

OUTCOME DEVALUATION OF A CONDITIONED REINFORCER: HEDONIC SHIFT VS.
SIGNALING PERSPECTIVES

by

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1. Introduction

Events in the environment, whether connected by time or causality, can change an animal in ways that change its behavior. This behavior can be preparatory or goal directed. Preparatory behavior is based on the occurrence of one event reliably predicting the occurrence of another event, whereas so called goal-directed behavior is based on contingencies (i.e., causal relationships) between certain behaviors and their outcomes (i.e., desirable or undesirable). While there are advantages to preparatory behavior (e.g., a warning call signals danger and results in freezing in preparation for that danger), it does not change the occurrence of events. Operant behavior, on the other hand, brings about events in their environment which are desirable, and prevents events which are harmful. For example, a male zebra finch has learned that when a female zebra finch lands near him, it is often followed by the opportunity to copulate. The male zebra finch will develop a preparatory response of approaching the female when she lands on the branch because copulation is the event most likely to follow. However, this preparatory response of approaching does not guarantee that the male will have the opportunity to copulate, as the female could fly away. This preparatory behavior is also passive, in that the male zebra finch must wait until presented with the female to make a response. Female zebra finches often approach males that are singing for mating. If the male zebra finch has learned that singing increases the likelihood that a female will land on his branch (increasing the chances of copulation), then singing in this situation is an operant response. Rather than being subject to events as they occur around him, the male zebra finch can directly influence the occurrence of those events.

In some instances, the value of an outcome changes, and animals adapt their behaviors to avoid an outcome they once sought out. Outcome devaluation occurs when an appetitive

stimulus (e.g., food) is paired with a painful stimulus (e.g., shock). Animals express the effect of this devaluation by changing their preparatory response in the presence of stimuli which predict that outcome (e.g., approaching to freezing) or decreasing whatever instrumental response produced that outcome. For example, a rat learns to press a lever for a food pellet reinforcer. After pressing the lever many times for food, consumption of a food pellet is now paired with a painful shock. The rat displays suppression of instrumental responding following this devaluation treatment. There are diverging theories on when and how the rat's behavior expressed the changed value of the food (i.e., a devaluation effect). By pairing the food with shock, signaling theory states that the rat will learn that the food predicts shock, and so will suppress its lever pressing to avoid the shock (Balleine & Dickinson, 1991). In this instance, the value of the food as an incentive for generating goal-directed behavior (i.e., its incentive value) has decreased. Hedonic shift theory, on the other hand, states that pairing the food with shock not only changes its incentive value, but also its affective value (Garcia, 1989). Rather than decreasing behavior to avoid the food, the rat will develop an aversion to the food because its affective value has shifted from appetitive to aversive. In other words, devaluation resulted in a change not in what the outcome *predicts*, but how it *tastes* (Balleine, 2011). An important prediction of hedonic shift theory is that animals can only learn about the changed value of the food by tasting the food again after the devaluation. The taste of the food generates a disgust reaction, which allows the animal to learn about the changed affective properties of the food, and thereby its changed incentive value. Thus, the subsequent suppression of behavior is due to a change in both the affective and incentive value of the outcome, which occurs only after reexposure to that outcome (Balleine & Dickinson, 1991; Balleine, 2001; Garcia, 1989).

These dueling theories make important predictions about the way humans and animals adapt their behavior when the value of something that once produced behavior has changed. While signaling posits that the behavior is suppressed because the organism is avoiding the outcome, hedonic shift stresses the formation of an aversion to the outcome, one that is long-standing and resistant to extinction (Garcia, 1989). For example, if a child who once liked and admired a doctor is given a shot from the doctor, does the child avoid that doctor in the future because he predicts pain or because the child doesn't like the doctor anymore? If he later encountered the same doctor at a grocery store, would that exposure decrease (i.e., extinction of the doctor signaling pain) or increase (i.e., reexposure to the doctor completes the hedonic shift) avoidance of that doctor? Doctors are different than food in that they are not biologically significant. Many theories of conditioning focus on what organisms learn about the occurrence of events in their environment, how these influence behavior (whether preparatory or operant) and how changing the value of an outcome influences both what the animal learns and how they behave.

1.1 Reevaluation Studies in Classical Conditioning

Pavlovian conditioning occurs when a neutral stimulus (e.g., tone) is repeatedly paired with a biologically significant, unconditioned stimulus (e.g., food). The unconditioned stimulus (US) naturally elicits an unconditioned response (UR; e.g., salivation). Through repeated presentations, the neutral stimulus becomes a conditioned stimulus (CS) and elicits a response appropriate to that of the unconditioned response (UR). Once the conditioned response (CR) is reliably elicited during the CS, the organism is said to have developed an associative link between the occurrence of these events, and it is the activation of this link that produces the CR. Several theories sought to characterize this conditioning process by identifying what and how

stimuli are linked by association. Historically, a CR was viewed as behavior elicited directly by the CS, through a stimulus-response (S-R) connection where the CS is linked directly to the CR (Domjan, 2003). Alternatively, it has been argued that the CS acts as a substitute for the US, and the CR occurs because of the activation of what the animal has learned about the US, called the US representation. This stimulus-stimulus (S-S) theory of learning asserts that the associative link containing the CS and the US become linked during conditioning, not the CS and UR (Pavlov, 1927).

Outcome reevaluation (or US reevaluation) is a common method used to determine the associative links of the events that occur in classical conditioning. This method involves changing (e.g., decreasing, in the case of devaluation) the incentive value of the US from appetitive to aversive, or aversive to appetitive, after conditioning has taken place (Balleine, 2001; Dickinson, 1989; Domjan, 2003; Holland & Rescorla, 1975). If the US representation is critical to the generation of a CR, as in S-S learning theory, then changing the value of the US should immediately affect the magnitude of the CR. However, if the presence of the CS is all that is needed to elicit the CR, then changing the incentive value of the US postconditioning (i.e., in the absence of additional CS-US pairings) should have no immediate effect on the CR (Holland & Rescorla, 1975; Holloway & Domjan, 1993). There are several ways to devalue a US, including pairing it with an aversive stimulus (e.g., shock) or changing the motivating value of the US (e.g., satiation).

Holland and Rescorla (1975) employed a basic US devaluation experiment in which a tone CS was repeatedly paired with food pellets. A CR was defined as exploration for food during the tone. After conditioning, some rats were allowed free access to the same food pellets used during training until they were satiated, and then were tested immediately. Satiated rats

showed suppressed food exploration compared to control rats in the presence of the tone, which indicates that the changed value of the US altered the magnitude of the CR. Additionally, they used rotation to induce sickness following ingestion of the food pellets to devalue the US. Those rats who received rotation looked for food less during the tone than control rats. These findings support S-S theory because the devaluation of the US suppressed the occurrence of the CR (Holland & Rescorla, 1975).

Holloway and Domjan (1993) showed that revaluing the US after it had been devalued reinstated the occurrence of the CR. In a sexual approach conditioning procedure, male Japanese quails were allowed access to a female quail located behind two automatic doors. The quails were conditioned to approach during the opening of the first door with a CS (a block with feathers) mounted above it, and then the opening of the second door revealed the presentation of the actual US, the female quail. The US was devalued by altering the light/dark cycle of the living quarters of the quails. During winter, male quails engage in less mating behavior, and therefore the motivational value of the female quail during winter is much lower than during seasons where there is more daylight. Following training, Holloway and Domjan (1993) reduced the light and increased the dark cycle for half of the quails, while the other half were kept on the normal 12/12 hour schedule. The short light cycle group showed less conditioned approach during the CS, which again supports S-S theory, as the value of the US had decreased. In addition, the devalued group was gradually re-introduced to the 12/12 hour light/dark cycle, essentially re-instating the motivational value of the US. The revalued group showed a spontaneous increase of their approach during the CS after just one test session, which indicates that the increased value of the US effectively reinstated the value of the CS (Holloway &

Domjan, 1993). If conditioned approach had remained the same despite the light/dark cycle manipulation, then S-R theory would have been supported.

Support for the S-S learning theory over S-R learning theory has also been found in aversive USs. Rescorla (1973) trained rats to lever press for food pellets. Following acquisition of the lever press response, rats received several presentations of a houselight CS followed by a loud noise US, during which lever pressing was suppressed. Some rats then received several presentations of the US (i.e., habituation) in the operant chamber with and without the lever present. Rats who experienced US habituation postconditioning, both in the presence and absence of the lever, pressed more than rats who did not experience any postconditioning changes to the US. Thus, by habituating the aversive US (similar to satiating an appetitive US), its motivational value decreased and diminished the freezing CR allowing for more lever pressing (i.e., less conditioned suppression). Rescorla (1974) also showed that inflating (rather than habituating) the US after conditioning resulted in a stronger suppression CR. Rats were trained to lever press for food, then received a phase of fear conditioning in which a flashing houselight (CS) was followed by shock (US). All subjects then received an exposure session to the US alone, with a less intense shock, more intense shock, or the same intensity shock as in training. Rats who received a higher intensity shock pressed less than any other group, indicating that the aversive value of the US was inflated. Exposing the rats to a shock that was less intense than the original US, however, resulted in a devaluation, and therefore less conditioned suppression than the more intensity and same intensity groups. Research indicates that S-S learning occurs during formation of a CR for both appetitive and aversive USs. Devaluation, reevaluation, and inflation alter the ability of the CS to elicit the CR. It should be noted that S-R learning is not entirely absent during US devaluation. Studies show some decrease in responding

regardless of group (i.e., a general motivational effect), but also that a reliable amount of instrumental responding persists even after devaluation (Holland & Rescorla, 1975; Holloway & Domjan, 1993). If the reinforcer has been completely devalued, which in most experiments is confirmed by rejection of the reinforcer, then only S-R can explain continued pressing. The pairing of the context (S) and the aversive event, which occurs in both paired and unpaired groups, is sufficient to explain the decreased responding across groups. Despite both of these behavioral observations, S-S learning is supported by the reliably larger suppression of responding for the paired as compared to unpaired group.

While S-S theory has been supported in first-order Pavlovian conditioning, mixed results have been found for second-order CSs (Holland & Rescorla, 1975; Rescorla, 1973; 1974; Rizley & Rescorla, 1972). A second-order CS is created when, after first-order training, it has been repeatedly paired with a first-order CS, but is never paired with the US (Domjan, 2003). S-S theory would predict that the second-order CS would activate and subsequently enter the CS-US associative link to form a three link chain [i.e., CS2- (CS1-US)] S-R theory, however, would predict that the second-order CS would elicit the CR on its own, without the need for any links to the US or the first-order CS (i.e., CS2-CR), as during training the second-order CS was repeatedly paired with the CR that occurred to the first-order CS. While it has been found that devaluing the US through habituation diminishes the ability of a first-order CS to elicit a CR, a second-order CS actually maintains its ability to elicit a CR despite devaluation (Rescorla, 1973; Rizley & Rescorla, 1972). Additionally, Rescorla (1974) tested the inflation of a shock to increase conditioned suppression in the presence of a second-order CS. Rats were trained with pairings of a light (first-order CS) and shock (US) until they reliably suppressed lever pressing in the presence of the light. Then, rats received repeated pairings of a tone (second-order CS)

followed by the light CS until they reliably suppressed lever pressing in the presence of the tone also. Rats then received exposure sessions to different shock intensities in the presence of the light, and were finally tested for conditioned suppression in the presence of the tone. Similar rates of conditioned suppression were found for both the control and second-order groups, indicating that the inflation of the aversive shock US did not affect the CR in the presence of the second-order CS (Rescorla, 1974). These results support S-R learning theory because the lack of an effect of US or first-order CS devaluation on a second-order CR indicates that neither the first-order CS or the US are present in the associative link acquired during second-order conditioning.

Overall, most research in Pavlovian conditioning supports the S-S learning assertion that, during conditioning, the CR changes in a manner that involves the current value of the US. This has been found with both appetitive and aversive USs. In second-order Pavlovian conditioning, however, the CR remains unaffected when the value of both the US and the first-order CS have been changed. These results support the S-R assertion that the second-order CS doesn't develop a link with the first-order CS or US, but instead acts directly to produce the CR. While theories of classical conditioning and devaluation studies inform about the nature of preparatory responses, there are also theories about what is learned during the formation of operant responses.

1.2 Reevaluation Studies in Instrumental Conditioning

While classical conditioning studies highlight the importance of responding to events that commonly occur together in the environment, the CR is often subject to the causality of such events. That is, the response doesn't change the events themselves. For example, after a CS is paired with shock, a rat will freeze during the CS, which does not alter the likelihood of the

shock occurring. It is important that organisms also learn responses that can directly increase the probability of appetitive outcomes and decrease the occurrence of aversive outcomes. In instrumental conditioning, the animal performs a response in the presence of stimuli, and the outcome is delivered contingent on the response (Domjan, 2003). There are three events present during instrumental conditioning: the preceding stimulus or stimulus context (S), the response made in the presence of these stimuli (R), and the outcome contingent on the performance of the response (O).

Just as S-R learning dominated early theories of classical conditioning, Thorndike's Law of Effect, which asserted that instrumental responding was driven by an S-R association, was one of the first theories on the nature of the associative structure formed during instrumental conditioning. While Thorndike (1911) acknowledged that behavior followed by appetitive consequences is likely to be repeated and behavior followed by aversive consequences is likely to be reduced, he believed that the role of the reinforcer was to solidify a connection between the contextual cues (S) and the instrumental response (R) (Thorndike, 1911). Theorists of this time shied away from the idea that an animal could develop an expectancy of a reward, as this was difficult to test and deemed superfluous (Domjan, 2003). In opposition to S-R theory, response-outcome (R-O) expectancy theory asserted that animals not only learn about the outcome, but perform the instrumental response due to the expectancy of the outcome that will follow.

R-O theory specifies that the contingency between the response and the outcome, and the value of the outcome as a reinforcer are critical for the acquisition and emission of an instrumental response. Changing either the R-O contingency or the value of the outcome should subsequently change instrumental responding. In support of R-O expectancy theory, Adams and Dickinson (1981) used an outcome devaluation experiment to demonstrate that rats formed an

associative link between a specific response and a contingent reinforcer. They used a conditioned taste aversion procedure similar to that first used by Garcia, Kimeldorf, and Koelling (1955), which involved pairing sucrose (a preferred reinforcer over water) with harmful radiation. Following just one pairing of the reinforcer and radiation, the animal exhibited suppressed consumption of sucrose (Garcia et al., 1955). Adams and Dickinson (1981) utilized this conditioned taste aversion procedure after training rats to lever press for a reinforcer, but used an LiCl injection instead of radiation. They also included sessions in which a non-contingent reinforcer was delivered in the same context without the lever present. One group of rats received a LiCl injection upon consumption of the contingent reinforcer, another group received the injection following consumption of the non-contingent reinforcer, and the remaining rats received an unpaired injection. Rats were then tested with extinction of the lever press response and re-acquisition of the lever press response for the contingent reinforcer.

S-R theory would predict that outcome devaluation would have no immediate effect on instrumental responding. The outcome gradually drives acquisition of the instrumental response, and likewise, in extinction, the absence of the outcome would gradually reduce responding. R-O theory, on the other hand, would predict that the devalued group would show immediate suppression of lever pressing. Results showed that both the contingent and non-contingent outcome were successfully devalued, as rats wouldn't consume the devalued reinforcer when given the opportunity (Adams & Dickinson, 1981). Additionally, the contingent devalued group showed more suppression of the lever press response than both the non-contingent devalued group and the unpaired group, and was the only group that did not re-acquire the lever press response for the devalued contingent reinforcer. This shows that the rats learned that pressing the lever would result in the contingent outcome, and so suppressed the lever press response when

the outcome was made aversive (Adams & Dickinson, 1981). While the results do support R-O theory, expectancy theory is limited by the lack of importance placed on contextual stimuli. As the popularity of the S-S learning theory of classical conditioning increased, so too did the theories of exploring the interaction of S-S and instrumental S-R (Domjan, 2003; Mowrer, 1960; Rescorla & Solomon, 1967).

Two process learning theory describes the application of Pavlovian S-S theory to instrumental behavior (Kruse, Overmier, Konz, & Rokke, 1983; Mowrer, 1960). Although there are different instantiations of two process learning theory, they all add an S-S, or stimulus-outcome (S-O), process to an S-R process. The S-R process is similar to Thorndike's Law of Effect in that the presence of the contextual stimuli make it more probable that the animal will perform the instrumental response. The second process, S-O, is the result of repeated delivery of the outcome in the presence of contextual stimuli. The S-O process was originally conceived as serving a motivational function that mediates (i.e., enhance or suppress) instrumental responses emitted in the presence of the same S (Domjan, 2003). Two-process theory, unlike Thorndike's Law of Effect, argues that the outcome functions as more than just an impetus for forming an S-R association, but is part of the learning that supports instrumental responding (Gray, 1975).

Unlike Thorndike's S-R learning, the results of Adams and Dickinson (1981) can be explained by motivational two process theory. The first process, S-R learning, predicts that there will be a high probability of lever pressing after training. The second process, S-O learning, predicts that motivation mediated by the outcome further increases activity, thereby increasing the frequency of the instrumental response beyond that of the S-R process alone. Adams and Dickinson (1981) found that rats suppressed instrumental responding for a devalued outcome due to a change in the value of the outcome (O) in the R-O contingency. Two process theory, on the

other hand, attributes the suppression of responding for the devalued outcome as the removal of the S-O process that previously energized responding. Without the additional motivation to respond from the second S-O process, responding decreased to levels solely supported by the S-R process. According to motivational two process theory, a decrease in responding on the devalued item is due to a loss of outcome mediated motivation, rather than a change in the response-outcome contingency (Bindra, 1974; Rescorla & Solomon, 1967; Trapold & Overmier, 1972).

