on outcome-selective transfer effects. Allman, DeLeon, Cataldo, Holland, and Johnson (2010) trained human adults in a stock market paradigm to associate particular symbols and responses with particular money currencies. In a first PIT test (without explicit feedback on the amount of earned money), participants preferred responses associated with the same outcome as that predicted by the presented Pavlovian cue (i.e., they exhibited specific PIT). Immediately before a second PIT test (again without explicit feedback on the amount of earned money), instructions made one of the currencies worthless. This devaluation treatment selectively reduced responses to those stimuli associated with the devalued currency, eliminating selective transfer to responses working for this currency. Responding for the nondevalued currency was, however, still elevated by presentations of symbols (Pavlovian cues) associated with that currency. In sum, the ability of stimuli to excite responses associated with the same outcome depended on the current value of the outcome, suggesting that the value of the outcome modulated the strength of the PIT effect.

With the present state of research it is not clear why most studies failed to observe an influence of posttraining reinforcer devaluation on outcome-selective transfer while the study of Allman et al. (2010) did not. Hogarth and Chase (2011) discuss as possible reasons two differences: (1) It is possible that currencies in the study of Allman et al. (2010) were represented predominantly in terms of their value rather than their perceptual identity, compared with biological rewards, which may be represented by both sensory features and incentive values. As a consequence, seeking a monetary outcome is mediated more by access to incentive values, while biological reward-seeking is mediated by both sensory features and incentive values. (2) Allman et al.'s stock market instructions to devalue the outcomes were perhaps more effective than the devaluation treatments used in the other studies such as specific satiety, taste aversion, and health warnings. For example, animals and humans exposed to the latter treatments may have ceased consumption at a time when some reinforcer properties remained valuable (for evidence see e.g., Collwill & Rescorla, 1990). Hogarth and Chase (2011), for instance, used specific satiety to devalue a tobacco outcome. Although smoking a cigarette before a transfer test reduced the participants' craving and working for cigarettes during the test, the magnitude of outcome-selective transfer was not affected by the devaluation treatment. The response rate for the tobacco outcome was however still considerable high (> 40%), indicating that devaluation of smoking was not very strong. Furthermore, regular smokers typically know that a state of satiety is only temporary. Accordingly, it is plausible that the tobacco reinforcer retained some value following the devaluation, maintaining outcome-selective transfer during the test.

The Present Research

The present research was conducted to examine more closely whether aversive outcomes following posttraining devaluation reduce the strength of cue-elicited responses in a PIT test. In contrast to Allman et al, however, our participants worked for biological reinforcers (lemonades) in the PIT experiments. A lemonade was devalued by pairing it with very bad-

tasting Tween 20, which reliably produces a strong taste aversion (Baeyens, Crombez, Hendrickx, & Eelen, 1995). We expected to replicate the results of Allman et al. with this strong devaluation treatment provided that the effect of aversive outcome devaluation is not specific for secondary reinforcers. More precisely, in a first PIT test, and before devaluation of an outcome, participants should press a response key more often during the presentation of a stimulus cue that is associated with the same outcome relative to conditions with unrelated cues. In a second PIT test, after the devaluation of a lemonade, Pavlovian cues associated with the devalued outcome should cease to elevate responding for that outcome, while Pavlovian cues associated with the nondevalued outcome should still augment responding for the same outcome. Observing this result would confirm that an influence of devaluation effects on specific PIT is not specific to secondary (monetary) reinforcers and is also obtained with primary (biological) reinforcers when the devaluation is of high magnitude. Alternatively, it is possible that cue-elicited responding is unaffected even after a strong devaluation of the associated outcome; this result would suggest that values of monetary reinforcers and biological reinforcers are accessed differently during a PIT test.

Experiment 2 used the same procedures as Experiment 1 with the single exception that participants did not consume the lemonades immediately after each transfer test. In line with classic research on avoidance gradients (Miller, 1944) and temporal discounting (Ainslie & Haslam, 1992), we expected that this procedural change reduces the effectiveness of the devaluation treatment and hence the averseness of the devalued lemonade, because consumption of that lemonade is more distal or it can be avoided completely (e.g., by not consuming the earned lemonade after the experiment). Accordingly, we expected that PIT effects are more robust in this experiment, observing transfer even to responses that procure a disgusting lemonade.

Experiment 1

Method

Participants

Twenty-seven volunteers (23 women, 8 left-handers) with an age between 21 and 43 years ($M = 26.2$) participated in exchange for payment. The experiment was approved by an ethics committee and all participants provided written consent. Participants were asked to abstain from drinking 1 to 2 hours before taking part in the study. Four participants did not pass the Pavlovian contingency tests (see Procedure below).

Design

The experiment had a 2 (transfer test: before devaluation vs. after devaluation) x 2 (Test Block 1 vs Test Block 2) x 3 (Pavlovian association: yellow drink vs red drink vs neutral outcome) x 2 (instrumental association: yellow drink vs red drink) within-subjects design. Each participant worked through two transfer tests, one before and one after the devaluation treatment. Each transfer test was composed of two blocks with 30 trials each. In each trial, a Pavlovian cue was presented that was paired either with the red lemonade or the yellow lemonade or with a neutral outcome (a wooden cylinder box), and two response keys were made available during this time period that worked for the red or yellow lemonade, respectively. In addition, the following factors were counterbalanced across participants: (1) the assignment of the outcomes (yellow drink vs. red drink vs. neutral outcome) to the Pavlovian cues (ingredients); (2) the assignment of the outcomes to left and right response keys; (3) a yellow or red coloring of a lemonade (Sprite[®], 7 Up[®]); (4) a devaluation of the yellow or red lemonade before the second transfer test.

Apparatus and Material

Participants were seated at a distance of about 60 cm from a 17" VGA color monitor. Stimulus presentation and measurement of response latencies were controlled by a software timer with video synchronization. Participants pressed the keys "j" and "k" of the computer keyboard with the index and middle fingers of their dominant hand.