To further elucidate the findings of Adams and Dickinson (1981), Colwill and Rescorla (1985) trained two different responses with two different outcomes, and then devalued one of those outcomes. R-O theory would predict that just the response contingent on the devalued outcome should be suppressed, while the other response should be maintained. Motivational two process theory, however, predicts that devaluing one of the outcomes should affect both instrumental responses equally. Because the motivation to respond is driven by an S-O association, both outcomes indiscriminately motivate responding (Bindra, 1974). Thus, both responses should show decrements for rats who experienced devaluation of either outcome. Rats were trained to lever press for sucrose and pull a chain for food pellets. Some rats received LiCl injections following consumption of sucrose, while others were made ill after eating the food pellets. An extinction test was conducted in which all rats were given a choice test between lever pressing or chain pulling. Results showed that rats suppressed the instrumental response on which the devalued reinforcer was contingent, but maintained a steady rate of responding for the other reinforcer (Colwill & Rescorla, 1985). These results supported R-O theory over motivational two process theory, as only the instrumental response on which the devalued outcome was contingent decreased.

Another procedure used to test motivational two-process theory was transfer of control, during which a CS was presented during ongoing instrumental behavior (Kruse et al., 1983; Rescorla, 1990; Domjan, 2003). If an excitatory CS was presented, motivational two-process theory predicts that more instrumental responding would be observed more in the presence than in the absence of the CS. Kruse et al. (1983) and Rescorla (1990) used transfer of control experiments to demonstrate that the S-O association is not limited to the context itself, but can be mediated by specific stimuli, such as a visual stimulus like the lever or chain. Rescorla (1990) used transfer of control with rats to show that an S-O link was specific to reinforcers that differed only in taste. In Phase 1, rats received Pavlovian pairings of a light or tone that signaled a nose poke would result in bitter or sour water. In Phase 2, rats learned to lever press for the bitter water and chain pull for the sour water without the presence of the light CS or the tone CS from the first phase. Finally, rats were tested for acquisition of the instrumental response in the presence of the CS that had resulted in the same, or a different outcome. For example, on a same trial, if the light was a CS for bitter water, then making a lever press response in the presence of the light (rather than the tone) was a correct response. On a different trial, making a chain pull response in the presence of the light was a correct response. Rats' performance on same trials was better than on different trials (Rescorla, 1990). These results complicate a generalized motivation account of two-process theory by showing that rats learned the fastest when the CS and the instrumental response resulted in the same outcome. Generalized motivation should enhance both responses equally (Gray, 1975; Rescorla & Solomon, 1967). These results could indicate an outcome specific motivation account, where the S in the S-R and S-O learning processes is not a general context, but specific contextual stimuli, such as a lever. However, there are only vague conceptions of how different stimuli would motivate different responses. These

results also complicate a purely R-O account. It is unclear how an S-O association in Rescorla (1990) would increase the value of the O or alter the R-O contingency, which are the only two ways to enhance the instrumental response within an R-O account. Alternatively, a specific-expectancy mediation model states that the concept of S-O associations as motivational can be dismissed, and instead, the O elicited by the S-O association acts a kind of discriminative stimulus for a particular response (Trapold & Overmier, 1972). This leads to an S-O-R conception of learning. Rescorla proposed an alternative, consistent with Skinner's early conception of an S-R-O three-term contingency (1938; 1969), which placed the three terms into a hierarchical structure, S(R-O).

A limitation of two-process theory is that the separate S-R and S-O components do not accurately reflect that a pairing of the context (S) and the outcome will only occur if the animal makes the specific instrumental response. Thus, instrumental conditioning is limited by a conditional relation in which S is followed by O only when the instrumental response occurs (Domjan, 2003). Rather than forming associative structures of S-O Pavlovian contingencies, S(R-O) theorists argue that, when in the presence of certain stimuli (S), the animal learns about the instrumental contingency, or that a certain response (R) results in a specific outcome (O). Just as S-S Pavlovian theorists use outcome reevaluation to show that the CR is mediated by a CS-US associative link, S(R-O) theorists use outcome devaluation to show that certain stimuli mediate learning about response-outcome contingencies. These studies utilize methods including satiation of the outcome to decrease the motivational control of the reinforcer (Balleine & Dickinson, 1998), changes in the outcome mediated by drug state (Balleine, Ball, & Dickinson, 1994), and through conditioned taste aversion (Adams & Dickinson, 1981; Balleine & Dickinson, 1991; Colwill & Rescorla, 1985).

While outcome devaluation studies in instrumental conditioning have primarily supported S(R-O) theories, there has been a divide in how devaluation changes the representation of the reinforcer. Signaling theory states that pairing the outcome with illness forms a new associative link where the outcome serves as a predictor of or signal for illness, as in traditional aversive conditioning studies (Domjan, 2003). This, in turn, decreases the incentive value of the outcome and suppression responses generated by the outcome. Hedonic shift theories, however, stress that it is not a change in what the outcome predicts, but in its core, unconditional affective properties. Outcome devaluation changes the affective value of the reinforcer from appetitive to aversive, and animals can only learn about its changed value through direct contact with the sensory properties of the reinforcer after devaluation has occurred. Only after the changed affective value of the reinforcer has been learned does the incentive value decrease and demonstrate subsequent suppression of responding, coined incentive learning. Recent studies have supported hedonic shift theory and the need for subsequent reexposure to the devalued stimulus to show a change in instrumental responding (Balleine & Dickinson, 1991; Balleine & Dickinson, 1998; Balleine, Garner, Gonzalez & Dickinson, 1995; Lopez, Balleine & Dickinson, 1992)

1.3 Signaling vs. Hedonic Shift Theory of Outcome Devaluation

1.3.1 Affective vs. incentive value.

While much evidence supports the assertion that animals learn about the outcomes of specific behaviors, there is much debate over how the animal comes to learn about the reinforcer or US. In order for a stimulus to generate and maintain a response, it must have both affective and incentive value. Affective value is what makes a stimulus appetitive or aversive (Pavlov, 1927; Garcia, 1989; Gray, 1975). Incentive value is how well that stimulus can generate or maintain behavior, and is based on the affective value of that stimulus (Balleine, 2001; Garcia,

1989). Affective value can be described as the “likeability” of a stimulus, how “good” or “bad” it is, such as the palatability of food (Wassum et al., 2009). Incentive value is the reinforcing properties of a stimulus, or how desirable a stimulus is (Balleine, 2001). The affective and incentive values of a stimulus shift in concordance with one another, but are functionally different (Wassum et al., 2009). Outcome devaluation serves to decrease the value of an outcome, but how? Signaling theory posits that only the incentive value of the outcome is changed. When food is paired with shock, the food itself still has positive affective properties; the animal still likes it. However, the incentive value of the food no longer supports behavior (Balleine & Dickinson, 1991).

According to signaling, what is generated in outcome devaluation is an *avoidance* of the outcome. Contrarily, hedonic shift theory asserts that a change in the affective value of a stimulus must occur before its incentive value can change (Balleine & Dickinson, 1991; Garcia, 1989). When the outcome is devalued, its affective value shifts from appetitive to aversive, and its incentive value decreases as a result. After all, if you don’t like something, why would you work for it? If the outcome is not contacted after devaluation, the incentive value will remain unchanged, and the outcome will continue to support behavior (Balleine & Dickinson, 1991; Garcia, 1989). Hedonic shift learning occurs in two phases: evaluative conditioning, where the affective value of a stimulus is assigned, and incentive learning, where the incentive value is updated upon contact with the outcome following a devaluation procedure.

1.3.2 Evaluative conditioning.

Since Pavlov (1927), theories of learning separate USs and CSs by the types of responses they elicit (Klein, 2009). Contemporary theories assume that USs elicit innate reflexes (Domjan, 2003). A UR when presented with food should be to approach and consume it, whether that food

is encountered before or after any conditioning has occurred. CSs in Pavlovian conditioning and instrumental responses are generated only after they have been paired with a US; thus, they are learned about, not innate (Balleine, 2001). If a UR is elicited upon the animal's first encounter with the US, then the affective value of the US, and therefore its incentive value, must be innate.

Pavlov (1927) adhered to a behavioral definition of the affective value of the US, which asserts that the UR elicited from the presence of the US is learned through experience. Rather than being born with the innate affective value of a US, Pavlov (1927) argued that a UR is acquired *after* the first presentation of the US. Thus, Pavlov (1927) did not actually consider a UR to the sight or smell of food (US) as innate, but “acquired in the course of the animal's own existence” (pp. 22). Rather, the sensory and perceptual properties of the food become paired with a physiologically based motivational system, which contains chemosensory stimuli that are activated upon the first consummatory contact with the food (Balleine, 2001; Garcia, 1989). When the animal first consumes the food, a nutritive motivational system is activated. The sensory properties of the food are paired with the activation of this motivational system, and thereby the positive affective value of the food is established (Pavlov, 1927). Evaluative conditioning is the process of assigning affective value to a stimulus, based on the activation of an appetitive motivational system, or an aversive motivational system. The true US in this sense is not the taste or smell of the food, but activation of the motivational system (Garcia, 1989).

In support of an acquired US affective value, and a learned UR, through evaluative conditioning, Pavlov (1927) found that puppies who were kept on a strict diet of milk did not salivate at the sight or smell of solid food as puppies who had been allowed to eat solids salivated. This indicated that the UR of salivation was learned when the puppy first ate the food, and was able to pair the sensory properties of the food with the activated nutritive system. More

recently, Changizi, McGehee, and Hall (2002) found that rat pups who had never been food deprived did not exhibit food exploration behaviors. When the pups were allowed to eat when food deprived, however, they began to exhibit food seeking behaviors. When the pups were satiated, they were not motivated to eat food. So, when the food was ingested, it did not result in the activation of the appetitive motivation system (or perhaps very little activation), and the affective value of the US remained unlearned. However, when rats were food-deprived, the nutritive value of the food was high, and thus the affective value of the food was high (Changizi, McGehee, & Hall, 2002). This, in turn, assigned a high incentive value to the food, and generated food exploration behaviors (Garcia, 1989; Pavlov, 1927).

Outcome devaluation procedures also inherently capture the effects of evaluative conditioning, as they involve pairing the sensory properties of the US with a different motivational system (Garcia, 1989). The conditioned taste aversion effect found by Garcia et al. (1955) demonstrated that certain types of outcome devaluation procedures produce a change in the affective value of the reinforcer. When the ingestion of food is paired with illness, the experience of nausea activates an aversive motivational system, a disgust system (Garcia, 1989). Via evaluative conditioning, the sensory properties of the food (i.e, its taste) are paired with this disgust system, and the affective value of the food changes from appetitive to aversive. In nature, the taste of a food is often associated with its nutritive value; sweet-tasting foods provide calories, while bitter-tasting foods are associated with toxicity (Berridge, 2000). Rescorla (1990) provided evidence that animals can learn about two different response-outcome contingencies when the outcomes only differ in taste, which supports the assumption that the taste of a food and its nutritive properties are processed separately (Garcia, 1989). In an experimental setting, the taste of an outcome can be manipulated so that it is a motivationally arbitrary feature; lemon-

flavored water is not more substantial than orange-flavored water. However, if only given lemon-flavored water when thirsty, and orange-flavored water when satiated, the lemon-flavored water is preferred over orange (Berridge, 1991). The lemon taste of the water ingested while water-deprived was used as a cue of the high affective value of that water. The orange-flavor, on the other hand, was never ingested when the animal needed water (Berridge, 1991). Evaluative conditioning allows animals to learn about cues which are associated with things they need (i.e., appetitive stimuli) and with things they don't need (i.e., aversive stimuli).

Outcomes can also be revalued. In addition to devaluing two different water outcomes which differed only in taste, Rescorla (1990) also revalued the two outcomes in a different experiment. Rats were trained to lever press for bitter water and chain pull for sour water, and then experienced reevaluation with one of the outcomes by following its delivery with sucrose. The instrumental response contingent on the revalued outcome took longer to extinguish compared to the non-revalued outcome response, indicating that the incentive value of the revalued outcome had increased by being paired with sucrose (Rescorla, 1990). This form of evaluative conditioning would have paired the sensory properties of the water with the nutritive system activated by ingesting sugar, thereby increasing the incentive value and changing the original US representation.

Overall, research indicates that the affective value of all stimuli, even those considered “unconditioned” are acquired through evaluative conditioning. This fundamental learning process precedes any subsequent Pavlovian and instrumental conditioning, and establishes the encoding of the US on which predictive and adaptive learning is based. The initial pairing of the cues of the US and the nutritive feedback essentially establish the affective value of the US through Pavlovian conditioning. The activation of the nutritive system is the “true” US, while the

cues of the US are in this sense CSs (Pavlov, 1927). Subsequent evaluative conditioning also occurs when the US has been revalued, or paired with a different motivational system, such as in conditioned taste aversion studies. Changes in the affective value of a stimulus result in behavioral changes which are resistant to extinction (Steiner, Infurna, & Spear, 1980) and occur even when the pairing of the food and the illness is separated by long delays (Garcia, Ervin, & Koelling, 1966; see Freeman & Riley, 2009 for a review). A second process, incentive learning, refers to how the animal learns about the changed incentive value of the US when it has been revalued.

1.3.3 Incentive learning.

Garcia (1989) argued that conditioned taste aversion was the result of two processes. First, an effective pairing of the taste of the food with the illness would result in activation of the disgust system and a diminished affective value of the food through evaluative conditioning (Garcia, 1989). Second, when the animal subsequently makes contact with the food after the devaluation, a new UR is elicited from the taste of the food. A typical UR in response to the taste of food is salivation, or an appetitive movement of the mouth, termed an orofacial fixed action pattern (Forestell & LoLordo, 2003). After pairing the taste of the food with illness, the orofacial fixed action patterns of rats and humans shift from appetitive to rejecting (Berridge, 2000; 2001). It is not until the new disgust UR is elicited from contact with the sensory properties of the US that the animal learns about the decreased value of the food, termed incentive learning. Incentive learning is a process in which a response, generated by contact with a devalued outcome, updates the incentive value of that outcome via a negative feedback loop (Balleine, 2001; Garcia, 1989).

Signaling theory is another, and perhaps simpler, account of outcome reevaluation. Derived from traditional accounts of aversive conditioning, signaling theory states that pairing

the reinforcer with illness forms an associative link in which the outcome now acts as a signal or predictor for the occurrence of illness. Therefore, outcome devaluation is the product of learning that a previously appetitive response-outcome contingency now results in an outcome which predicts illness. This expectation leads to a subsequent suppression of that instrumental response. According to signaling, the affective value of the outcome has not changed, but its incentive value has changed because the outcome now signals something aversive (Balleine, 2001; Balleine & Dickinson, 1991). Contrarily, hedonic shift theory states that the outcome does undergo a change in both affective and incentive value. That is, the affective properties of the outcome shift from appetitive to aversive (indicated by a distaste reaction upon consumption), and it also no longer holds value as a reinforcer after devaluation. A change in value does not suppress outcome-seeking behavior until the animal is reexposed to the outcome (i.e., consummatory contact with food). Signaling predicts the opposite effect: reexposing the animal to the outcome should actually weaken its predictive effects, because this is an instance in which the outcome is not followed by illness. This, in turn, should subsequently increase outcome-seeking behavior.

Past reward devaluation studies failed to capture the different predictions of signaling and hedonic shift theories because the common procedure involved multiple pairings of the outcome and the aversive event (Balleine, 2001). This confounded the second process of hedonic shift theory, which states that reexposure is required for the animal to learn about the latent change in incentive value of the reinforcer.

Garcia (1989) was the first to propose the hedonic shift theory in conditioned taste aversion, followed shortly by Balleine & Dickinson (1991). Balleine & Dickinson (1991) showed that, with only a single pairing of the outcome and illness, suppression of the

instrumental response was not observed. Rats were trained to lever press for sucrose, and then received an injection of LiCl to make them ill. One group was reexposed to the outcome the day after the injection, while the other group received an equal amount of time in the operant chamber without reexposure. Those rats who were reexposed showed suppression and failed to reacquire the lever press response for sucrose. Reexposure was also tested in a different operant chamber than where instrumental conditioning occurred, and the results were the same, further ruling out two-process theories as the stimulus context was different for reexposure. Finally, Balleine & Dickinson (1991) trained rats to lever press and chain pull for sucrose and pellets respectively, then devalued both of the reinforcers. However, only one reinforcer was reexposed. The instrumental outcome contingent on the reexposed reinforcer was suppressed more than for the reinforcer not reexposed. All of these results support hedonic shift theory, which stresses that reexposure through consumption of the reinforcer is needed to learn about its changed incentive value through its new evaluative connection with the disgust system. Signaling, on the other hand, would predict that reexposing the reinforcer would actually weaken the devaluation because it is an instance in which the outcome is not followed by illness. Balleine (2001) replicated and extended these findings and those of Rescorla (1990) to show that devaluation and reexposure to reinforcers that only differ in flavor also supports hedonic shift theory. The perceptual and sensory properties of the US are linked with the disgust system during devaluation. As a result, motivationally arbitrary features such as smell and taste are important for learning about the changed affective value.