Lemonades were Sprite[®] and 7 Up[®] that were rated similarly in an informal taste test with three students. The lemonades were colored in red and yellow using food coloring. A drink was devalued by mixing Tween 20 (Polysorbate 20) into a drink (1:100 ml), which is a colorless substance without smell.

Stimuli

Pavlovian cues were six pictures of different spices (brown sugar, cardamom, honey, mint, lime, aniseed). Outcomes in the Pavlovian training were a picture of a drinking glass filled with yellow lemonade, a picture of a glass filled with red lemonade, and a picture of a wooden cylinder box (storage can). Each outcome was paired with a different set of two spices in the Pavlovian phase and the assignment of a stimulus pair to one of the three outcomes was counterbalanced across participants.

For the instrumental training, 20 pictures of drinking glasses filled with yellow lemonade and 20 pictures of a drinking glasses filled with red lemonade were presented. Each picture series showed an empty drinking glass in the first picture and a completely filled drinking glass in the last picture; intermediate pictures showed drinking glasses filled with increasing amounts of a lemonade.

Procedure

Table 1 gives an overview of the experimental procedure that was adapted from Allman et al. (2010). After signing an informed consent, participants ate salt pretzels while reading the welcome instructions for the experiment. Then, they were asked to rate how thirsty they are at the moment on a scale ranging from 0 (not at all) to 9 (very much).

Stage 1: Taste-and-rate task

Participants were asked to taste each lemonade (25 ml) and to rate the taste on a scale ranging from 0 (disgusting) to 9 (delicious).

Stage 2: Pavlovian training

This stage was introduced by the following instructions (translated in English language):

You will now learn the ingredients of both lemonades. In each trial, you will see a picture of an ingredient followed by a picture of the associated lemonade or a picture of a storage can, respectively. Find out the ingredients of both lemonades and what spices belong to the storage can.

Important: Press the spacebar when a lemonade glass is displayed on the screen. No button press is necessary when the storage can appears.

Participants observed ten pairings of each ingredient with an outcome, resulting in 10 blocks with 6 trials each. Each ingredient was presented on the screen for 1 s, and following an interval of 50 ms, the outcome (either a yellow or a red drink or a storage can) was presented on the screen for 2 s. The intertrial interval (ITI) ranged between 0.5 s and 1.5 s. To ensure sufficient attention to the events on the screen, participants were instructed to press the space bar when a drinking glass appears on the screen (see Allman et al., 2010, for a similar procedure). An error message appeared for 5 s if the spacebar was (not) pressed during the presentation of a storage can (lemonade).

After training, participants were asked to indicate the contingencies between the ingredients and the outcomes. In each trial, a picture of an ingredient was presented on the screen; below the ingredient, the three outcomes were presented and participants were to indicate the outcome with which this ingredient was paired during the training phase by pressing designated buttons. Each ingredient was presented once, and the order of their presentation was randomized. A message informed the participant after each button press whether the assignment was correct or incorrect. If one or more assignments were incorrect, the Pavlovian training was repeated but this time with half the number of training trials (30 trials). After the retraining, a second Pavlovian contingency test was performed. If the participant failed again to provide the correct answers, the experiment ended and he or she was asked to work on another, unrelated experiment for the remaining time. This happened with four participants of the sample.

Stage 3: Instrumental training

For this stage, following instructions (translated in English) were presented on the screen:

In this phase, you should fill lemonade in two drinking glasses by pressing repeatedly two buttons. The response buttons have a green label. Each button pours another lemonade into a glass. Find out what lemonade is poured into a drinking glass with button presses.

Note: You must press a button repeatedly in order to produce a visible filling of a glass. The order of the keypresses is however unimportant. When a glass is completely filled, the corresponding button is deactivated. The task is complete when BOTH glasses are completely filled with lemonade.

Attention: When a lemonade glass appears on the screen, press the spacebar to save your progress.

During this stage, a black fixation cross was presented on a white background while participants responded on two concurrent fixed ratio nine schedules (FR9 schedule based on the procedure of Allman et al., 2010). Response keys were the buttons “j” and “k” with a green label attached to them. One response key worked for the red lemonade, while the other response key worked for the yellow lemonade. Participants were able to switch responding between keys, and if they did so before the FR9 criterion for a key had been reached they could complete the requirement for that key when they returned to it. Once a key had been pressed nine times, a picture of a lemonade was presented as a corresponding response outcome on the screen for 2 s. Presses of the response keys during this time did not contribute to the FR tallies; instead, participants were to press the spacebar during this time to acknowledge the filling of a lemonade glass and to save the progress that they have made with filling that glass. If the spacebar was not pressed, an error message appeared and the last filling of the lemonade glass was not counted (for a similar procedure see Allman et al., 2010). With each presentation, the drinking glass was filled with more lemonade of a corresponding color for that particular key. When the glass was full, a corresponding message appeared on the screen that prompted participants to stop responding with that particular key. The task continued until both drinking glasses were filled with lemonades.

Each response key was pressed 180 times at minimum for a presentation of all 20 pictures of a picture series. Keypresses counting towards the presentation of a lemonade picture were

repeated if the spacebar was not pressed during the presentation of the drink picture. After the instrumental training, participants were asked to indicate the instrumental contingency relation by pressing the response keys that poured red and yellow lemonades into the glasses, respectively. In the case of an incorrect assignment, the instrumental training was repeated with half the number of outcome presentations (i.e., 10 pictures per lemonade glass). However, this never happened in this experiment.

Stages 4 and 5: Transfer test and consumption

Following instructions (translated in English) were given for this stage:

You will now earn “real” lemonade with your keypresses. But be watchful: Keypresses are counted only during the presentation of a picture on the screen. Which picture is presented on the screen is however unimportant and it does not influence your gain of lemonade.

Note: The more frequently you press a key, the more lemonade you will earn. The frequency of your keypresses thus determines how much lemonade you will get.

Important: In this phase, lemonade glasses won’t be shown anymore . Therefore, it is not necessary to press the spacebar.

Each of the six ingredients that were presented during the Pavlovian phase were presented in randomized order in a block. Participants worked through 10 blocks (60 trials total). Each ingredient was presented on the screen for 8 s; the next ingredient appeared after a blank period of 2 s. Keypresses were recorded in every phase of a trial but they counted for lemonades only during the presentation of the picture of an ingredient. This task feature was introduced to minimize motor exhaustion and to direct the participant’s attention to the events on the screen. Once a key had been pressed nine times, 2.5 ml were added to the tally of a lemonade. Response outcomes (pictures of lemonades) were however not presented during this stage (corresponding formally with an extinction test). Participants were reminded to perform multiple keypresses if no or only a single key press was registered during the presentation of an ingredient; these trials were repeated at the end of a block in randomized order.

Previous human revaluation studies have demonstrated a devaluation effect with test blocks ranging between 10 and 30 trials (Hogarth & Chase, 2011; Schwabe & Wolf, 2009; Valentin, Dickinson, & O'Doherty, 2007) and for durations between one and three minutes (Klossek, Russell, & Dickinson, 2008; Tricomi, Balleine, & O'Doherty, 2009). Therefore, a transfer test was divided into two test blocks with 30 trials each. Following each test block, a screen informed the participant about how much yellow and red lemonade he or she has earned in this block. Using the FR9 tally, participants could earn a maximum of 50 ml of each lemonade in a test block (which was reached with 180 presses of a response key). The experimenter filled the specified amounts (in ml) of red and yellow lemonades in two small cups and the participant was asked to empty both cups.

Stages 6 to 10: Pavlovian and instrumental retraining; outcome devaluation with taste of drink; Transfer Test 2 and consumption

Before devaluation, the Pavlovian training (Stage 6) and the instrumental training (Stage 7) was repeated with half the number of trials in each stage. This re-training served to reestablish the Pavlovian (Stage 2) and instrumental contingencies (Stage 3) following Transfer Test 1 (in extinction). After the retraining, and prior to the devaluation treatment, participants rated again their thirst. Then, one of the lemonades was devalued with Polysorbate 20. Instructions explicitly stated that the taste of one lemonade has changed; however, the nature of this change was not explained. Participants were then asked to taste both lemonades again (without rating). Following the tasting (Stage 8), participants worked through a second transfer test (Stage 9) that was identical with the first transfer test. For the consumption phase (Stage 10), participants were again asked to empty both cups. An experimenter recorded the residual amount of liquid if a participant refused to empty a cup with lemonade.

Following Stage 10, a manipulation check of the devaluation treatment was performed. Participants could freely choose which of the two lemonades they want to drink. An experimenter recorded the choice and the amount of lemonade that was poured in the drinking

glass for immediate consumption. Finally, participants were thanked, debriefed, and paid for participation.

Results and Discussion

Thirst was rated higher ($M = 6.8$, $SD = 0.9$) at the first measurement point (before Stage 1) relative to the second measurement point (before Stage 8) ($M = 5.1$, $SD = 2.2$), $t(23) = 4.29$, $p < .001$. The taste of Sprite[®] ($M = 5.5$, $SD = 2.0$) and 7 Up[®] ($M = 5.4$, $SD = 2.2$) was rated very similar in Stage 1 ($F < 1$), irrespective of their color ($F < 1$). Participants earned and consumed $M = 41$ ml ($SD = 14.5$) lemonade in the first transfer test (collapsed across both test block). In the second transfer test, participants earned $M = 42$ ml ($SD = 13.5$) of the nondevalued lemonade and $M = 13$ ml ($SD = 18.0$) of the devalued lemonade. In the manipulation check of the devaluation treatment following Stage 10 (free selection of one of the two lemonades), all participants chose the nondevalued lemonade.

Responses during the presentation of the ingredient picture (8 s) and during the ITI (2 s) were summed up for analyses of the response rate. This was done because participants often continued to press keys for a short period of time after the disappearance of an ingredient picture. However, results were basically the same when only responses rates during ingredient presentations were analyzed. Table 2 reports the mean number of keypresses in each transfer test as a function of the presented Pavlovian cue and the test block. Outcome-selective transfer was assessed with a comparison of the instrumental responses rate (RO1 or RO2, respectively) in the presence of Pavlovian cues associated with the same outcome (SO1 or SO2, respectively) relative to the response rate in the baseline condition with presentations of neutral Pavlovian cues that have no instrumental association (SO_n). Comparisons were also made with conditions in which the Pavlovian cues had relations to the other lemonade. Such comparison does however not only involve a Pavlovian priming of the response associated with the same (devalued) outcome but also a Pavlovian priming of the response associated with the alternative (nondevalued) outcome that produces response interference. Thus, a comparison with a baseline

condition involving neutral cues is better suited for this present research purpose. The counterbalanced assignment of the ingredients to the outcomes had no effect on the results in this experiment and in the subsequent experiment; therefore, analyses were collapsed across this factor in the subsequent analyses.

Before Devaluation (Transfer Test 1)

In a repeated-measures analysis of variance (ANOVA) of the keypresses with Pavlovian cue (paired with outcome 1 vs. outcome 2 vs. neutral outcome), instrumental response (paired with outcome 1 vs. outcome 2), and test block (first vs. second) as factors only the interaction between Pavlovian cue and instrumental response reached significance, $F(2, 44) = 17.01, p < .001$. As expected, Pavlovian cues selectively enhanced the frequency of responses that worked for the same outcome relative to neutral cues, $t(22) = 4.31, p < .001$. By contrast, Pavlovian cues associated with a different outcome reduced the response rate relative to the baseline condition, showing a suppression of cue-incongruent responses, $t(22) = -3.61, p < .05$. Latter finding confirms that the response elevation was specific for the response associated with a matching outcome. All other effects were not significant (with $ps > .50$).