1.3.4. The importance of the current motivational state.

Tolman's (1949) incentive learning theory places importance on the current motivational state of the animal during instrumental conditioning. He claimed that it is through incentive

learning, and not evaluative conditioning, that animals encode the biological significance of a stimulus (Balleine, 2001). Incentive learning does not take place during every single consumption of the reinforcer, but only upon the first presentation of the US or when the value of the US has changed. Thus, during outcome devaluation, incentive learning is necessary for a hedonic shift to occur. Tolman (1949) stressed that the animal's current motivational state affects performance of the instrumental response by modulating the value assigned to the reinforcer. If the outcome holds no value to the animal in its current state (i.e., food when the animal is satiated but thirsty), then it will not learn about the current or changed value of that outcome. As described earlier, the US can also be devalued by decreasing the motivational control of the US through satiation (Balleine, 2001). Dickinson & Dawson (1988) found that sucrose is a more effective reinforcer when rats are thirsty, and food pellets when rats are hungry. However, this difference was only made apparent when rats were given non-contingent exposure to the food pellets when food deprived or the sucrose when water-deprived. These results show that while primary motivational shifts (i.e. from hunger to satiation) result in incentive learning about the changed value of the reinforcer, motivation is only one of the factors which control instrumental behavior.

Additionally, Lopez, Balleine, & Dickinson (1992) varied the motivational state (i.e. hungry or thirsty) of rats during reexposure after devaluation. Rats were trained to lever press for sucrose while they were hungry or thirsty. Then, the sucrose was paired with LiCl. Because sucrose is a more effective reinforcer when rats are thirsty than when they are hungry (Dickinson & Dawson, 1988), the sucrose is more valuable for thirsty rats. If current motivational state controlled responding, as Tolman (1949) emphasized, then hungry rats who were reexposed should not show as much of a devaluation effect because they have not encountered the sucrose

in a thirst deprived state. Rats reexposed to sucrose when thirsty should show a traditional devaluation effect. Contrarily, what Lopez et al. (1992) found was an overall effect of reexposure, regardless of motivational state at the time of reexposure. In other words, both hungry and thirsty reexposed rats showed similar levels of suppression after devaluation. Incentive learning is not always conditional upon motivational state, as Tolman (1949) emphasized. While changes in motivational state (i.e. from hungry to satiated) can decrease the incentive value of food, the value of the outcome can be changed in other ways. Thus, a rat, whether hungry or satiated, will show a devaluation effect after reexposure to a food that has been paired with illness. Logically, this makes sense that the current motivational state of the animal does not determine whether devaluation actually changes an organism's behavior to reduce contact with that outcome. It is important that behavior is adaptive in avoiding harmful things, even if they don't have use to the animal at the current time (Lopez et al., 1992).

1.4 Additional Devaluation Topics

1.4.1 Generality of hedonic shift theory.

The accumulated evidence supports a hedonic shift theory of outcome devaluation over a signaling account. However, the generality of the hedonic shift theory has come into question in recent research (Balleine, 2001). To our knowledge, all of the support for hedonic shift comes from studies which employ a conditioned taste aversion procedure. Garcia (1989) claimed that conditioned taste aversion induces illness which activates a disgust system, and that the gastric feedback from this system makes the reinforcer taste bad. However, not all outcome devaluation involves an illness that induces vomiting. Further, there are different types of aversive events which could be paired with the sensory properties of the outcome, such as a painful shock. Additionally, Garcia (1989) places emphasis on consummatory contact with the food to activate

the gastric feedback of the disgust system. He argues that a change in the affective value of an outcome (i.e., a hedonic shift) only occurs with devaluation procedures which activate nutritive motivational systems, such as the disgust system.

If hedonic shift occurs only for stimuli which are ingested and for reactions which induce gastric feedback, then this necessitates separate processing systems for nausea and for other aversive stimuli. In fact, Darwin (1872) was the first to separate the experience of disgust, as facilitated by nausea, from pain. Disgust, Darwin (1872) argued, is a specifically evolved psychological mechanism for generating behaviors which aid in the avoidance of pathogens. These behaviors rely on cues of pathogens, rather than identification of toxins themselves, because they are often too small (Curtis, de Barra & Aunger, 2011). Facial expressions of disgust are universal across species (Curtis, de Barra & Aunger, 2011; Panksepp, 2007) and are discriminable from expressions of pain (Kunz, Peter, Huster & Lautenbacher, 2013). Behaviors motivated by disgust are activated by a gut-defense system, while behaviors motivated by pain are activated by a skin-defense system (Garcia, 1989; Kunz et al., 2013; Provenza, 1995; Richardson & McNally, 2003). Because the experience of pain and disgust serve two different purposes, the avoidance of predators and pathogens respectively, animals learn to use different cues for each of these aversive outcomes. Skin defense systems are activated by visual and auditory stimuli which are accompanied with the sensation of pain (Provenza, 1995), such as the sound of a tiger growling before it bites into a gazelle's neck. CSs which are associated with pain are what Garcia (1989) referred to as distal cues, or cues which occur outside the organism. Gut defense systems, on the other hand, rely on proximal cues, or internal cues, such as the taste of food to aid the organism in toxin avoidance (Provenza, 1995; Richardson & McNally, 2003). The qualitative differences in cues used to generate behaviors from the skin-defense and gut-

defense systems results in selective associations (Garcia, 1989), in which certain pairings of cues and incentives are more readily and easily learned than others. Rats more readily learned about a distal CS paired with a painful shock than a distal CS paired with nausea, and vice versa (Garcia et al., 1966). These selective associations, Garcia (1989) argued, are why hedonic shift only occurs when taste cues are paired with nausea. Distal cues are weak signals of toxins when they are not paired with the taste of a food.

Changes to the affective value of a stimulus, or hedonic shift, are much stronger and resistant to extinction than that of CSs in traditional aversive conditioning procedures (see Freeman & Riley, 2009, for a review). Reevaluation procedures which do not involve activation of a nutritive or disgust system do not involve affective processing, but rather, involve a change in the predictive value of cues (i.e., signaling). Thus, the use of an aversive stimulus that does not produce illness, and subsequent gastric feedback, to devalue food (e.g., pairing the taste of food with shock) will not result in conditioned taste aversion (Garcia et al., 1966; Garcia, 1989). Indeed, the pairing of food and natural aversive illnesses which do not induce nausea, such as a respiratory allergic reaction, results in conditioned taste avoidance, but not conditioned taste aversion (Pelchat, Grill, Rozin & Jacobs, 1983). Hedonic shift theory necessitates that for incentive learning to occur, the animal must be reexposed to the food and experience a disgust response, which updates the affective properties of the food (i.e., the animal doesn't like the food anymore) and subsequently the incentive value of the food (i.e., the animal suppresses behavior supported by that food). These disgust reactions are unique to procedures which produce conditioned taste aversion, but not conditioned taste avoidance (Parker, Rana, & Limebeer, 2008). Conditioned taste avoidance is mediated through signaling, or conditioned fear, rather than a change in the affective properties of the food (Garcia, 1989).

Rescorla (1992) argued against hedonic shift theory by hypothesizing that the LiCl used in the Balleine and Dickinson (1991) reexposure study was not strong enough to actually devalue the reinforcer with a single pairing. Rats were trained to lever press for sucrose and pull a chain for pellets, then one of the reinforcers was devalued with a single injection of LiCl. Rescorla (1992) used a hypertonic, or more powerful, concentration of LiCl. Results showed a devaluation effect without reexposure. In addition to the concentration of LiCl, Rescorla (1992) claimed that the reexposure effect found by Balleine and Dickinson (1991) suffered from other procedural errors. In particular, they used thirsty rats rather than hungry rats and they administered LiCl after response-contingent outcomes, rather than free operant outcomes.

In response to Rescorla (1992), Balleine & Dickinson (1992) argued that because Rescorla (1992) used a hypertonic injection of LiCl, this caused somatic discomfort (i.e., pain) along with illness. They argued that the more painful injection expanded the aversive effects of the illness by causing immediate discomfort, and involved signaling rather than hedonic shift. Balleine & Dickinson (1992) found that when the rats were given the more painful hypertonic injection under anesthesia (and thus inhibiting the experience of the somatic discomfort), reexposure was still required for suppression to occur. These results could suggest that an outcome paired with physical pain does not undergo the same kind of evaluative conditioning of one paired with gastric illness. If outcome devaluation through pairing with an immediately painful stimulus causes a signaling effect rather than a hedonic shift, then this provides evidence for the presence of motivational systems for different aversive events (Balleine, 2001). However, this could also suggest that simultaneously pairing two different types of aversive events (i.e., pain and illness) with food could overshadow the need for incentive learning and thus eradicate

the need for reexposure. Research has not been conducted using just one type of overtly painful stimulus (e.g., shock).

Additionally, Balleine, Garner, & Dickinson (1995) found that administering an anti-emetic, which prevents vomiting and other symptoms that accompany the LiCl injection, prevented devaluation of the outcome. Rats who received the anti-emetic following the LiCl injection showed similar rates of suppression to the control group. Thus, it seems that rats need to experience the activation of the specific disgust system by pairing the taste of the US with illness (specifically vomiting) to experience outcome devaluation. There has been little research conducted with reinforcers other than food. Because of the emphasis hedonic shift theory places on reexposure through direct consummatory contact, it is questionable whether the theory would generalize to reinforcers that are not ingested (Garcia, 1989). In addition to conditioned taste aversion and changes in satiety, research has found evidence of incentive learning in outcome reevaluation mediated by drug state (Balleine, Ball, & Dickinson, 1994) and sexual rewards (Woodson & Balleine, 2002).

At some level, there does seem to be interactions between processing cues and the outcomes themselves. When distal cues are first paired with taste, conditioned taste aversion can still occur. Holland (1981) paired an auditory CS with food, and then that CS with illness, and observed disgust reactions in the presence of the devalued CS. The conditioned taste aversion was developed through a process Garcia (1989) coined as taste potentiation, in which the devaluation of a cue which is associated with a taste expectancy will result in a hedonic shift in the same way as if the taste itself was devalued. It should be noted, however, that the disgust reactions in response to the devalued CS were much lower than those observed in the presence of

devalued USs (Holland, 1981). There is very little research that has addressed the limits and nature of this kind of devaluation, such as whether reexposure is necessary.

1.4.2 Neural bases of hedonic shift theory.

In order to address the issue of the generality of hedonic shift theory, recent research has aimed to identify the neural bases of evaluative conditioning and incentive learning. Both Rescorla (1990) and Balleine and Dickinson (1998) showed that incentive learning occurs in devalued outcomes which differ only in taste (i.e., same caloric density). This suggests that neural structures involved in taste processing would also be involved in incentive learning. Balleine and Dickinson (2000) trained rats to perform two instrumental responses for two different outcomes, and then allowed free access of one of the outcomes until the rats were satiated. The gustatory region of the insular cortex is involved in taste processing. When this was lesioned, rats were still able to detect the devalued outcome on which they had been satiated (i.e., they suppressed consumption of this outcome). Lesioned rats, however, did not show suppression of the outcome-contingent response, and instead performed both responses equally as compared to pre-devaluation (Balleine & Dickinson, 2000). These results suggest that motivationally arbitrary features such as taste and smell are encoded during incentive learning and help the animal learn about the value of a particular outcome. Berridge (1991) found that rats satiated on milk showed increased aversive taste reactivity responses when reexposed with milk, but not when presented with sugar. Incentive learning involves changes detected in the sensory properties of food, not just general shifts in motivation.

Further, the nucleus accumbens (Brog et al., 1993) and the basolateral amygdala (BLA) (Yamamoto, Azuma, & Kawamura, 1984), both involved in reward processing, have been found to maintain reciprocal connections with the gustatory region of the insular cortex. When the BLA

was lesioned, Balleine, Killcross, & Dickinson (2003) did not find an outcome devaluation effect with rats. It was concluded that BLA lesioned rats failed to encode the outcome compared to sham rats, and thus could not learn about the outcome-action contingency. Because BLA lesioned rats could not encode the sensory features of the outcome, they could not associate these features with the incentive value, and incentive learning could not take place.

Opioids have been studied as possible contributors to the encoding of the affective or reward value of outcomes during evaluative conditioning. Wassum, Ostlund, Maidment, & Balleine (2009) infused naloxone, an opioid antagonist which inhibits the effects of opioids, into the nucleus accumbens shell of rats. When rats were food deprived, naloxone infused rats did not show increased licking responses for sucrose, despite being food deprived. This indicates that they could not encode the affective value (i.e. palatability) of the sucrose. These same rats, however, exhibited incentive learning as evidenced by an increase in instrumental actions that previously resulted in the delivery of sucrose. When naloxone was infused into the BLA, the opposite effect was observed. BLA infused rats showed no issue in encoding the increased palatability of the sucrose when food deprived, but exhibited no outcome reevaluation effect in their instrumental responses. These results suggest that opioid-mediated changes in palatability of the outcome and incentive value of the outcome are doubly dissociated. That is, evaluative conditioning (i.e., palatability) and incentive learning (i.e., incentive value) are mediated by different neural processes, further supporting hedonic shift theory.

1.4.3 Associative structure of a conditioned reinforcer.

In Pavlovian conditioning, there is substantial evidence that a second-order CS is encoded into an associative structure with the CR, but not the US. Outcome devaluation does not affect the conditioned response in the presence of the second-order CS (Holland & Rescorla,

1975; Rescorla, 1973, 1974; Holland & Rescorla, 1975). Much less is known about the associative structure of a conditioned reinforcer (CDR; Balleine, 2001; Dickinson, 1989). A neutral stimulus becomes a CDR (i.e., a CS) through multiple pairings with a primary reinforcer (i.e., a US). A CDR is able to support the acquisition of an instrumental response contingent on the CDR alone, which has no innate, biological significance (Domjan, 2003). There are two possibilities for the associative structure of a CDR. First, it could be an extension of the R-O contingency, such that when the response is followed by the CDR, a direct representation of the primary reinforcer is activated (i.e., $R \rightarrow S \rightarrow O$). Second, it could be driven by an S-O association, such that the delivery of a CDR activates a general appetitive arousal rather than a specific representation of the outcome (i.e., $S \rightarrow O \rightarrow R$). In this way, the stimuli in the context become associated with the delivery of the reinforcer, and the specific response contingent on that reinforcer is not encoded for CDRs (Rescorla & Solomon, 1967).

Parkinson, Roberts, Everitt, and Di Ciano (2005) explored the function of a light as a CDR and as a CS. Rats were trained in an operant chamber with two levers, and a light above each lever. Rats received Pavlovian training in which a light CS was followed by food, and a neutral light was followed by no food. Rats then received sessions where they had free access to sucrose or simply remained in the operant chamber without the levers or lights. Following the sucrose sessions, the rats were injected with LiCl. Because they were injected and reexposed to sucrose a total of four times, Parkinson et al. (2005) was not able to investigate the effects of hedonic shift vs. signaling theories. Following devaluation, rats were tested for magazine approach and the acquisition of a lever press response for the light CS and the neutral light. Although rats showed suppression of magazine approaches during the presence of the light CS compared to the neutral light, they did acquire a lever press response with the delivery of the

light CS as a CDR. This suggests that the ability of a stimulus to act as a CDR is not affected by US devaluation. This, in turn supports the activation of a more general appetitive arousal, rather than the CDR being present in an associative structure with the original US representation (Parkinson et al., 2005).

Overall, research indicates that the ability of a CDR to support instrumental behavior is not hindered by outcome devaluation. However, Parkinson et al. (2005) was the only study to date to actually test the effect of outcome devaluation on a CDR. This study is further limited on its contribution to hedonic shift theory by the fact that the acquisition of an instrumental response for the CDR was tested, and multiple pairings of the food and illness were used. That is, Parkinson et al. (2005) devalued the outcome before any instrumental conditioning occurred. Hedonic shift theory deals with goal-directed behavior, and what factors motivate the animal to perform actions. The associative structure of the CDR, whatever it may be, had not been formed before devaluation. Also, by using multiple pairings, Parkinson et al. (2005) failed to see whether reexposure to the sucrose was necessary to mediate acquisition of an instrumental response for the CDR. More research is needed on the resistance of a CDR to outcome devaluation after the instrumental response for the CDR has already been acquired.

1.5 The Current Study

This research sought to address the gap in the literature on the generalizability of hedonic shift theory from conditioned taste aversion studies to other types of outcome devaluation, which include painful stimuli that do not produce illness and conditioned reinforcers which are not ingested. The value of a CDR paired with food was altered through one or more post- acquisition pairings of the CDR with shock. This procedure allowed for investigations into how the CDR

supports instrumental responding, and whether outcome devaluation of a CDR by pairing it with a painful shock will support previous findings of hedonic shift theory.

Rats received Pavlovian pairings of sucrose with an audiovisual stimulus, which served as a CDR. After Pavlovian training, rats were trained to lever press for the CDR. Rats then received a session with either a single pairing of the CDR with a shock (i.e., Paired Reexposure and Paired without Reexposure groups), two pairings (i.e., Two Paired group), or the CDR and shock unpaired (i.e., Unpaired Reexposure and Unpaired without Reexposure groups). The following day, half of the rats from each group were reexposed (i.e., Unpaired Reexposure and Paired Reexposure groups) to the CDR. The remaining half (i.e., Unpaired without Reexposure, Paired without Reexposure, and Two Paired group) were exposed to the operant chamber but in the absence of any nominal events. During a reevaluation test, the rats were given the opportunity to press the lever in the absence of the CDR or any other nominal events. Finally, a second test was conducted to measure the ability of the CDR to support reacquisition of the instrumental response.

It was expected that the CDR would gain biological strength through repeated Pavlovian pairings (i.e., audiovisual stimulus → sucrose) in Phase 1. In Phase 2, the operant response was expected to be acquired due to its contingency with the CDR. After Phase 3, rats who received one or two pairings of the audiovisual stimulus and were reexposed to the CDR were expected to suppress responding during the reevaluation test as compared to the unpaired groups. Parkinson et al. (2005) found that pairing the primary reinforcer with LiCl did not disrupt the ability of a CDR with which it was paired to support instrumental behavior. However, the current experiment is more similar to taste potentiation. If the value of the CDR is needed to maintain the response, then devaluing the CDR by pairing it with shock should disrupt responding during

the reevaluation test. During the reacquisition phase, the response will be directly paired with the CDR (as in Phase 2). It is predicted that the one pairing with reexposure and two pairing groups would not reacquire the response.

How much the instrumental response is affected by devaluation during the reevaluation and reacquisition tests differs between the hedonic shift and signaling accounts. With respect to hedonic shift theory, rats in the Paired without Reexposure group would show more instrumental behavior (i.e., less suppression) during the reevaluation test relative to the Paired Reexposure and Two Paired groups. During reacquisition, the Paired without Reexposure would receive reexposure to the CDR after the first lever press. Consequently, Paired without Reexposure was anticipated not to reacquire the lever press, but due to the delayed timing of reexposure would be predicted to respond more than the Paired Reexposure and Two Paired groups. Rats in group Two Paired were already effectively reexposed to the CDR with the second pairing, and were expected to show suppressed responding during reevaluation and no reacquisition. Finally, it was expected that rats in the Unpaired groups would not show suppression in reevaluation, and would reacquire the lever press response for the CDR. Signaling theory, on the other hand, predicts the opposite for the Paired Reexposure—that reexposure would weaken the devaluation effect, not enhance it, and that this group should show less suppression and a faster reacquisition rate. Additionally, the Two Paired group should show the most suppression and the slowest reacquisition rate because the predictive strength of the outcome for illness was twice as strong as both Paired groups. Lastly, it was predicted that nose poking would decrease for all both Paired and Two Paired groups without the need for reexposure because this is a CR which is devalued overtly through contextual cues (Balleine et al., 1995; Balleine et al., 2005).

1.5.1 Pilot study.

A pilot study was conducted to evaluate parameters for the proposed study. Rats ($n = 16$) received 14 sessions of Pavlovian pairings of an audiovisual CS followed by access to sucrose. Then, acquisition of lever pressing for the CDR was measured over two sessions. Rats were split into two groups, paired ($n = 8$) and unpaired ($n = 8$). The paired group received a 30-second presentation of the CDR, followed by a 4-second, 1 m-A shock. The termination of the CDR and the onset of the shock overlapped for the paired group, and the unpaired group experienced a 3-minute interval between the two events. Following devaluation, all subjects received a reevaluation test (Test 1), in which lever press responses were nonreinforced. The next day all rats were reexposed to the CDR, then received a second reevaluation test (Test 2). Finally, in the reacquisition phase, lever presses once again resulted in the CDR.

It was predicted that the results of this pilot study would support hedonic shift theory over signaling theory. Following acquisition of a lever press response for the audiovisual CDR, it was expected that rats in both groups would show similar levels of suppression during Test 1. It was also expected that there would be some decrease in responding for both the paired and unpaired groups from the pairing of the shock with the operant box itself. Signaling accounts would predict that the paired group would show more suppression than the unpaired group because reexposure is not required to elucidate the effects of devaluation.

Following reexposure, however, it was predicted that the paired group would show more suppression of lever pressing than the unpaired group in Test 2. Signaling theory would actually predict the opposite: that suppression in the paired group would decrease due to the weakening effects of reexposure. The results of Test 1 and Test 2 were compared using a mixed measures analysis of variance (ANOVA).

A 2 (Group: unpaired vs. paired) by 2 (Reexposure: Test 1 vs. Test 2) mixed measures ANOVA was conducted on rats' suppression ratio of lever press responses, with reexposure as the within subjects factor. This analysis revealed a main effect of reexposure, $F(1, 12) = 8.39, p = .01$, with more suppression across groups in Test 2 than Test 1. There was no main effect of group, and no significant two way interaction, $ps > .38$. These results indicate that the lever press response for all subjects decreased due to general effects of extinction, but no effect of devaluation was observed.

After reexposure, it was predicted that the paired group would be slower and more resistant to reacquire lever pressing for the CDR than the unpaired group. An ANOVA was conducted on the ratio of lever pressing before devaluation versus during the reacquisition phase for both groups. A reacquisition ratio was calculated by dividing the total number of lever presses during the first session of reacquisition by the sum of the total lever presses of the first session of reacquisition and the last session on conditioned reinforcement. A one-way ANOVA conducted on the reacquisition ratio revealed that there was no main effect of group, $F(1, 9) = .59, p = .46$.

Overall, these results indicate that over Test 1, Test 2, and reacquisition, the long period of time without sucrose caused extinction of the lever press response, rather than a sufficient devaluation from pairing the CDR with shock. The lack of a difference in suppression between groups in Test 1 could be support for hedonic shift theory, but the lack of a difference after reexposure and no effect of the shock pairing for the paired group during reacquisition suggests that one pairing of the shock and the CDR may not have been sufficient to cause devaluation. Finally, the lever press response had already begun to extinguish from Test 1, suggesting a within-subjects experiment was not ideal for measuring the effects of reexposure.

Unlike in the pilot study, where the compound stimulus and the shock overlapped, as is typical in aversive conditioning studies, it was determined that there should be a temporal gap between the termination of the compound stimulus and the beginning of the shock. In traditional conditioned taste aversion studies, there is a temporal gap between the consumption of food and the onset of illness. Studies which have used painful hypertonic LiCl injections found that, when rats were given immediate somatic discomfort, there was no reexposure effect (Balleine & Dickinson, 1992; Rescorla, 1992). By mirroring the temporal gap in conditioned taste aversion studies, it was predicted that the effects of the painful shock will result in a reexposure effect.

2. Experiment 1a Method

2.1 Subjects

Subjects included 40 female experimentally-naïve Long-Evans rats (*Rattus norvegicus*) obtained from Invigo Laboratories (Indianapolis, IN) and approximately one year old. All subjects were pair-housed in translucent plastic tubs with a substrate of wood shavings in a vivarium maintained on a 12-hour dark/12-hour light cycle. All experimental manipulations were conducted during the light portion of the cycle. A progressive food restriction schedule was imposed over three weeks prior to the beginning of the experiment, until all rats were within 80-85% of their free feeding weight. Rats were weighed three times a week during the experiment to make sure they did not fall below the food deprivation percentages. All animals were handled daily for 30 seconds during the week prior to the initiation of the study. All research conducted was approved by Texas Christian University's Institutional Animal Care and Use Committee.

2.2 Apparatus

All tests occurred in a standard operant chamber measuring 30 x 25 x 20 cm (l x w x h) housed within a sound and light-attenuating environmental isolation chest (Med Associates). The

wall and ceiling of the chamber were composed of clear Plexiglas and the floor was constructed of stainless-steel rods measuring 0.5 cm in diameter, spaced 1.5 cm center-center. These steel bars were used to transmit shock during devaluation sessions. The chamber was equipped with a food dispenser capable of delivering chocolate-flavored pellets (50% sucrose w/w). The operant chamber included two retractable levers on either side of the magazine. A discrete light and speaker capable of presenting tones of different frequencies were located at the top rear of the chamber, above the levers. Ventilation fans in each enclosure and a white noise generator on a shelf outside of the enclosure ensured a consistent background noise of 75-dB (A).

2.3 Procedure

2.3.1 MagTrain.

For the first two days, the rats were trained to eat from the food magazine. The lever was not present in the operant box. A food pellet was delivered on a variable interval (VI) 60-second schedule, in which a food pellet was delivered over a variety of intervals which averaged one minute. The houselight remained illuminated throughout the duration of the session. All sessions began with a 120-sec adjustment period and lasted a maximum duration of 50 minutes.

2.3.2 Phase 1: Pavlovian.

Rats completed 8 sessions of Phase 1. The lever was not present during this phase. An audiovisual stimulus, consisting of a 3,000 Hz tone and a discrete light located above and to the right of the food magazine, was presented for 5-sec, followed by the delivery of a chocolate flavored pellet. The houselight was extinguished at the onset of the audiovisual stimulus and illuminated at its offset. The intertrial intervals (ITI) were delivered on a VI 120-s (60, 90, 120, 150, 180-sec) schedule. Sessions lasted for 25 minutes. Mastery to criterion for Phase 1 was a

discrimination ratio of .70. The total duration spent in the magazine both during and before the audiovisual stimulus was recorded in seconds.

The experimental room in which the operant chambers were located experienced several temperature and humidity issues, with occasional temperatures below 60 degrees Fahrenheit. These issues resulted in a two day interruption for Phase 1 after the sixth session. Rats completed two final sessions of Phase 1 after the interruption. Analyses were conducted to ensure all rats reached mastery to criterion in the final two sessions before being moved on to Phase 2.

2.3.3 Phase 2: Conditioned reinforcement.

For two consecutive sessions, rats were placed in the operant box with the active and inactive lever extended. Active lever presses were reinforced on a Random Ratio (RR) 2 schedule, in which the computer program pseudo-randomly determined whether each press to the lever would be reinforced. Reinforced active lever presses resulted in a 5-sec presentation of the audiovisual stimulus. The inactive lever remained extended for the duration of each session, but presses to it did not result in any nominal events. The position of the active and inactive levers was counterbalanced. Each session lasted for 60 trials or 30 minutes, whichever came first. The time of each lever press and nose poke duration were recorded in seconds. Additionally, the total number of active and inactive lever presses, and the number of lever presses in 5 minute bins were recorded. All rats were required to press each lever at least once to qualify for Phase 3.

2.3.4 Phase 3: Conditioned reinforcer devaluation. Before this phase, subjects were split into five groups: Explicitly Unpaired Reexposure ($n = 8$), Explicitly Unpaired without Reexposure ($n = 8$), Paired Reexposure ($n = 8$), Paired without Reexposure ($n = 8$), and Two Paired ($n = 8$). During this phase, the lever was retracted and no food pellets were delivered. For the Paired groups, after a three-minute adjustment period, the audiovisual stimulus was presented

for 5-sec, followed 5-sec later by a 4-sec, 1 mA unscrambled footstock. For the Two Paired group, a 3-minute interval was implemented following the termination of the first shock, followed by a second pairing of the audiovisual stimulus and the shock. For both Unpaired groups, the tone and the shock were presented at separate times, separated by an interstimulus interval (ISI) of three minutes. Subjects in all groups remained in the chamber with the houselight on for a total duration of 10 minutes.

2.3.5 Phase 4: Reexposure.

The day after Phase 3, all subjects were placed in the operant chamber with the lever retracted and the dipper arm inaccessible. For groups Unpaired Reexposure and Paired Reexposure, following a five minute adjustment period, the compound stimulus was presented one time for 5-sec. After, subjects in these groups remained in the chamber for an additional five minutes, so as to equate the session time to that of Phase 3. Subjects in groups Two Paired, Explicitly Unpaired without Reexposure and Paired without Reexposure remained in the chamber with only the houselight illuminated for the ten minute session.

2.3.6 Reevaluation Test.

On the following day, both levers were extended and lever press responses recorded for 30 minutes. Lever press responses were nonreinforced (i.e., not followed by food pellets or the audiovisual stimulus). The time of each lever press and the total nose poke duration for the session were recorded. The houselight remained illuminated for the duration of the session.

2.3.7 Reacquisition.

The day after the reevaluation test, rats were presented with a session identical to that of Phase 2, conditioned reinforcement. Both levers were extended, and presses to the active lever were reinforced with a 5-sec presentation of the audiovisual stimulus on an RR2 schedule. The

houselight extinguished at the onset of the audiovisual stimulus and illuminated at the offset. The time of each lever press and the total nose poke duration for the session were recorded.

3. Experiment 1a Results

3.1 Phase 1

A discrimination ratio was calculated for each session of Phase 1 by using the duration of nose pokes during the 5 seconds preceding the audiovisual CS (preCS period) and the 5 seconds during the CS. A discrimination ratio of .5 indicates equal amounts of nose poking during the preCS and CS periods, whereas a discrimination ratio of 1.0 indicates nose poking occurred only in the presence of the CS. Acquisition of the audiovisual stimulus as a CS was evaluated by analyzing discrimination ratios for Phase 1. The discrimination ratios from Phase 1 and lever press data from Phase 2 were analyzed to determine if there were any emergent group differences before differential treatment commenced in Phase 3.

Rats completed eight sessions of Phase 1. These first four sessions were collapsed into Block 1, and the last four sessions into Block 2. A five (Group: Unpaired Reexposure, Unpaired without Reexposure, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Block: 1 vs. 2) mixed measures analysis of variance (ANOVA), with group as the between-subjects factor, was conducted on discrimination ratios (See Figure 1). There was a main effect of block, $F(1, 35) = 115.23, p \leq .001, \eta^2_p = .77$, with discrimination ratios improving from Block 1 ($M = .55, SE = .02$) to Block 2 ($M = .74, SE = .01$). There was no main effect of group or interaction, $F_s \leq .71, p_s \geq .16, \eta^2_{ps} \leq .18$.

Rats were considered to have met mastery to criterion for Phase 1 when their discrimination ratios reached .7. Discrimination ratios for each group on sessions seven and eight

were entered into a single sample *t*-test against a constant of .5. Thus, all rats reached mastery to criterion for Phase 1 within eight sessions and were subsequently moved on to Phase 2.

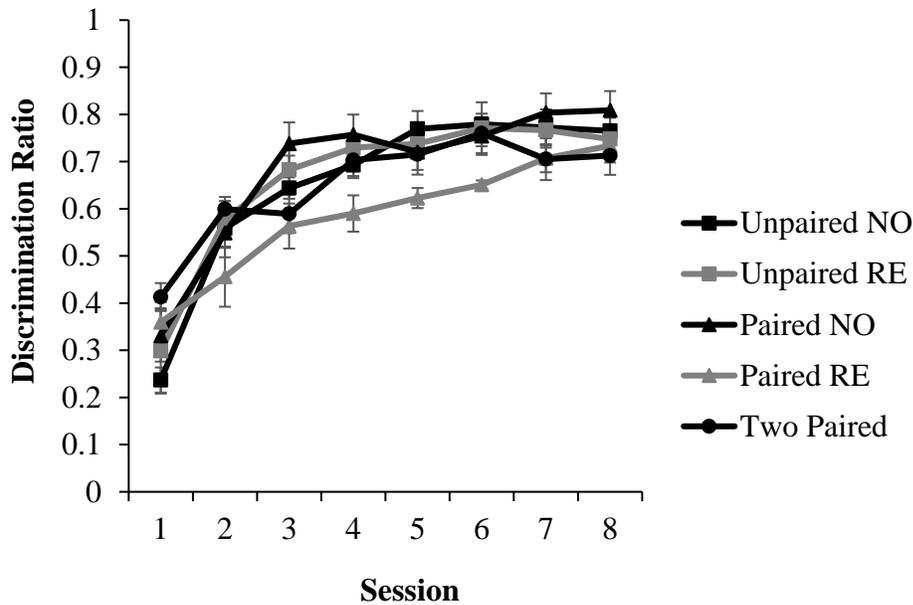


Figure 1 displays discrimination ratios for each session of Phase 1 of Experiment 1a. A discrimination ratio of 1.0 represents nose poking only during the CS, while a ratio of .5 represents nose poke equally with and without the CS. Errors bars represent standard error of the mean (SEM).

An additional analysis was conducted to identify any emergent group differences in total duration of nose pokes throughout each session. A five (Group: Unpaired Reexposure, Unpaired without Reexposure, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Block: 1 vs. 2) mixed measures ANOVA, with group as the between-subjects factor, on total nose poke duration revealed that there were no significant main effects or interactions, $F_s \leq 1.55$, $p_s \geq .21$, $\eta^2_{ps} \leq .15$. Overall, there were no group differences in Phase 1.

3.2 Phase 2

To examine emergent group differences in Phase 2, a five (Group: Unpaired Reexposure, Unpaired without Reexposure, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Session: 1 vs. 2) by two (Lever: active vs. inactive) mixed measures ANOVA, with

group as the between-subjects factor, was conducted on the total number of lever presses (See Figure 2). There was a significant main effect of session, $F(1, 35) = 15.00, p \leq .001, \eta^2_p = .30$, with decreased lever pressing from Session 1 ($M = 11.94, SD = 1.79$) to Session 2 ($M = 7.78, SD = 1.47$). There was also a main effect of lever, $F(1, 35) = 12.62, p = .001, \eta^2_p = .27$, with all rats pressing the active lever more than the inactive lever. There was no main effect of group, $F(1, 35) = .14, p = .96, \eta^2_p = .02$, and no significant interactions, $F_s \leq 1.12, p_s \geq .36, \eta^2_{ps} \leq .11$. These results indicate that rats pressed the active lever more than the inactive lever across both sessions of conditioned reinforcement training, but that lever pressing overall decreased over time.

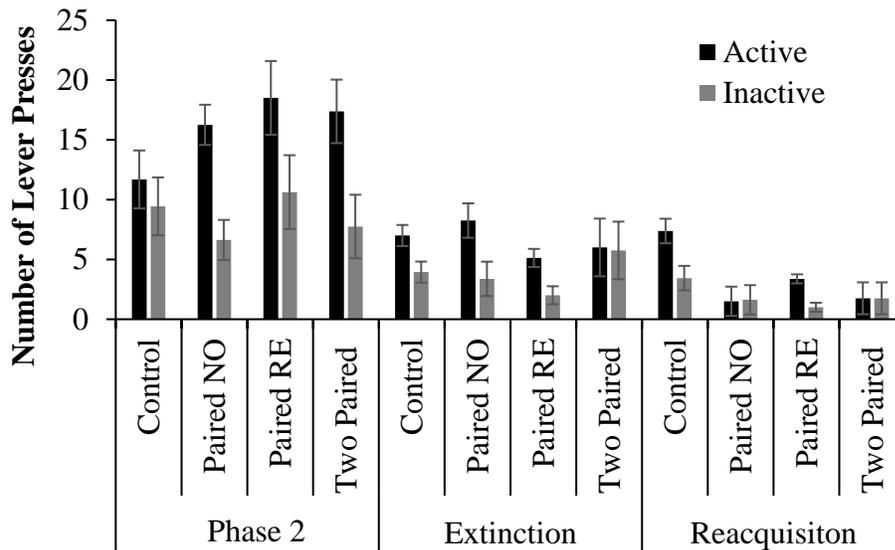


Figure 2. The total number of lever presses for Phase 2 (responding was reinforced on a random ratio-2), the Reevaluation Test, and the Reacquisition Phase of Experiment 1a. Values for Phase 2 were averaged across both sessions. The active lever was that which was associated with the conditioned reinforcer, and the inactive lever was nonreinforced. Error bars represent SEM.