After Devaluation (Transfer Test 2)

Analogous analyses were performed on the response rates in the second transfer test following the devaluation treatment (see Table 2). A repeated-measures ANOVA with Pavlovian cue (paired with devalued vs. nondevalued vs. neutral outcome), instrumental response (paired with devalued vs. nondevalued outcome), and test block (first vs. second) showed a main effect of instrumental response, $F(1, 22) = 25.21, p < .001$. Working for the devalued lemonade ($M = 2.9, SE = 1.24$) was dramatically reduced in comparison with keypresses for the nondevalued lemonade ($M = 17.2, SE = 2.66$), confirming that the devaluation treatment was strong and effective. Furthermore, the main effect of test block reached significance, $F(1, 22) = 8.17, p < .01$, indicating more keypresses during the first test block. The main effect of Pavlovian cue, $F(1, 22) = 3.60, p < .05$, and the two-way interaction

between Pavlovian cue and instrumental response were also significant, $F(2, 44) = 7.66, p < .01$, indexing an outcome-selective PIT effect. The three-way interaction with test block was not significant ($F < 1$); the data for the following analyses were therefore collapsed across both test blocks.

Nondevalued response. A repeated-measures ANOVA of the response rate with Pavlovian cue (paired with devalued vs. nondevalued vs. neutral outcome) as factor confirmed that working for the valued lemonade was still augmented by a matching Pavlovian cue, $F(2, 44) = 6.81, p < .01$. As shown in Table 2, response rate was highest when the Pavlovian cue was associated with the same (nondevalued) lemonade relative to conditions in which the Pavlovian cue was associated with a different (devalued) lemonade, $t(22) = 2.76, p < .05$, or with a neutral outcome, $t(22) = 2.63, p < .05$. Response rates in the presence of Pavlovian cues associated with the devalued lemonade and the neutral outcome were however not different, $t(22) = -1.36, p = .19$.

Devalued response. The pattern of results was different with the responses that worked for the devalued lemonade. Again, Pavlovian cues influenced the rate of responding according to an overall ANOVA, $F(2, 44) = 4.84, p < .05$. Response rate was lower in the presence of Pavlovian cues associated with the nondevalued lemonade relative to the baseline condition with neutral cues, $t(22) = -1.41, p < .05$, and the condition with cues associated with the devalued lemonade, $t(22) = -1.65, p < .05$. Most important, working for the devalued lemonade was *not* elevated by cues associated with the devalued lemonade relative to the baseline condition, $t(22) = 0.80, p = .43$. Thus, there was no reinforcer-specific transfer effect after devaluation of the outcome.

An additional analysis was performed that tested directly for a difference in the magnitude of transfer effects with devalued and nondevalued outcomes. Reinforcer-specific transfer effects were first computed separately for devalued and nondevalued responses by subtracting the response rate in the baseline condition from the response rate in the condition with a

matching cue. A repeated-measures ANOVA of the PIT effects with transfer test (first vs. second) and outcome (devalued lemonade vs. nondevalued lemonade) as factors produced a significant main effect of transfer test, $F(1, 22) = 6.43, p < .05$, and a significant interaction between transfer test and outcome, $F(1, 22) = 7.14, p < .05$. PIT effects were nearly identical for both lemonades in Transfer Test 1 (with $M = 4.9, 95\% \text{ CI } [2.2, 7.7]$), for outcome 1 and $M = 4.8, 95\% \text{ CI } [2.5, 7.1]$, for outcome 2). Following the devaluation treatment (i.e., in Transfer Test 2), by contrast, the PIT score was marginal for the devalued lemonade ($M = 0.2, 95\% \text{ CI } [-0.4, 0.9]$), while the size of transfer for the nondevalued lemonade remained relatively stable ($M = 3.7, 95\% \text{ CI } [0.8, 6.6]$). This difference in the magnitudes is also significant, $t(22) = -2.45, p < .05$, confirming that outcome-specific transfer is reduced following the devaluation of that outcome.

Experiment 2

Participants in Experiment 1 consumed the lemonades immediately after each test block. Accordingly, they experienced directly the (aversive) consequences of their actions after each test and they learned that executing the instrumental response during a test guarantees reinforcer consumption without further choice.¹ Motivational dynamics are however different with more distal presentations of reinforcers, because in this situation an animal or human is free to make the instrumental response but they can then reject the delivered reinforcer if it turns out to be aversive. In fact, numerous studies showed that losses and punishing events become less aversive to an individual when their delivery is delayed or when their occurrence can be avoided altogether (Crosbie, 1998). Thus, one would expect that the disruptive effect of our devaluation procedure on Pavlovian-to-instrumental transfer is similarly reduced when the consumption of the devalued lemonade is delayed.

Experiment 2 examined this hypothesis with a simple change of the task procedure. Instead of consuming the earned lemonades directly after each test block, participants were now told that the lemonade will be bottled and that they can take the bottles home with them at the

end of the experiment. Participants still drank a devalued lemonade before the second PIT test. However, we expected that a distal delivery or consumption of the earned (devalued) lemonade reduces the averseness of the reinforcer devaluation, and hence the disruptive effect of outcome devaluation on outcome-selective transfer. In short, we now expected significant transfer to responses that work for the devalued lemonade.

Method

Thirty-four volunteers (24 women, 4 left-handers) with an age between 19 and 57 years ($M = 25.8$) participated in exchange for payment. None of them had participated in Experiment 1. Three participants did not pass the Pavlovian contingency tests and one participant was unable to indicate the correct instrumental contingency after relearning. These participants worked on an unrelated experiment for the remaining time.

The experimental procedure was identical with the first experiment with the single change that there were no consumption phases (Stages 5 and 10). Participants still received a written summary of the amount of red and yellow lemonade that they have earned in each test block. However, they did not consume the lemonades after a test block. Instructions stated that the earned lemonade is filled in separate bottles after each transfer test, which they can take home with them. At the end of the experiment, participants were debriefed and they received a soda bottle (50 cl) of their choice irrespective of how much lemonade he or she has earned during the experiment.

Results and Discussion

Thirst was not rated differently at the first measurement point ($M = 6.2$, $SD = 1.9$) and at the second measurement point ($M = 6.2$, $SD = 2.0$), $|t| < 1$. The taste of Sprite[®] ($M = 5.2$, $SD = 2.1$) and 7 Up[®] ($M = 5.8$, $SD = 1.9$) was rated similarly in Stage 1, irrespective of their color (both $ps > .10$). In the manipulation check of the devaluation treatment (at the end of the experiment), 26 out of 30 participants preferred the nondevalued lemonade. The data sets of the participants who preferred the devalued lemonade were not included in the analyses for a

conservative test of the hypotheses. Responses during the presentation of an ingredient picture and during the ITI were again added up for analyses. Table 3 presents the mean number of keypresses in each transfer test as a function of the Pavlovian cue and the test block.