The preliminary analyses for Phase 1 and Phase 2 showed no emergent group differences. All rats successfully reached mastery to criterion for Phase 1 within eight sessions. Thus, all rats were kept in the same groups and moved on to Phase 3, the beginning of differential treatment.

3.3 Reevaluation Test

Both the active and inactive levers were present during the reevaluation test, and presses to both levers were nonreinforced. A five (Group: Unpaired Reexposure, Unpaired without Reexposure, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Lever: active vs. inactive) mixed measures ANOVA was conducted on total number of lever presses (See Figure 2). The results revealed a main effect of lever, $F(1, 36) = 11.52, p = .002, \eta^2_p = .24$, with rats pressing more on the active lever than the inactive lever. However, this difference was not qualified by a main effect of group or a group by lever interaction, $F_s \leq 1.16, p_s \geq .34, \eta^2_{ps} \leq .09$.

Because there was a high amount of variability across lever pressing for all groups, analyses were conducted on rats' suppression ratios. A suppression ratio for each individual rat was calculated by taking the number of active lever press responses during reevaluation and dividing them by the sum of active lever press responses during the reevaluation test and during Session 1 of Phase 2. Before conducting analyses, a t -test compared suppression ratios for each of the Unpaired groups, and revealed no differences, $t(13) = .48, p = .64$. Thus, both Unpaired groups were collapsed into one control group for the following analyses. A one-way ANOVA examined suppression ratios as a function of group and revealed no main effect of group, $F(1, 34) = 1.82, p = .16, \eta^2_p = .14$ (See Figure 3).

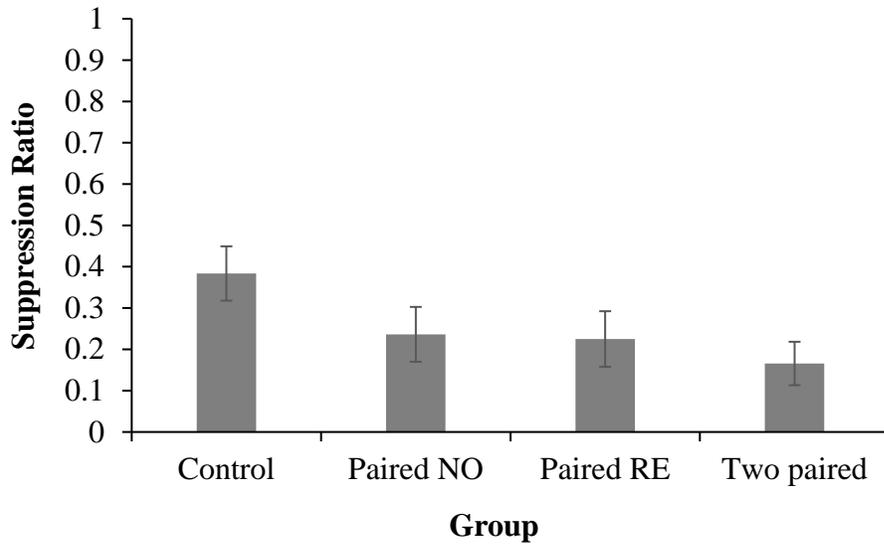


Figure 3. The suppression ratios for each group during the reevaluation test of Experiment 1a. Errors bars represent SEM.

A four (Group: Unpaired collapsed, Paired without Reexposure, Paired Reexposure, vs. Two Paired) by two (Lever press: first vs. second) mixed measures ANOVA examined latency to active lever press during the reevaluation test (See Figure 4). All results were non-significant, $F_s \leq 1.56$, $p_s \geq .22$, $\eta^2_{ps} \leq .16$.

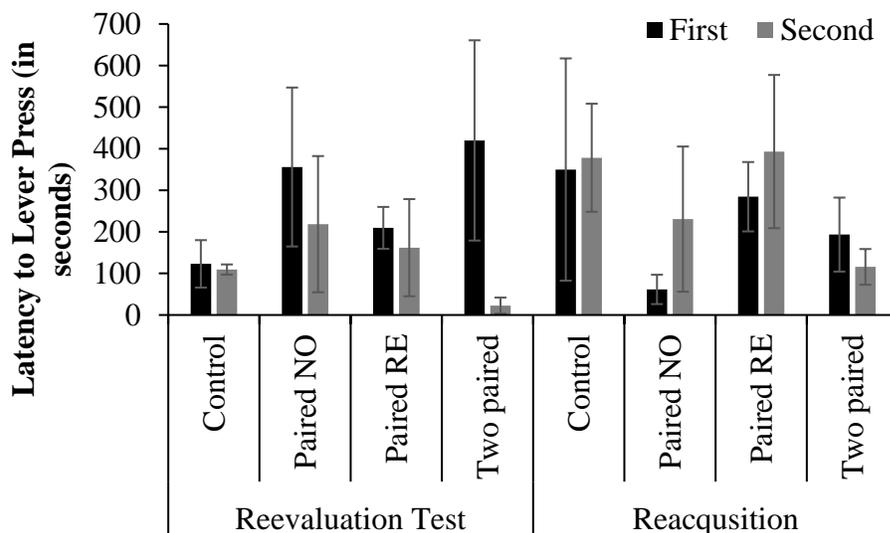


Figure 4. Latency to press the active lever in the reevaluation test and reacquisition phase of Experiment 1a. First refers to the latency from the beginning of the session to the first lever press, and second refers to the amount of time between the first and second presses. The timing of each lever press was measured in seconds. Errors bars represent SEM.

The rate of lever pressing was also recorded in six, five-minute bins throughout the 30 minute session. A 4 (Group: Unpaired collapsed, Paired without Reexposure, Paired Reexposure, vs. Two Paired) by six (Block: 1, 2, 3, 4, 5, vs. 6) mixed measures ANOVA was conducted on total number of active lever presses for each bin (See Figure 5). While there was no effect of group, $F(3, 36) = .22, p = .88, \eta^2_p = .02$, or interaction, $F(15, 180) = 1.01, p = .44, \eta^2_p = .08$, there was a main effect of block, $F(5, 180) = 4.46, p = .001, \eta^2_p = .11$. Pairwise comparisons using least significant difference (LSD) correction revealed that the rate of lever pressing in Block 1 was significantly higher than all other blocks, $ps \leq .05$. Additionally, Block 2 was higher than Block 4, $p = .046$, and Block 4 was higher than Block 5, $p = .04$. All other comparisons were non-significant, $ps \geq .07$. These results indicate that lever pressing extinguished for all groups after the first five minutes, although lever press rate overall was subject to high variability, as indicated by Figure 5. An additional one-way ANOVA, with group as the between-subjects factor, analyzed group differences in active lever presses within the first block of the reevaluation, but there was no effect of group, $F(3, 28) = .32, p = .81, \eta^2_p = .07$.

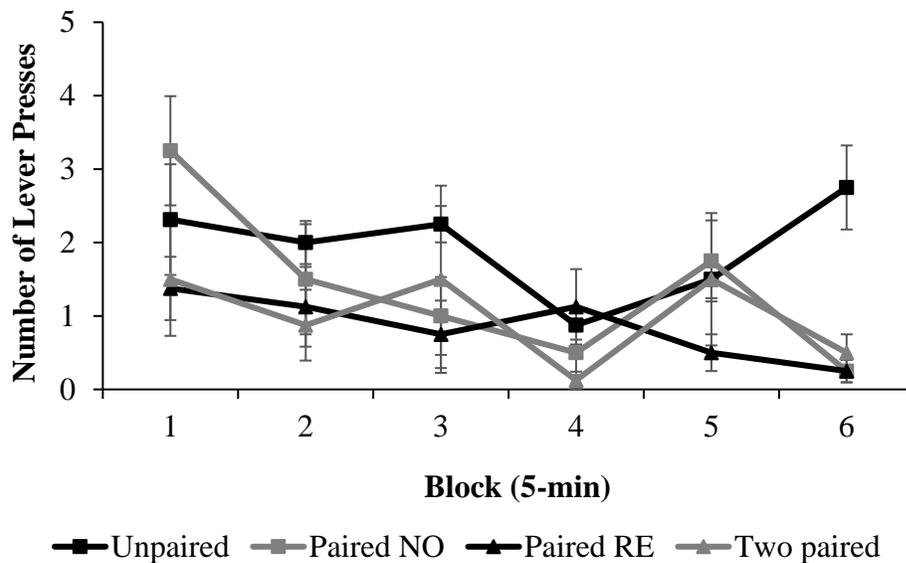


Figure 5. The active lever press rate for the reevaluation test of Experiment 1a. Errors bars represent SEM.

A nose poke duration suppression ratio was conducted for each rat by dividing the nose poke duration during the reevaluation test by nose poke duration during the reevaluation test and during the first session of Phase 1 (See Figure 6). A one-way (Group: Unpaired-collapsed, Paired without Reexposure, Paired Reexposure, vs. Two Paired) ANOVA was conducted on these suppression ratios. Results revealed a significant main effect of group, $F(3, 36) = 3.52, p = .03, \eta^2_p = .23$. Post-hocs using LSD correction showed that the suppression ratio for group Unpaired-collapsed was significantly higher than groups Paired without Reexposure and Two Paired, $ps \leq .044$, but not different from group Paired Reexposure, $p = .20$. All other comparisons were non-significant, $ps \geq .14$.

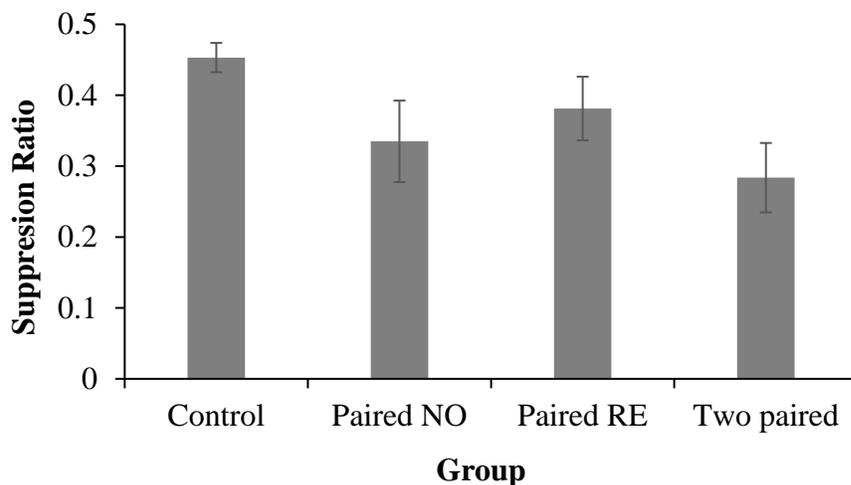


Figure 6. The nose poke duration suppression ratios for the reevaluation test of Experiment 1a. Errors bars represent SEM.

3.4 Reacquisition

To examine whether there were group differences in active lever presses, a 4 (Group: Unpaired collapsed, Paired without Reexposure, Paired Reexposure, vs. Two Paired) by 3 (Test: Phase 2 Session 1, Reevaluation Test, vs. Reacquisition) mixed measures ANOVA was conducted on total number of active lever presses (See Figure 2). While there was no main effect of group or an interaction, $F_s \leq 1.79, ps \geq .11, \eta^2_{ps} \leq .13$, there was a main effect of test,

$F(2, 72) = 20.76, p \leq .001, \eta^2_p = .37$. Rats pressed the active lever more during Phase 2 than either the reevaluation test or reacquisition phase, $ps \leq .001$. Rats also pressed more during the reevaluation test than during reacquisition, $p = .01$. Overall, rats pressed less with each subsequent phase.

Latency for the first and second bar press was measured in seconds. A 4 (Group: group: Unpaired collapsed, Paired without Reexposure, Paired Reexposure, vs. Two Paired) by 2 (Lever press: first vs. second) mixed-measures ANOVA was conducted on latency during reacquisition (See Figure 4). No main effects or interactions were significant, $F_s \leq .72, ps \geq .41, \eta^2_{ps} \leq .10$.

Differences in total number of presses to the active and inactive levers were analyzed using a similar ANOVA (See Figure 2). Results revealed marginal main effects of group, $F(1, 36) = 2.51, p = .07, \eta^2_p = .17$, and lever, $F(1, 36) = 2.71, p = .11, \eta^2_p = .07$, but no interaction, $F(3, 36) = 1.34, p = .28, \eta^2_p = .10$. Pairwise comparisons using Least Significant Difference (LSD) correction showed that group Unpaired collapsed press both levers significantly more than groups Paired without Reexposure and Two Paired, $ps \leq .04$, and marginally more than group Paired Reexposure, $p = .08$. All other comparisons were non-significant, $ps \geq .76$. Additionally, all rats pressed the active lever marginally more than the inactive lever, trending with results found in the reevaluation test.

The rate of lever pressing was recorded in six, five-minute bins throughout the 30 minute session. A 4 (Group: Unpaired collapsed, Paired without Reexposure, Paired Reexposure, vs. Two Paired) by 6 (Block: 1, 2, 3, 4, 5, vs. 6) mixed measures ANOVA was conducted on total number of active lever presses for each bin (See Figure 7). There was no main effect of block or interaction, $F_s \leq .31, ps \geq .80, \eta^2_{ps} \leq .03$. There was, however, a main effect of group, $F(1, 35) =$

3.34, $p = .03$, $\eta^2_p = .22$, in which group Unpaired collapsed had a higher rate of lever pressing than all other groups, $ps \leq .027$. All other comparisons were non-significant, $ps \geq .91$.

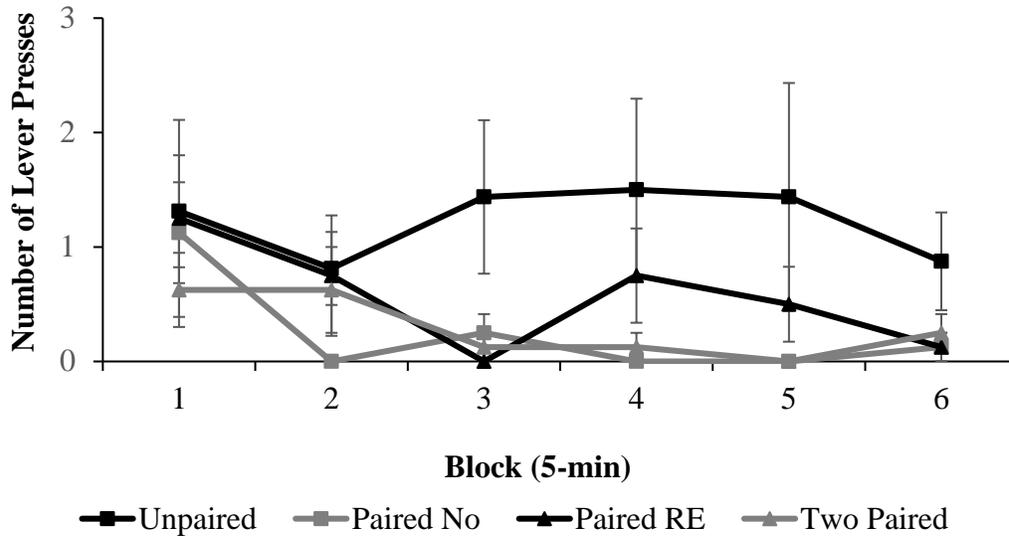


Figure 7. The active lever press rate for the reacquisition phase of Experiment 1a. Errors bars represent SEM.

A one-way ANOVA analyzed differences in total nose poke duration for each group, but revealed no effect of group, $F(3, 36) = .22$, $p = .88$, $\eta^2_p = .02$. See Figure 8.

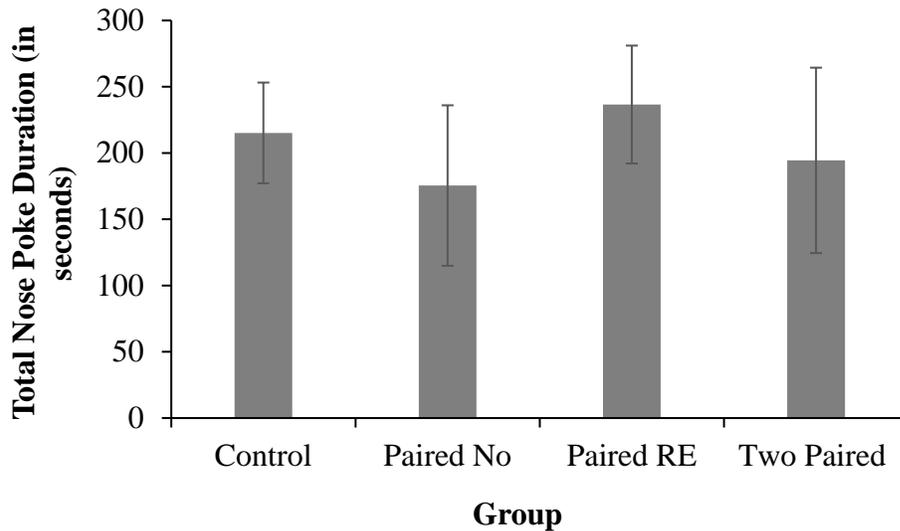


Figure 8. The total nose poke duration (in seconds) for the reacquisition phase of Experiment 1a. Errors bars represent SEM.