Before Devaluation (Transfer Test 1)

A repeated-measures ANOVA of the number of keypresses with Pavlovian cue (paired with outcome 1 vs. outcome 2 vs. neutral outcome), instrumental response (paired with outcome 1 vs. outcome 2), and test block (first vs. second) produced a main effect of test block, $F(1, 25) = 24.60, p < .001$, and a significant interaction between Pavlovian cue and test block, $F(2, 50) = 5.11, p < .01$. Keypresses were less frequent in the first test block relative to the second test block, especially when neutral Pavlovian cues appeared on the screen. Most important, the interaction between Pavlovian cue and instrumental response was significant, $F(2, 50) = 15.42, p < .001$, indicating an outcome-selective transfer effect. All other effects were not significant (with $ps > .20$).

Replicating the results of Experiment 1, the response rate was elevated when the instrumental and Pavlovian associations referred to the same outcome (lemonade) relative to baseline responding, $t(25) = 4.14, p < .001$. Furthermore, Pavlovian cues associated with a different outcome reduced the response rate relative to the baseline condition, $t(25) = -3.70, p < .01$. Latter finding again confirms that the response elevation is specific for a matching response and not a general transfer effect.

After Devaluation (Transfer Test 2)

In an ANOVA with Pavlovian cue (paired with devalued vs. nondevalued vs. neutral outcome), instrumental response (paired with devalued vs. nondevalued outcome), and test block (first vs. second), the expected main effect of instrumental response was significant, $F(1, 25) = 65.29, p < .001$. As expected from the devaluation treatment, keypresses for the devalued lemonade ($M = 3.8, SE = 1.06$) were markedly reduced in comparison with working for the nondevalued lemonade ($M = 29.4, SE = 2.68$) in both Test Block 1, $F(1, 25) = 61.03, p < .001$,

and Test Block 2, $F(1, 25) = 61.42, p < .001$. The devaluation effect was slightly stronger in the first compared to the second test block, even though this difference was not statistically reliable, $F(1, 25) = 3.30, p = .08$. Furthermore, there was a tendency to press the response keys less frequently during the second test block, $F(1, 25) = 3.56, p = .07$. The main effect of Pavlovian cue and the two-way interaction between Pavlovian cue and test block were not significant (with $ps > .10$). Most important for the present research, the two-way interaction between Pavlovian cue and instrumental response was significant, $F(2, 50) = 6.36, p < .01$. This interaction was further qualified by a three-way interaction with test block, $F(2, 50) = 3.20, p < .05$. The nature of the three-way interaction was examined in the following analyses.

Nondevalued response. A repeated-measures ANOVA of the response rate with Pavlovian cue (paired with devalued vs. nondevalued vs. neutral outcome) and test block (first vs. second) as factors yielded a significant main effect of test block (with fewer responses in the second block), $F(1, 25) = 5.65, p < .05$, a significant main effect of Pavlovian cue, $F(2, 50) = 6.52, p < .05$, and a significant interaction between both factors, $F(1, 25) = 3.90, p < .05$.

As shown in Table 3, response rate was highest when the Pavlovian cue was associated with the same (nondevalued) lemonade relative to conditions in which the Pavlovian cue was neutral, $t(25) = 2.54, p < .05$, or associated with a different (devalued) lemonade, $t(25) = 2.72, p < .05$. Response rates in the presence of Pavlovian cues associated with the devalued lemonade were also depressed relative to neutral cues, $t(25) = 2.14, p < .05$. This pattern of responding was more pronounced in the second test block relative to the first block.

Devalued response. In an analogous ANOVA, the main effect of test block ($F < 1$) and the interaction between test block and Pavlovian cue were not significant $F(2, 50) = 2.20, p = .12$. The main effect of Pavlovian cue reached however significance, $F(2, 50) = 4.91, p < .05$. Working for the devalued lemonade was depressed in the presence of cues associated with the other (valued) lemonade relative to conditions with neutral cues, $t(25) = -1.90, p < .05$ (one-sided), and with matching cues, $t(25) = -2.38, p < .05$. Most important, response rates were

augmented by cues associated with the devalued outcome relative to the baseline condition, $t(25) = 2.02$, $p < .05$ (one-sided). Thus, Pavlovian cues retained a capacity to motivate a matching response when the consumption of the devalued lemonade was more distal.

For a direct comparison, reinforcer-specific transfer effects were again computed for devalued and nondevalued responses separately by subtracting the response rate in the baseline condition from the response rate in the condition with a matching cue. In an ANOVA of the scores with transfer test (first vs. second) and outcome (devalued lemonade vs. nondevalued lemonade) as factors, the main effect of transfer test became significant, $F(1, 25) = 9.30$, $p < .05$. Transfer effects were stronger in the first transfer test (before devaluation) than in the second transfer test (after devaluation). The main effect of outcome and the interaction between both factors were however not significant (with both F s < 1). This result confirms that the magnitude of PIT was not different for devalued and valued outcomes.

General Discussion

The present research examined conditions in which outcome-selective transfer to a response is and is not sensitive to a devaluation of the outcome. Experiment 1 produced strong evidence that a devaluation of lemonades with taste aversion affects the magnitude of outcome-selective transfer: Stimulus cues associated with a valued outcome (lemonade) augmented responses associated with that outcome; in contrast, no specific PIT effect was observed following the devaluation of a shared outcome. This result replicates findings of an earlier study (Allman et al., 2010) but now with the use of biological reinforcers (lemonades), showing that effects of outcome devaluation on outcome-selective transfer are not specific to monetary reinforcers but are also obtained with more complex representations of primary reinforcers. Like in the study of Allman and colleagues, the devaluation of a reinforcer was very strong and presumably aversive to the participants. This is in our view a key difference to previous human PIT studies that observed no effect of outcome devaluation on outcome-selective with the

administration of relatively weak (but still effective) devaluation procedures (e.g., specific satiety or health warnings).