4. Experiment 1a Discussion

Hedonic shift theory posits that the effects of outcome devaluation will not be displayed in instrumental behavior until the organism has been reexposed to the outcome. Although all rats acquired the audiovisual stimulus as both a CS (in Phase 1) and a CDR (in Phase 2, as evidenced by more active lever pressing when compared to the inactive lever), the results of the reevaluation test revealed no selective group differences. All rats pressed the active lever the most in the first five minutes of the reevaluation test, and then lever pressing extinguished throughout the remainder of the session. As indicated by Figure 5, there was a high variability of lever pressing throughout the reevaluation test. While the results of this experiment did not support a reexposure effect, there was evidence that successful devaluation was achieved with a single pairing of the CDR and shock in the rate of lever pressing during the reacquisition test. During the reacquisition test, both Unpaired groups pressed the active lever more than all other groups, which demonstrated that paired devaluation prevented the CDR from supporting reacquisition of the instrumental response.

While lever pressing as a measure of devaluation was inconclusive for the reevaluation test, there was also some evidence for overt devaluation in the nose poke durations of each group, with the Unpaired groups nose poking more than the Paired without Reexposure and Two Paired groups, but not the Paired Reexposure group. Suppression of magazine entries for all groups who received a paired devaluation procedure, regardless of reexposure, is a replication of a common result in studies of hedonic shift (Balleine & Dickinson, 1991).

During Phase 2, lever pressing decreased from the first session to the second session, indicative of general extinction. This extinction of lever pressing was also found in the pilot study, which did not include an additional inactive lever. This suggests that the incentive value

of the audiovisual stimulus as an outcome for instrumental behavior decreases after a single session.

Overall, the results of Experiment 1a do not indicate that reexposure is needed to observe suppression of instrumental responding, but that the continued value of the CDR is necessary for maintaining instrumental responding. Rats in the Unpaired groups displayed neither a suppression of searching for food (i.e., magazine entries) or in reacquisition of lever pressing that produces the audiovisual stimulus as a CDR. While the need for reexposure, which is at the crux of hedonic shift theory, was not supported, the results were also inconsistent with signaling theory. Signaling theory posits that devaluation is evidenced in an immediate shift in instrumental behavior, without the need for reexposure. However, we observed no group differences during the reevaluation test. It is possible that both Unpaired groups showed suppression of responding during the reevaluation test due to contextual fear conditioning, in which the painful shock became associated with the context. Thus, contextual fear conditioning could have overshadowed any selective group differences in lever pressing during the reevaluation test. Responding most likely increased in the Unpaired groups during the reacquisition test because the reevaluation test was equivalent to a session of extinction of contextual fear conditioning (i.e., context exposure but no shock).

The results of Experiment 1a were mixed, with some evidence for devaluation but only when the CDR was reintroduced. The high variability during testing may have been due to temperature fluctuations, as well as the age of the rats. The rats used in Experiment 1a were all females and approximately one year old at the beginning of the experiment. Experiment 1b was intended as an exact replication of Experiment 1a. All training procedures and durations were identical to those of 1a, with the exception of the elimination of the unscheduled two-day break

in Phase 1. Additionally, because no differences between groups Unpaired without Reexposure and Unpaired Reexposure were found in any of the dependent measures, we only included one Unpaired without Reexposure group. Lastly, the subjects in Experiment 1b were younger (five months) than those of Experiment 1a, and both males and females were included as subjects.

5. Experiment 1b Method

Experiment 1b was a direct replication of Experiment 1a, utilizing younger rats, one less group, and without room temperature issues.

5.1 Subjects

Subjects included 32 (16 male, 16 female) experimentally-naïve Long-Evans rats (*Rattus norvegicus*) obtained from Invigo Laboratories, (Indianapolis, IN) and five months old at the onset of the experiment. All subjects were pair-housed in translucent plastic tubs with a substrate of wood shavings in a vivarium maintained on a 12-hour dark/12-hour light cycle. All experimental manipulations were conducted during the light portion of the cycle. A progressive food restriction schedule was imposed over three weeks prior to the beginning of the experiment, until all rats were within 80-85% of their free feeding weight. Rats were weighed three times a week during the experiment to make sure they did not fall below the food deprivation percentages. All animals were handled daily for 30 seconds during the week prior to the initiation of the study. All research conducted was approved by Texas Christian University's Institutional Animal Care and Use Committee.

5.2 Apparatus

The apparatus used was identical to the one used in Experiment 1a.

5.3 Procedure

5.3.1 MagTrain.

Two days of magazine training were implemented with the same procedure as in Experiment 1a.

5.3.2 Phase 1: Pavlovian.

The procedure for Phase 1 was identical to that of Experiment 1a. All rats received eight sessions, to equate the duration of Phase 1 in Experiment 1a. No temperature or humidity issues interrupted training.

5.3.3 Phase 2: Conditioned reinforcement.

The procedure for this phase was identical to that of Experiment 1a.

5.3.4 Phase 3: Conditioned reinforcer devaluation.

Before this phase, subjects were split into four groups: Explicitly Unpaired ($n = 8$), Paired without Reexposure ($n = 8$), Paired Reexposure ($n = 8$), and Two Paired ($n = 8$). Unlike in Experiment 1a, there was no Explicitly Unpaired Reexposure group. All other procedures were the same.

5.3.5 Phase 4: Reexposure.

All procedural details of this phase were the same as in Experiment 1a. Group Paired Reexposure was reexposed to the audiovisual stimulus, while groups Explicitly Unpaired, Paired without Reexposure, and Two Paired were not reexposed.

5.3.6 Reevaluation Test.

The reevaluation test was identical to Experiment 1a.

5.3.7 Reacquisition.

The reacquisition test was identical to Experiment 1a.

6. Experiment 1b Results

6.1 Phase 1

Acquisition of the audiovisual stimulus as a CS was evaluated by analyzing discriminations ratios for Phase 1 and no group differences were found. A four (Group: Unpaired, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Block: 1 vs. 2) mixed measures analysis of variance (ANOVA), with block as the within-subjects factor, was conducted on the discrimination ratios for Phase 1. While there was no main effect of group, $F(1, 3) = .39, p = .76, \eta^2_p = .04$, or two-way interaction, $F(3, 28) = .31, p = .82, \eta^2_p = .03$, there was a significant main effect of block, $F(1, 3) = 120.20, p \leq .001, \eta^2_p = .81$, with discrimination ratios significantly improving from the first four sessions to the last four sessions. Additionally, single sample *t*-tests analyzed discrimination ratios for each group during the last two sessions. All discrimination ratios were significantly above chance (.5), $ts \geq 4.48, ps \leq .001$.

6.2 Phase 2

For analysis of preexisting group differences in Phase 2, a four (Group: Unpaired, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Session: 1 vs. 2) by two (Lever: active vs. inactive) three-way mixed measures ANOVA was run on the total number of lever presses. Upon examining the descriptive statistics (See Figure 9), the number of lever presses for Group Unpaired was noticeably lower than for other groups. Results of the ANOVA indicated a trend toward a main effect of group, $F(3, 28) = 1.81, p = .17, \eta^2_p = .16$, and pairwise comparisons using Least Significant Difference correction showed that Group Unpaired pressed significantly less overall than all other groups, $ps \leq .04$. Due to evidence supporting an emergent group difference, the groups were reconfigured based on lever press performance before any differential treatment occurred in Phase 3.

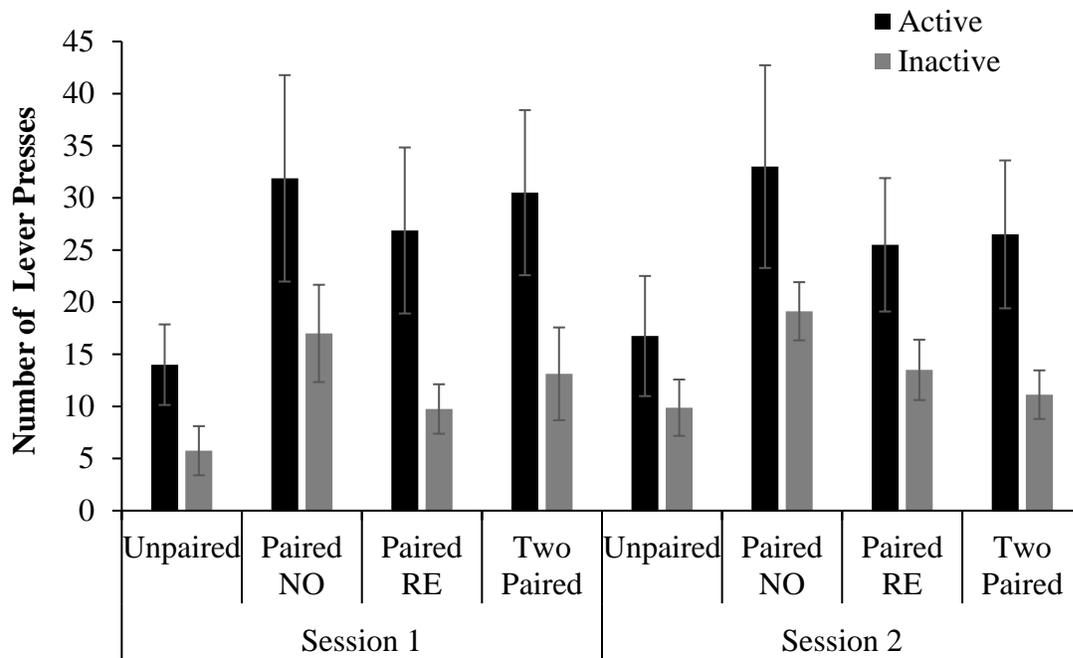


Figure 9. The total number of active and inactive lever presses across both sessions of Phase 2 in Experiment Ib, prior to performance matching. All subsequent figures for Experiment Ib represent performance matched groups. Errors bars represent SEM.

6.2.1 Performance matching.

The total number of lever presses in Phase 2 for each rat was calculated, and rats were sorted from least to most presses. Then, rats were assigned to groups so that each group had an evenly distributed array of low, moderate, and high lever presses for each rat. The squad, operant box, and sex of the rat were counterbalanced when re-assigning groups. All preliminary analyses for Phase 1 and 2 were re-run with the new group assignments to ensure that any emergent group differences were eliminated.

Using the performance-matched group assignments, a four (Group: Unpaired, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Block: 1 vs. 2) mixed measures analysis of variance (ANOVA), with block as the within-subjects factor, was conducted on the discrimination ratios for Phase 1 (See Figure 10). As expected, there was no main effect of group, $F(3, 28) = .84, p = .48, \eta^2_p = .08$. There was still a main effect of block,

$F(1, 28) = 128.71, p \leq .001, \eta^2_p = .82$, with better performance during the last four sessions than during the first four sessions. Finally, there was no significant two-way interaction, $F(3, 28) = .99, p = .41, \eta^2_p = .10$. A similar ANOVA was run with total nose poke duration as the dependent variable, and again revealed no significant main effects or interactions, $F_s \leq 1.59, p_s \geq .21, \eta^2_{ps} \leq .15$. Overall, the results of the performance matched groups were comparable to those of the using the original group assignments for Phase 1.

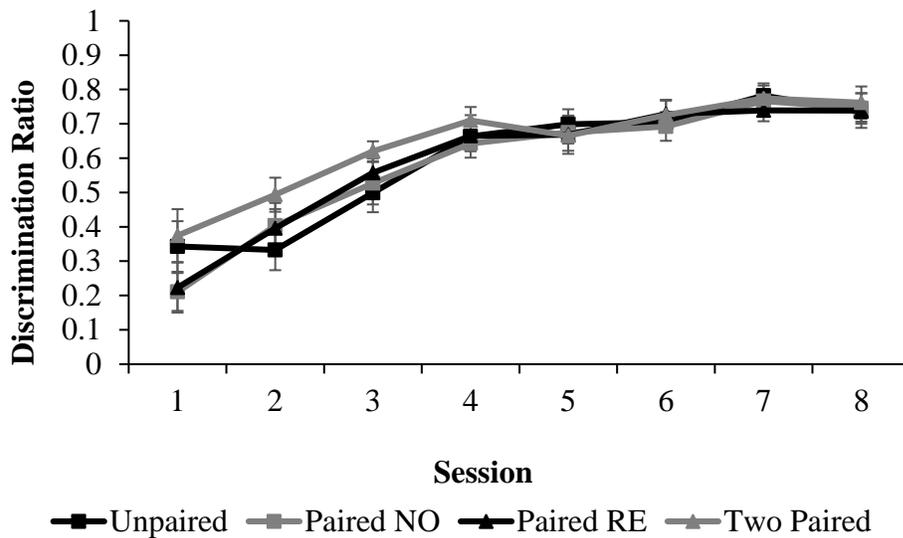


Figure 10. Discrimination ratios for each session of Phase 1 of Experiment 1b. A discrimination ratio of 1.0 represents nose poking only during the CS, while a ratio of .5 represents nose poke equally with and without the CS. Errors bars represent SEM.

The total number of lever presses for Phase 2 were re-examined using the new group assignments. Upon examining the descriptive statistics (See Figure 11), the lever presses for each group are more evenly distributed. To confirm this, a four (Group: Unpaired, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Session: 1 vs. 2) by two (Lever: active vs. inactive) three-way mixed measures ANOVA was conducted on the total number of lever presses. Firstly, the significance of the main effect of group significantly increased, $F(3, 28) = .02, p = .99, \eta^2_p < .01$, indicating that performance matching eradicated the previously identified group differences in Phase 2. There was a significant main effect of the type of lever,

$F(1, 28) = 19.36, p \leq .001, \eta^2_p = .41$, with rats pressing the active lever more than the inactive lever. All other main effects and interactions were non-significant, $F_s \leq .95, p_s \geq .27, \eta^2_{ps} \leq .13$.

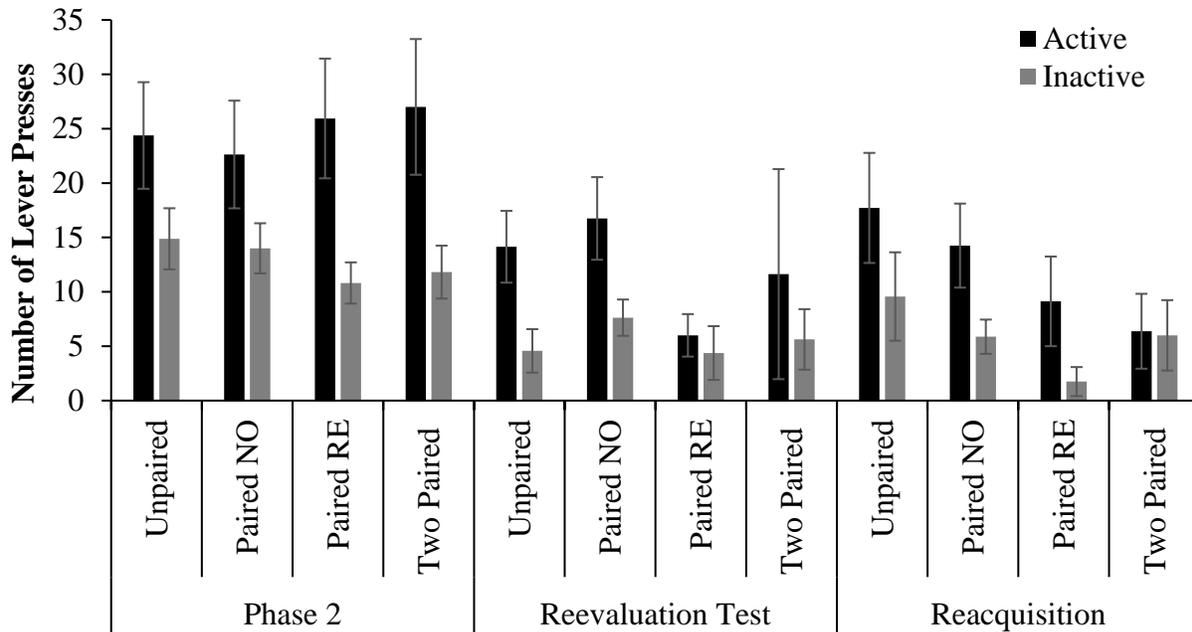


Figure 11. The total number of lever presses for Phase 2, the Reevaluation Test, and the Reacquisition Phase for Experiment 1b. Values for Phase 2 were averaged across both sessions. The active lever was that which previously or presently resulted in the conditioned reinforcer, and the inactive lever was nonreinforced. Errors bars represent SEM.

Overall, re-assigning groups based on lever press performance removed any preexisting group differences. All rats successfully reached mastery to criterion in Phase 1 within eight sessions. Additionally, one rat in group Unpaired did not press either lever at all in Phase 2, and was subsequently eliminated from all additional analyses.

6.3 Reevaluation Test

After devaluation and reexposure, rats were placed in the operant box for a 30-minute, nonreinforced reevaluation test. During this test, both the active and inactive levers were present. A four (Group: Unpaired, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by two (Lever: active vs. inactive) mixed measures ANOVA analyzed the total number of lever presses for each rat (See Figure 11). The results revealed a main effect of lever, $F(1, 27) = 4.88$,

$p = .04$, $\eta^2_p = .15$, but no main effect of group, $F(3, 27) = .85$, $p = .48$, $\eta^2_p = .09$ or two-way interaction, $F(3, 27) = .38$, $p = .77$ $\eta^2_p = .04$. Overall, rats pressed the active lever more than the inactive lever.

In order to take into account the high variability of lever pressing in each group (particularly in Group Two Paired, See Figure 11), suppression ratios were conducted for each rat. These were calculated by dividing the total number of active lever presses during the reevaluation and dividing them by the total sum of active lever presses during the reevaluation test and during Session 1 of Phase 2.

A one-way ANOVA with group as the between-subjects factor analyzed differences in active lever press suppression ratios (See Figure 12). The results revealed a significant main effect of group, $F(3, 27) = 5.44$, $p = .01$. Post-hoc comparisons using LSD correction indicated that suppression ratios for groups Paired Reexposure and Two Paired were significantly lower than those for groups Unpaired, $ps \leq .05$, and Paired without Reexposure, $ps \leq .003$. There was no difference in lever pressing between rats in groups Paired Reexposure and Two Paired, $p = .97$, and between Unpaired and Paired without Reexposure, $p = .26$. These results suggest that groups Paired Reexposure and Two Paired pressed less than the other groups during the reevaluation test.

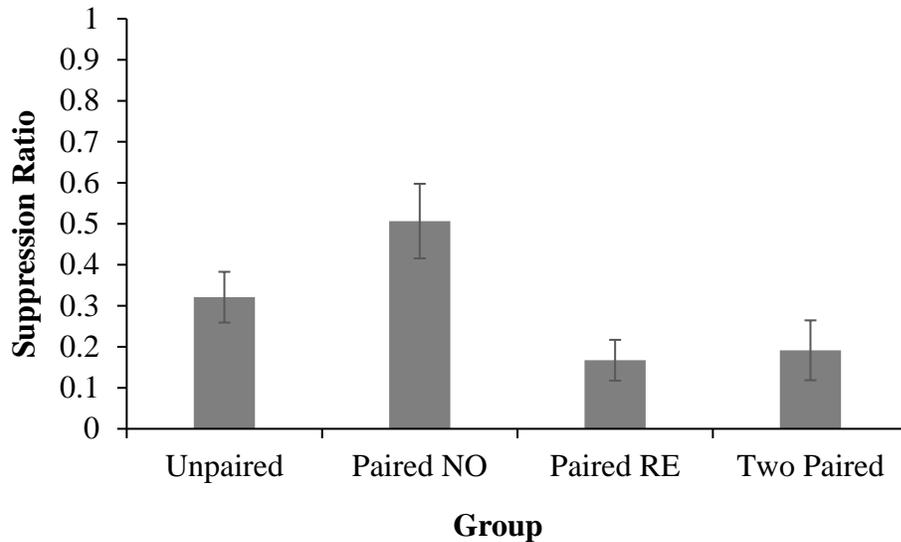


Figure 12. The suppression ratios for each group during the reevaluation test of Experiment 1b. A suppression ratio of .5 indicates equal amounts of pressing during Phase 2 and during the test, while a value of zero indicates completed suppression of responding during test. Errors bars represent SEM.

The rate of lever pressing during the reevaluation test was measured in six, five minute bins (See Figure 13). To analyze changes in the rate of lever pressing, a 4 (Group: Unpaired, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by 6 (Block: 1, 2, 3, 4, 5, vs. 6) mixed measures ANOVA was conducted with block as the within-subjects factor. While there were no main effects of block, $F(5, 135) = .51, p = .77, \eta^2_p = .02$, or group, $F(3, 27) = .67, p = .58, \eta^2_p = .07$, there was a marginally significant two-way interaction, $F(15, 135) = 1.60, p = .08, \eta^2_p = .15$.

To further elucidate the two-way interaction, simple main effect analyses using LSD correction were utilized. Results of the follow-up tests indicated group differences in the first two blocks of the reevaluation test. In Blocks 1 and 2, group Unpaired pressed significantly more than group Two Paired, $ps \leq .04$, and group Paired without Reexposure pressed more than both the Paired Reexposure and Two Paired groups, $ps \leq .03$. Group Unpaired and group Paired Reexposure demonstrated no differences in lever pressing for each block, $ps \geq .26$. Lever press rates for group Two Paired did not differ except for a marginally significant increase in Block 4

as compared to Blocks 1, 2, 5, and 6, $ps \leq .07$. Group Paired without Reexposure demonstrated a decrease in lever pressing from Block 1 to Blocks 3 and 6, $ps \leq .05$, and from Block 2 to Block 6, $p = .02$. This group also showed a surge in responding in Block 5 as compared to Blocks 3 and 6, $ps \leq .02$. All other comparisons were non-significant, $ps > .05$. These results indicate that there were group differences in the first two blocks of the reevaluation test, and relatively stable rates of responding in all groups, except for sudden increases in responding for the Paired without Reexposure and Two Paired groups in the latter half of the test.

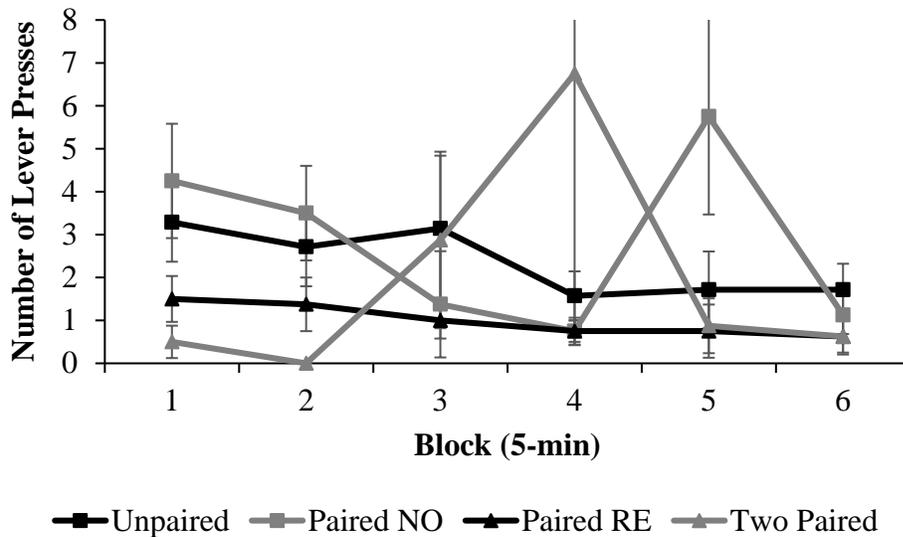


Figure 13. The active lever press rate for the reevaluation test of Experiment 1b. Errors bars represent SEM.

An additional 4 (Group: Unpaired, Paired Reexposure, Paired without Reexposure, vs. Two Paired) by 2 (Lever press: first vs. second) mixed measures ANOVA was conducted on the latency (in seconds) to the first and second press the active lever (See Figure 14). There were no main effects of lever press or group, $F_s \leq 1.28$, $ps \geq .27$, $\eta^2_{ps} \leq .05$. There was, however, a marginally significant two-way interaction, $F(3, 27) = 2.42$, $p = .09$, $\eta^2_p = .21$. Simple main effect analyses using LSD correction indicated that group Two Paired waited marginally longer to press the lever for the first time than group Unpaired, $p = .06$. When analyzing within-group

differences in latency, simple main effect analyses revealed that Group Two Paired waited significantly longer to press the lever the first time as compared to the second time, $p = .03$. All other comparisons were non-significant, $ps > .05$. These results suggest minimal differences in latency to lever press during the reevaluation test.

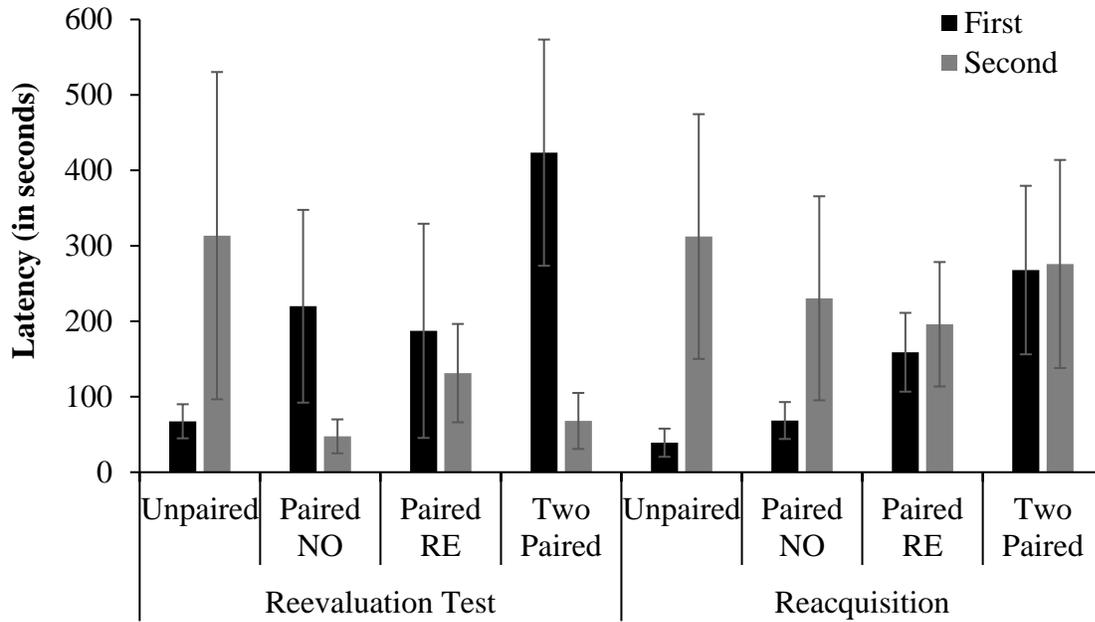


Figure 14. Latency to press the active lever in the reevaluation test and reacquisition phase of Experiment 1b. First refers to the latency from the beginning of the session to the first lever press, and second refers to the amount of time between the first and second presses. The timing of each lever press was measured in seconds. Errors bars represent SEM.

Finally, a one-way ANOVA with group as the between-subjects factor compared the total nose poke duration for each group (See Figure 15). The results of the ANOVA revealed no effect of group, $F(3, 27) = .92, p = .45, \eta^2_p = .02$.

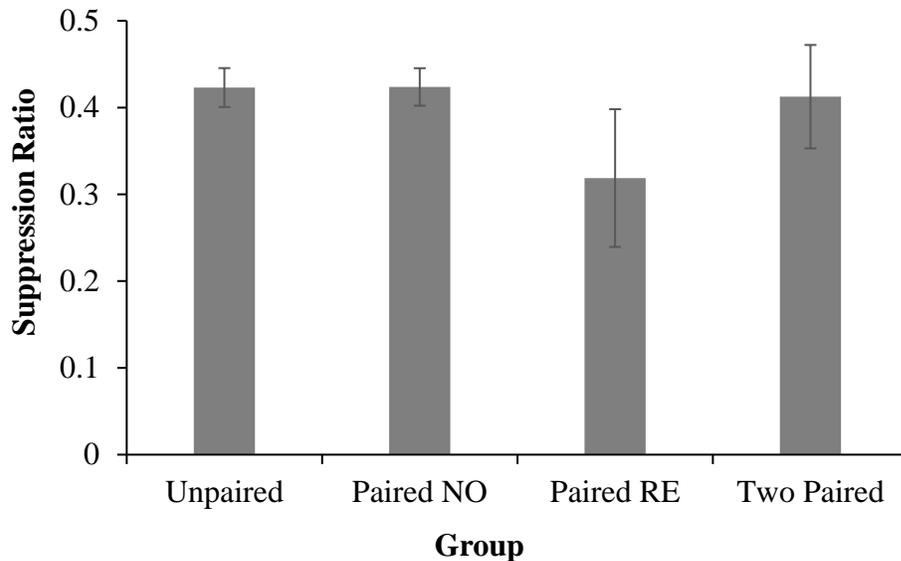


Figure 15. The nose poke duration suppression ratios for the reevaluation test of Experiment 1b. A suppression ratio of .5 represents no decrease in nose poking from Phase 2 to the reevaluation test, while a value of zero represents total suppression of nose poking during the reevaluation test. Errors bars represent SEM.

Overall, the results of the reevaluation test demonstrated performance differences by group, with more suppression of lever pressing in groups Paired Reexposure and Two Paired as compared to groups Unpaired and Paired without Reexposure.

6.4 Reacquisition

During the reacquisition test, rats were placed in the operant box with both the active and inactive lever, and the active lever once again resulted in the presentation of the audiovisual CDR. To examine differences in active lever presses throughout the duration of the experiment, a 4 (Group: Unpaired, Paired without Reexposure, Paired Reexposure, vs. Two Paired) by 3 (Test: Phase 2 Session 1, Reevaluation Test, vs. Reacquisition) mixed measures ANOVA was conducted on the total number of active lever presses (See Figure 11). There was a main effect of test, $F(2, 54) = 13.67, p \leq .001, \eta^2_p = .34$, in which rats pressed the lever during Phase 2 significantly more than during the reevaluation test or reacquisition, $ps \leq .001$. Rats pressed

equally during both tests, $p = .91$. There was no main effect of group, $F(1, 27) = .60, p = .62, \eta^2_p = .06$, and no significant two-way interaction, $F(6, 54) = .52, p = .79, \eta^2_p = .05$.

As a more direct measure of reacquisition, a 4 (Group: Unpaired, Paired without Reexposure, Paired Reexposure, vs. Two Paired) by 2 (Lever: active vs. inactive) two-way mixed measures ANOVA was conducted on the total number of lever presses, with group as the between-subjects factor (See Figure 11). There was a main effect of lever, $F(1, 27) = 8.75, p = .006, \eta^2_p = .25$, in which the total number of responses to the active lever was higher than those to the inactive lever. All other effects and interactions were non-significant, $F_s \leq 1.76, p_s \geq .18, \eta^2_{ps} \leq .16$.

The rate of lever pressing was measured in six, five minute bins throughout the duration of the 30 minute session. A 4 (Group: Unpaired, Paired without Reexposure, Paired Reexposure, vs. Two Paired) by 6 (Block: 1, 2, 3, 4, 5, vs. 6) mixed measures ANOVA examined the rate of active lever pressing during the reacquisition phase (See Figure 16). While there was no main effect of group, $F(3, 27) = 1.49, p = .24, \eta^2_p = .14$, or two-way interaction, $F(15, 135) = 1.29, p = .21, \eta^2_p = .13$, there was a marginally significant main effect of block, $F(5, 15) = 2.21, p = .06, \eta^2_p = .08$. Pairwise comparisons indicated that rats pressed the active lever at the same rate for the first three blocks, $p_s \geq .37$. Lever pressing significantly decreased from Block 1 to Block 4, $p = .007$, and marginally decreased from Block 1 to Blocks 5 and 6, $p_s \leq .08$. Additionally, rats pressed the lever marginally more in Block 2 as compared to Block 4, $p = .06$, and in Block 3 as compared to Block 4, $p = .05$. Overall, these results demonstrate a general decrease in lever pressing in the second half of the reacquisition session.

Upon examining the descriptive statistics for the active lever press rate during reacquisition, there were noticeable differences in pressing during the first block (See Figure 16).

To further elucidate these differences, a separate one-way ANOVA was run on the total number of active lever presses during the first block, with group as a between-subjects factor. The results demonstrated a significant main effect of group, $F(3, 27) = 4.01, p = .02, \eta^2_p = .45$. Pairwise comparisons showed that rats in group Unpaired pressed significantly more than the rats in groups Paired Reexposure and Two Paired, $ps \leq .02$, but at the same rate as rats in group Paired without Reexposure, $p = .57$. Additionally, rats in group Paired without Reexposure pressed marginally more than in group Paired Reexposure, $p = .07$, and significantly more than those in group Two Paired, $p = .02$. Finally, the rats in groups Paired Reexposure and Two Paired pressed at comparable rates in the first block, $p = .61$.

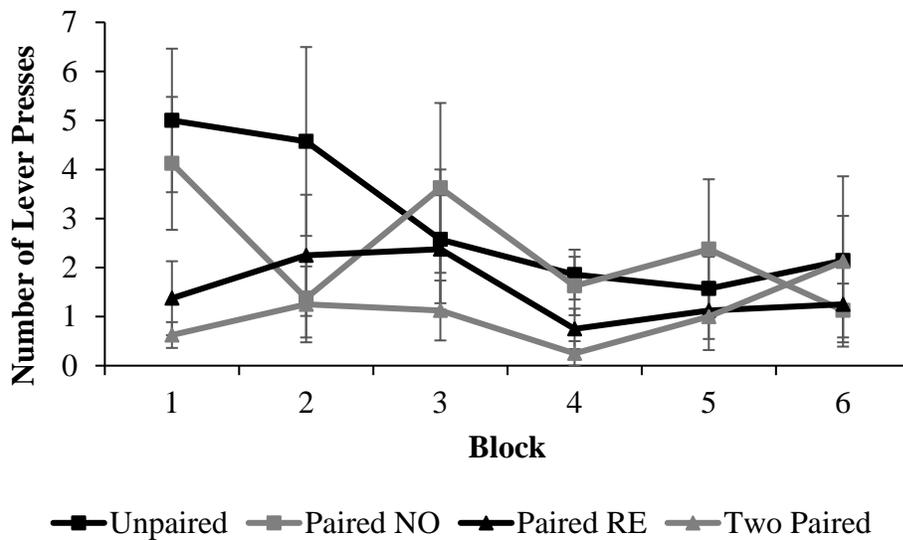


Figure 16. The active lever press rate for the reacquisition phase of Experiment 1b. The total number of active lever presses was recorded for each 5-minute block of the 30-minute session. Errors bars represent SEM

An additional mixed measures ANOVA examined latency to press the active lever as a function of Group (Unpaired, Paired without Reexposure, Paired Reexposure, vs. Two Paired) and Lever press (first vs. second). There were no significant main effects or interactions, $F_s \leq 2.15, ps \geq .15, \eta^2_{ps} \leq .16$ (See Figure 14).