Experiment 2 used the same procedures as Experiment 1 but this time participants did not consume the earned lemonade after each test block. With this setup, a specific PIT effect was still observed following outcome devaluation. Pavlovian signals of a devalued outcome retained a capacity to motivate the response that procures that devalued outcome, which is in line with previous reports of robust outcome-selective PIT effects following reinforcer devaluation (e.g., Hogarth & Chase, 2011; Watson et al., 2014). Based on classic research on avoidance gradients (Miller, 1944) and temporal discounting (Ainslie & Haslam, 1992), we expected that the bad-tasting lemonade becomes less aversive to the participants when the consumption of that lemonade is delayed and/or can be avoided altogether. In fact, satiation failed to reduce cue-elicited food-seeking in the study of Watson et al (2014) even when the devalued food was consumed immediately following a PIT test. Thus, it is plausible that a reduction in the averseness of the devalued lemonade, and not the temporal delay itself, was the key difference between Experiment 1 and 2.

Limitations of the Study

In addition to differences in the devaluation treatment, other factors could have contributed to the eliminated PIT effect following devaluation that was observed in Experiment 1. One very basic concern is that baseline responding following devaluation was too low for being affected by the Pavlovian cues. However, this explanation presupposes that outcome-selective transfer is under voluntary control, which is at odds with current theorizing about automatic associative processes driving the PIT effect (e.g., Balleine & Ostlund, 2007; Hogarth, Balleine, Corbit, & Killcross, 2013). Even more important, selective transfer to a devalued response was observed in Experiment 2 despite a highly depressed response rate. Latter finding confirms that a low response rate does not generally prevent outcome-selective transfer (for a

thorough discussion of floor and ceiling effects in PIT studies see also Colagiuri & Lovibond, 2015).

In our experiments, instrumental outcomes were not delivered during the PIT tests, corresponding formally to an extinction test. Participants were however explicitly informed that the R-O contingencies are also effective during the transfer test, which is a difference to rodent studies, in which animals do not possess this knowledge. Thus, some caution is warranted when drawing analogies between animal studies and our study. It should be noted, however, that other human studies used instructions similar to ours for a PIT test and they observed no reduction of outcome-selective PIT following devaluation (e.g., Hogarth & Chase, 2011). Thus, these instructions do not appear to make a critical difference.

Finally, it is possible that our participants developed response strategies that are based on some declarative or explicit propositional representations of the contingencies (Greve, 2001). For instance, participants may have responded for outcome-selective transfer in the first test by using the following verbal action rule: “If it is an ingredient of the yellow drink, I press the key that earns the yellow drink; if it is an ingredient of the red drink, I press the other key.” However, on devaluation of, let’s say, the yellow drink, the verbal action rule must have changed: “Since this is an ingredient of the yellow drink, which is now disgusting, it is pointless responding on the key that earns this drink.” It should be noted that participants were explicitly instructed to ignore the ingredient pictures during the PIT test, but they may have ignored this request. Hence, the present study (like any other human PIT study with freely elected and cued response conditions) cannot rule out verbal action rules of this sort, and more research is needed on this issue. For instance, future research may include questionnaires that directly ask for explicit strategies. Furthermore, variable ratio schedules can be used that make the contingencies less transparent and explicit for the participants. In this respect, it would be valuable to examine the effects of more complex or abstract tasks on the display of outcome-selective transfer following

devaluation , given that such tasks are typically less amenable to an encoding in a propositional format (De Houwer, 2009).

Conclusion

The present experiments show that posttraining devaluation of a primary reinforcer (a lemonade) affects outcome-selective transfer when the devaluation treatment results in an aversive outcome that is consumed immediately. This finding is not only of theoretical interest but also of practical importance. According to the present analysis, it should be possible to reduce transfer effects underlying unwanted action tendencies such as drug-taking with devaluation treatments that render drug-effects aversive (see e.g., Rose, Behm, Murugesan, & McClernon, 2010, for a strong devaluation of smoking). Future research may examine more systematically whether such an intervention approach is useful.

REFERENCES

- Adams, C. D. (1980). Post-conditioning devaluation of an instrumental reinforcer has no effect on extinction performance. *Quarterly Journal of Experimental Psychology*, *32*, 447–458. doi:10.1080/14640748008401838
- Allman, M. J., DeLeon, I. G., Cataldo, M. F., Holland, P. C., & Johnson, A. W. (2010). Learning processes affecting human decision making: An assessment of reinforcer-selective Pavlovian-to-instrumental transfer following reinforcer devaluation. *Journal of Experimental Psychology: Animal Behavior Processes*, *36*, 402–408.
- Ainslie, G., & Haslam, N. (1992). Hyperbolic discounting. In G. Loewenstein & J. Elster (Eds.), *Choice over time* (pp. 57–92). New York: Russell Sage Foundation.
- Asratyan, E. A. (1974). Conditional reflex theory and motivational behavior. *Acta Neurobiologiae Experimentalis*, *34*, 15–31.
- Baeyens, F., Crombez, G., Hendrickx, H., & Eelen, P. (1995). Parameters of human evaluative flavor-flavor conditioning. *Learning and Motivation*, *26*, 141–160. doi:10.1016/0023-9690(95)90002-0
- Balleine, B., & Dickinson, A. (1991). Instrumental performance following reinforcer devaluation depends upon incentive learning. *The Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology*, *43B*, 279–296.
- Balleine, B. W., & Ostlund, S. B. (2007). Still at the choice-point: Action selection and initiation in instrumental conditioning. In B. W. Balleine, K. Doya, J. O’Doherty, & M. Sakagami (Eds.), *Reward and decision making in corticobasal ganglia networks*. (pp. 147–171). Malden: Blackwell Publishing.
- Bouton, M. E., Winterbauer, N. E., & Todd, T. P. (2012). Relapse processes after the extinction of instrumental learning: Renewal, resurgence, and reacquisition. *Behavioural Processes*, *90*, 130–141. doi:10.1016/j.beproc.2012.03.004

- Bray, S., Rangel, A., Shimojo, S., Balleine, B., & O'Doherty, J. P. (2008). The neural mechanisms underlying the influence of Pavlovian cues on human decision making. *The Journal of Neuroscience*, *28*, 5861–5866.
- Colagiuri, B., & Lovibond, P. F. (2015). How food cues can enhance and inhibit motivation to obtain and consume food. *Appetite*, *84*, 79–87. doi:10.1016/j.appet.2014.09.023
- Cohen-Hatton, S. R., Haddon, J. E., George, D. N., & Honey, R. C. (2013). Pavlovian-to-instrumental transfer: Paradoxical effects of the Pavlovian relationship explained. *Journal of Experimental Psychology: Animal Behavior Processes*, *39*, 14–23. doi:10.1037/a0030594
- Colwill, R. M., & Rescorla, R. A. (1990). Effect of reinforcer devaluation on discriminative control of instrumental behavior. *Journal of Experimental Psychology: Animal Behavior Processes*, *16*, 40–47.
- Corbit, L. H., & Balleine, B. W. (2005). Double dissociation of basolateral and central amygdala lesions on the general and outcome-specific forms of Pavlovian-instrumental transfer. *The Journal of Neuroscience*, *25*, 962–970.
- Crosbie, J. (1998). Negative reinforcement and punishment. In K. A. Lattal & M. Perone (Eds.), *Handbook of research methods in human operant behavior* (pp. 163–189). New York: Plenum Press.
- De Houwer, J. (2009). The propositional approach to associative learning as an alternative for association formation models. *Learning & Behavior*, *37*, 1–20.
- De Wit, S., & Dickinson, A. (2009). Associative theories of goal-directed behaviour: a case for animal–human translational models. *Psychological Research*, *73*, 463–476. doi:10.1007/s00426-009-0230-6
- De Wit, S., Niry, D., Wariyar, R., Aitken, M. R. F., & Dickinson, A. (2007). Stimulus-outcome interactions during instrumental discrimination learning by rats and humans. *Journal of Experimental Psychology: Animal Behavior Processes*, *33*, 1–11.

- Everitt, B. J., & Robbins, T. W. (2005). Neural systems of reinforcement for drug addiction: From actions to habits to compulsion. *Nature Neuroscience*, *8*, 1481–1489. doi:10.1038/nn1579
- Greve, W. (2001). Traps and gaps in action explanation: Theoretical problems of a psychology of human action. *Psychological Review*, *108*, 435–451.
- Hogarth, L. (2012). Goal-directed and transfer-cue-elicited drug-seeking are dissociated by pharmacotherapy: Evidence for independent additive controllers. *Journal of Experimental Psychology: Animal Behavior Processes*, *38*, 266–278.
- Hogarth, L., Balleine, B. W., Corbit, L. H., & Killcross, S. (2013). Associative learning mechanisms underpinning the transition from recreational drug use to addiction. *Annals of the New York Academy of Sciences*, *1282*, 12–24. doi:10.1111/j.1749-6632.2012.06768.x
- Hogarth, L., & Chase, H. W. (2011). Parallel goal-directed and habitual control of human drug-seeking: Implications for dependence vulnerability. *Journal of Experimental Psychology: Animal Behavior Processes*, *37*, 261–276.
- Hogarth, L., Dickinson, A., Wright, A., Kouvaraki, M., & Duka, T. (2007). The role of drug expectancy in the control of human drug seeking. *Journal of Experimental Psychology: Animal Behavior Processes*, *33*, 484–496.
- Holland, P. C. (2004). Relations Between Pavlovian-Instrumental Transfer and Reinforcer Devaluation. *Journal of Experimental Psychology: Animal Behavior Processes*, *30*, 104–117.
- Holmes, N. M., Marchand, A. R., & Coutureau, E. (2010). Pavlovian to instrumental transfer: A neurobehavioural perspective. *Neuroscience & Biobehavioral Reviews*, *34*, 1277–1295. doi:10.1016/j.neubiorev.2010.03.007
- Klossek, U. M. H., Russell, J., & Dickinson, A. (2008). The control of instrumental action following outcome devaluation in young children aged between 1 and 4 years. *Journal of Experimental Psychology: General*, *137*, 39–51.

- LeBlanc, K. H., Ostlund, S. B., & Maidment, N. T. (2012). Pavlovian-to-instrumental transfer in cocaine seeking rats. *Behavioral Neuroscience*, *126*, 681–689. doi:10.1037/a0029534
- Lovibond, P. F., & Colagiuri, B. (2013). Facilitation of voluntary goal-directed action by reward cues. *Psychological Science*, *24*, 2030–2037. doi:10.1177/0956797613484043
- Miller, N. E. (1944). Experimental studies of conflict. In J. M. Hunt (Ed.), *Personality and the behavior disorders*. (pp. 431–465). Oxford, England: Ronald Press.
- Ostlund, S. B., & Balleine, B. W. (2008). On habits and addiction: An associative analysis of compulsive drug seeking. *Drug discovery today. Disease models*, *5*, 235–245. doi:10.1016/j.ddmod.2009.07.004
- Rescorla, R. A. (1994). Transfer of instrumental control mediated by a devalued outcome. *Animal Learning & Behavior*, *22*, 27–33.
- Rose, J. E., Behm, F. M., Murugesan, T., & McClernon, F. J. (2010). Silver acetate interactions with nicotine and non-nicotine smoke components. *Experimental and Clinical Psychopharmacology*, *18*, 462–469. doi:10.1037/a0021966
- Schwabe, L., & Wolf, O. T. (2009). Stress prompts habit behavior in humans. *The Journal of Neuroscience*, *29*, 7191–7198. doi:10.1523/JNEUROSCI.0979-09.2009
- Shin, Y. K., Proctor, R. W., & Capaldi, E. J. (2010). A review of contemporary ideomotor theory. *Psychological Bulletin*, *136*, 943–974.
- Talmi, D., Seymour, B., Dayan, P., & Dolan, R. J. (2008). Human Pavlovian-instrumental transfer. *The Journal of Neuroscience*, *28*(2), 360–368.
- Trapold, M. A., & Overmier, J. B. (1972). The second learning process in instrumental learning. In A. A. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 427–452). New York: Appleton-Century-Crofts.
- Tricomi, E., Balleine, B. W., & O'Doherty, J. P. (2009). A specific role for posterior dorsolateral striatum in human habit learning. *European Journal of Neuroscience*, *29*, 2225–2232. doi:10.1111/j.1460-9568.2009.06796.x

- Urcuioli, P. J. (2005). Behavioral and associative effects of differential outcomes in discrimination learning. *Learning & Behavior*, *33*, 1–21.
- Valentin, V. V., Dickinson, A., & O'Doherty, J. P. (2007). Determining the neural substrates of goal-directed learning in the human brain. *The Journal of Neuroscience*, *27*, 4019–4026. doi:10.1523/JNEUROSCI.0564-07.2007
- Watson, P., Wiers, R. W., Hommel, B., & de Wit, S. (2014). Working for food you don't desire. Cues interfere with goal-directed food-seeking. *Appetite*, *79*, 139–148. doi:10.1016/j.appet.2014.04.005
- Weingarten, H. P. (1983). Conditioned cues elicit feeding in sated rats: a role for learning in meal initiation. *Science*, *220*(4595), 431–433. doi:10.1126/science.6836286

FOOTNOTE

1 Participants had of course the right to refuse consumption of the lemonade. However, there was presumably a social pressure to comply with the experimenter's request to drink up, which explains why only one participant refused to drink the devalued lemonade that was earned during a transfer test.

Table 1

Summary of experimental procedure

Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7	Stage 8	Stage 9	Stage 10
Taste- and-rate	Pavlovian training	Instrumental training	Transfer Test 1	Consumption	Pavlovian retraining	Instrumental retraining	Taste (devaluation)	Transfer Test 2	Consumption
Taste	S1→ YD		S1: R1 vs R2		S1→ YD			S1: R1 vs R2	
YD	S2→ YD	R1→ YD	S2: R1 vs R2	Drink YD	S2→ YD	R1→ YD	Taste YD	S2: R1 vs R2	Drink YD
	S3→ RD		S3: R1 vs R2		S3→ RD			S3: R1 vs R2	
Taste	S4→ RD		S4: R1 vs R2		S4→ RD			S4: R1 vs R2	
RD	S5→ NO	R2→ RD	S5: R1 vs R2	Drink RD	S5→ NO	R2→ RD	Taste RDdev	S5: R1 vs R2	Drink RDdev
	S6→ NO		S6: R1 vs R2		S6→ NO			S6: R1 vs R2	

Note. Stimuli (S) were six ingredient pictures, responses (R) were left and right button presses (counterbalanced as R1 and R2), outcomes (O) were a red drink (RD), a yellow drink (YD), and a picture of a wooden storage can (neutral outcome, NO). Each transfer test comprised two test blocks with 30 trials each, and each test block was followed by a consumption phase. Devaluation (dev) of yellow and red drinks with Tween 20 was counterbalanced across participants. Experiment 2 was identical with Experiment 1 with the exception that there were no consumption phases (Stages 5 and 10).

Table 2

Mean number of left and right button presses (counterbalanced as RO1 and RO2) in Experiment 1 as a function of Pavlovian stimulus, test block, and transfer test. Standard deviation is shown in parentheses.

		Transfer Test 1		Transfer Test 2	
		RO1	RO2	RO1dev	RO2
Test Block 1	SO1	15.5 (11.0)	8.0 (9.7)	4.6 (8.6)	16.9 (15.6)
	SOn	10.8 (9.6)	11.7 (8.2)	4.2 (8.0)	18.7 (13.9)
	SO2	8.0 (9.6)	15.7 (10.5)	2.2 (5.5)	22.1 (14.7)
Test Block 2	SO1	16.5 (12.7)	5.6 (9.3)	2.5 (6.5)	13.7 (14.6)
	SOn	11.4 (10.2)	11.0 (9.3)	2.4 (6.3)	13.9 (13.3)
	SO2	6.3 (10.1)	16.7 (13.7)	1.5 (4.3)	17.7 (13.7)
Total	SO1	16.0 (10.6)	6.8 (8.7)	3.5 (6.8)	15.4 (13.7)
	SOn	11.1 (9.3)	11.4 (8.2)	3.2 (6.7)	16.2 (12.7)
	SO2	7.1 (9.2)	16.2 (10.8)	1.8 (4.7)	19.9 (13.3)

Table 3

Mean number of left and right button presses (counterbalanced as RO1 and RO2) in Experiment 2 as a function of Pavlovian stimulus, test block, and transfer test. Standard deviation is shown in parentheses.

		Transfer Test 1		Transfer Test 2	
		RO1	RO2	RO1dev	RO2
Test Block 1	SO1	20.2 (13.4)	10.1 (13.1)	5.8 (12.1)	27.5 (18.7)
	SOn	12.1 (10.4)	15.2 (12.2)	3.2 (5.4)	30.6 (15.4)
	SO2	8.5 (12.0)	22.7 (14.3)	1.7 (4.1)	33.8 (14.8)
Test Block 2	SO1	22.5 (15.3)	11.2 (16.6)	8.0 (13.1)	22.8 (17.3)
	SOn	17.4 (13.9)	18.3 (14.3)	3.1 (5.0)	28.3 (14.0)
	SO2	10.1 (16.5)	25.6 (16.7)	1.1 (3.2)	33.0 (12.7)
Total	SO1	21.3 (14.0)	10.7 (14.5)	6.9 (11.9)	25.2 (17.5)
	SOn	14.5 (11.8)	16.6 (12.6)	3.2 (4.9)	29.5 (14.4)
	SO2	9.3 (13.4)	24.1 (15.0)	1.4 (2.6)	33.4 (13.4)