Finally, a one-way ANOVA examined total nose poke duration during reacquisition, with group as the between-subjects factor (See Figure 17). There was no effect of group, $F(3, 27) = 1.86, p = .16, \eta^2_p = .12$.

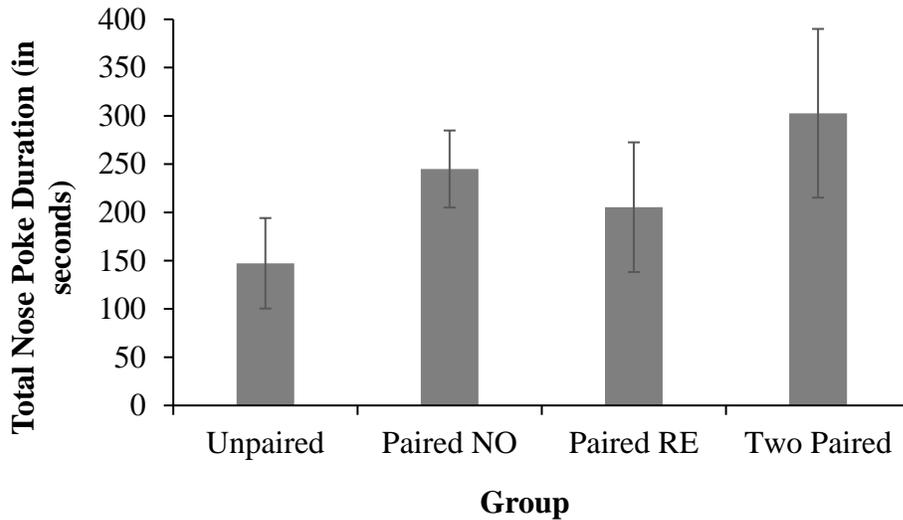


Figure 17. The total nose poke duration (in seconds) for the reacquisition phase of Experiment 1b. Errors bars represent SEM.

Overall, these results indicate that there were group differences in the first block of reacquisition, but responding in all groups was subject to general extinction over the 30 minute session.

7. Experiment 1b Discussion

After a single pairing of the CDR and a painful shock, it was expected that only the group reexposed to the shock would show a subsequent suppression of lever pressing. All rats acquired the CR to the CDR in Phase 1. After performance matching, the variability in lever pressing during Phase 2 was evenly distributed across all four groups. All rats also acquired the audiovisual stimulus as a CDR in Phase 2, as indicated by the higher number of presses on the active lever, as compared to the inactive lever. Based on the results of the reevaluation test, reexposure to the CDR after a single devaluation treatment was necessary to observe a

subsequent suppression of lever pressing. Those rats in group Paired without Reexposure did not demonstrate suppression, and pressed at rates similar to rats in the Unpaired group. Rats in group Two Paired, who were reexposed during the devaluation session rather than the day after, showed similar suppression of lever pressing as compared to the Paired Reexposure group. Additionally, a similar pattern of suppression was observed during the reacquisition test. During the first block of reacquisition, rats in groups Unpaired and Paired without Reexposure pressed more than rats in the Paired Reexposure or Two Paired groups.

Unlike in the pilot study and Experiment 1a, there was no evidence of a decrease in active lever pressing from Session 1 to Session 2. While the lack of extinction in Phase 2 could be due to correcting procedural errors of Experiment 1a and using younger rats, suppression ratios for the reevaluation test were calculated the same way. In order to calculate these suppression ratios, we used the number of active lever presses from Session 1 of Phase 2.

While the pattern of response suppression among groups supports the need for reexposure to the devalued outcome, there was no evidence of overt devaluation through a decrease in nose poke duration. A decrease in nose poke duration for groups which have received paired devaluation, regardless of whether they were reexposed, is a common finding in studies which support the reexposure effect (Balleine & Dickinson, 1991). However, in Experiment 1b, there were no group differences in nose poke durations during the reevaluation test. In fact, all groups showed little suppression of nose poking during the reevaluation test as compared to Phase 2, before devaluation occurred. The nose poke durations of rats in Experiment 1a showed that rats in groups Unpaired and Paired Reexposure spent more time in the food magazine than rats in groups Paired without Reexposure and Two Paired. These results do not provide complete support for overt devaluation because group Paired Reexposure should

have also spent less time in the food magazine. The lack of a solid finding of overt devaluation through reduced nose poke duration could be due to the removed nature of the CDR. Previous research examining devaluation and the boundaries of hedonic shift theory used primary reinforcers as outcomes, such as food. Rather than a primary reinforcer, our study devalued an audiovisual stimulus, which held no biological significance prior to training. Parkinson et al. (2005) found reduced nose poking when the primary reinforcer with which the CDR was paired was devalued, but the CDR continued to support the acquisition of new behaviors. Consequently, the lack of nose poke suppression could be a unique finding of devaluation studies using CDRs.

8. General Discussion

These experiments aimed to address gaps in the research in two ways. Firstly, we wanted to determine whether a CDR could be devalued. Secondly, we wanted to evaluate the generality of hedonic shift theory by using reinforcers other than food and devaluation procedures that did not involve illness. The results of Experiment 1b indicated that 1) devaluation of reinforcer which was not primary or food-related does show a reexposure effect, and 2) the continued potency of the CDR was needed to maintain instrumental responding.

The results of both experiments indicated that a CDR can be devalued when paired with a single shock. This is in direct contrast to the maintenance of conditioned responding in the presence of the second-order CS after US devaluation (Holland & Rescorla, 1975; Rescorla, 1973; 1974). Those findings indicated that responding in the presence of a second-order CS is not dependent on the current value of the US. Repeated pairings of the second-order CS and the CS-CR during training created a type of S-R reflexive responding, such that responding during the second-order CS does not retrieve representations of the first-order CS or the US. The

second order CS-CR associative structure is consistent with the finding that complete extinction of the first-order CR does not eliminate responding to the second-order CS (Rescorla, 1979). Similar to the removed nature of the second-order CS from the US, Parkinson et al. (2005) demonstrated that acquisition of a stimulus as a CDR is also resistant to devaluation of a US. After pairings of a light CS and food, the food was devalued with illness, and subsequent CRs (i.e., magazine approaches) in the presence of the light CS were also extinguished. Although Pavlovian responding in the presence of the light CS was suppressed, the light was still able to function as a CDR to support the acquisition of lever pressing. Like the second-order CS, the results of Parkinson et al. (2005) demonstrated that the value of the CDR as an outcome is not dependent on the current value of the US with which it was paired. The documented resistance of second-order CSs and CDRs to outcome devaluation are prime examples of the ability of a single stimulus to possess both inhibitory first-order properties and excitatory second-order properties (Holland & Rescorla, 1975; Rescorla & Solomon, 1967). Rescorla (1973) described the duality of some stimuli in a procedure of Pavlovian aversive conditioning. In first-order conditioning, the subject learns that the presentation of the first-order CS was followed by a painful stimulus. In second-order conditioning, however, the subject learned to fear the second-order CS without having a detailed memory of the painful US. Similarly, in the case of instrumental conditioning, the subject responds not for the CDR because it retrieves the memory of the food itself, but because it incites a general state of appetitive arousal (Rescorla & Solomon, 1967; Parkinson et al., 2005). Thus, acquisition of the light CS as a CDR is attributed to the rats' memory of "feeling good" during the presence of the CS, rather than a detailed memory of the CS as a predictor of the devalued US.

Previous research examining the resistance of second-order CSs and CDRs to outcome devaluation implies that the associative structure of the CDR is not dependent on the continued potency of the primary reinforcer, but our results indicate otherwise. Rats in Experiment 1b demonstrated diminished instrumental responding after a single pairing of the CDR and shock. Additionally, they demonstrated resistance to reacquire the response when the CDR was delivered, a replication of findings from traditional outcome devaluation studies (Balleine & Dickinson, 1991). If instrumental responding for the CDR was based on the activation of a general arousal from previous Pavlovian training and the current value of the primary reinforcer, then instrumental responding should have been maintained at similar rates for pre- and post-devaluation.

It is possible that devaluation of the CDR in Experiment 1b was the result of a form of mediated conditioning, whereby the CDR activated an experience of the original US (CDR-US) that was paired with the shock during Phase 3 (Holland, 1981; Garcia, 1989). However, if this were the case, then one would also expect to see a decrease in nose poke duration for the paired groups, which we did not get in Experiment 1b. Instead, rats in all groups showed equal amounts of time spent in the feeding niche for pre- and post-devaluation. Given the failure to replicate a suppression of magazine approaches for the US (Balleine & Dickinson, 1991), our results do not say for certain whether the value of the primary reinforcer was altered by devaluation of the CDR. However, when looked at through the lens of hedonic shift theory, our results do imply that responses acquired via a CDR as an outcome are sensitive to the current value of the CDR.

Beyond exploring the associative structure of the CDR, we were also interested in testing the generality of the hedonic shift theory. Do evaluative conditioning and incentive learning occur when the devaluation procedure involves outcomes which are not food and aversive

stimuli which do not involve nausea or gastric reactions? According to Garcia (1989), activation of a nutritive (e.g., disgust) system via consummatory behaviors is the only way to process the affective value, and changes to the affective value, of a stimulus. Therefore, because our devaluation procedure did not use illness and did not devalue food, suppression of instrumental responding should have been observed for all paired groups, regardless of whether or not they were reexposed to the CDR. The observed lack of suppression in the Paired without Reexposure group in Experiment 1b is in direct contrast to the prediction of hedonic shift that the reexposure effect is specific to conditioned taste aversion procedures. Because reexposure to the devalued CDR was needed to produce a suppression in responding, both the affective and incentive value of the CDR were changed. The pairing of the CDR and shock resulted in a change in the affective value of the CDR from appetitive to aversive, and the reexposure to the CDR updated its incentive value based on the changed affective value. Our results provide evidence of the generality of hedonic shift theory beyond conditioned taste aversion procedures. They also imply that affective processing may occur with motivational systems other than those that are nutritive, such as with skin-defense systems.

The results of Experiment 1a, however, were inconclusive. This may have been the result of temperature fluctuations during the experiment, and possible age-related differences in learning and performance. In both rats and humans, ageing is directly related to decreases in cognitive functioning such as memory (Burk et al., 2002; Gallagher & Colombo, 2005; Haider et al., 2014) and in decreased functionality of goal-directed behavior due to decreased motivation (Okuda, Roozendaal, & McGaugh, 2004; Van der Staay, 2002). Research has demonstrated that older rats (typically aged 18-24 months) perform worse than young rats (typically aged 3-6 months) on behavioral tasks of both short-term and long-term memory, and on well-documented

Morris Water Maze and elevated plus maze tests (Burk et al., 2002; Gallagher & Colombo, 2005; Haider et al., 2014). The prefrontal cortex is involved in determining the incentive value of stimuli which are the outcomes of goal-directed behavior (Gallagher, McMahan, & Schoenbaum, 1999) and in learning about changes in the value of the outcome (Bentosela & Mustaca, 2003), and aged rats have demonstrated prefrontal cortex deficits (Bentosela et al., 2006). While we did use rats aged one year in Experiment 1a, they were still outside the age range for what are considered old rats in typical studies. One year old rats fall within the middle-aged range, neither young, nor old. There have also been age differences demonstrated between young and middle-aged rats. Specifically, Bentosela et al. (2006) demonstrated age differences in young and middle-aged rats in a reward devaluation paradigm. In addition to age-related retrieval failures of reward devaluation, there is evidence to suggest that the aversive state incited by the devaluation is less intense in older rats (Wood, Daniel, & Papini, 2005). These findings indicate that the inconclusive results of Experiment 1a were possibly influenced by age-related deficits, such as failure to retrieve the initial or changed incentive value of the CDR, and a less intense aversion state caused by the devaluation itself.

Although the results of the reevaluation test in Experiment 1b supported a hedonic shift of the value of the CDR, the failure of the Paired without Reexposure group to resist reacquisition of the CDR was not anticipated. Hedonic shift theory posits that, once the outcome is reexposed, an aversion is substantiated which is resistant to extinction. Because the CDR was made contingent upon lever pressing during reacquisition, it was predicted that the Paired without Reexposure group would decrease lever pressing after the first delivery of the CDR. Instead, the Paired without Reexposure group maintained responding at levels comparable to the Unpaired group. The nature of this experiment was largely novel, and it is unknown whether the

behavior of the Paired without Reexposure group is a replicable finding of hedonic shift theory. We expect that the failure of the Paired without Reexposure group to show a reexposure effect during re-acquisition is due in part to the length of time between devaluation and reexposure. Rats in group Paired Reexposure were reexposed 24 hours after devaluation, while rats in group Paired without Reexposure did not experience the reexposure of the CDR until 72 hours later. Balleine & Dickinson (1991) also found that a long delay between devaluation and reexposure did not result in suppression of instrumental responding. Additionally, it has been demonstrated that devaluation procedures facilitated via taste potentiation result in more graded response suppression than traditional conditioned taste aversion procedures (Garcia, 1989; Holland, 1981). Because our experiment used a stimulus which was not a primary reinforcer, it is likely that the effects of the devaluation are weaker, and more subject to decrement over time.

A common procedure in studies analyzing hedonic shift theory, and devaluation in general, involves training two different instrumental responses with two different outcomes (Colwill & Rescorla, 1985; Rescorla, 1991). By training two different responses with two different outcomes, the interpretation of the results of devaluation are stronger than if just using one instrumental response and one outcome. If only using one instrumental response and outcome, any subsequent decrease in instrumental responding could be explained by the pervasive effects of the devaluation, or by contextual conditioning. While our experiments did have the advantage of using two different experimental responses, we did not deliver two different outcomes contingent on these responses. In Phase 2, rats were presented with two levers, positioned to the left and right of the feeding niche. One of these levers, the active lever, resulted in the delivery of the audiovisual stimulus. The other lever, the inactive lever, resulted in no outcome, and was thus neutral. More responses on the active lever as compared to the inactive

lever was our criterion for successful acquisition of the audiovisual stimulus as a CDR. Future research could use separate outcomes on different levers to extend the current findings.

It is possible that more activity on the active lever could also be due to some primary reinforcing effects of a discriminable stimulus change, or the primary reinforcing effects of lights or tones themselves. The illumination of a light as a reinforcer has also been examined (Barry & Symmes, 1963; Goodrick, 1970; Lockard, 1963; Roberts, Marx, & Collier, 1958). The stimulus-change hypothesis states that responses which result in discriminable changes maintain or increase the probability of those responses occurring again (Goodrick, 1970). Studies examining the stimulus change hypothesis typically have an instrumental response which produces a distinct change in the context, such as a lever press which results in the onset or offset of a light (Lockard, 1963). When responding on a preferred lever produced the illumination of an overhead floodlight, rats switched to the unpreferred lever (Barker et al., 2010). Goodrick (1970) trained two groups of rats with two different levers. One of the levers was active, and resulted in either an intermediate light onset or light offset. The other lever was inactive, and did not result in an outcome. The active lever was preferred because it produced a discriminable change (Goodrick, 1970). One could argue that our criterion for successful acquisition of a CDR (i.e., more responses on the active lever) is not due to the pairing of a previously arbitrary audiovisual stimulus. Experiment 1a and 1b used a seminal procedure of conditioned reinforcement, the new-response method (Olausson, Jentsch, & Taylor, 2004; Sosa, Valerio dos Santos, & Flores, 2011; Williams, 1994). The new-response method of conditioned reinforcement pairs an arbitrary stimulus with a primary reinforcer, such as food, and then demonstrates acquisition of a new response which produces the arbitrary stimulus. Although there is evidence that a light can serve

as a primary reinforcer, our study met all of the requirements for creating a CDR using the new response method (Parkinson et al., 2005; Sosa et al., 2011).

Our results largely lend support to a hedonic shift of the affective value of the CDR from appetitive to aversive. A procedure that shares similarities with that of Experiment 1a and 1b is that of counterconditioning, a process by which naturally emitted responses by an aversive US are modified when paired with an appetitive US or primary reinforcer (Pearce & Dickinson, 1975). For example, when shock is repeatedly paired with food, the CR of dogs shifts from jumping to salivation. Rather than acting as an aversive US, the shock became an appetitive CS, which generated a CR which signaled the expectancy of food (Erofeeva, 1921). The modification of an aversive UR to an appetitive CR is attributed to dual activation of positive and negative central motivational systems (Gray, 1975; Konorski, 1967; Miller, 1963; Rescorla & Solomon, 1967). Appetitive stimuli selectively activate the positive system, and aversive stimuli activate the negative system. These motivational systems parallel those typically described in hedonic shift theory (Garcia, 1989; Balleine, 2001). The difference between hedonic shift theory and counterconditioning is how they view activation of these motivational systems. According to hedonic shift theory, an effective devaluation treatment (e.g., a conditioned taste aversion procedure) pairs the food with an aversive motivational system (e.g., a disgust system). When the food is encountered again, it no longer activates a positive motivational system (Garcia, 1989). Explanations of counterconditioning, however, posit that counterconditioning creates a stimulus which is dually activated by these positive and negative systems (Pearce & Dickinson, 1975). Both counterconditioning and outcome devaluation involve altering responses from a change in the affective properties of a stimulus. However, while hedonic shift asserts that a change in affective value occurs along a continuum, counterconditioning attributes the response

modification to the stimulus acting as both an appetitive CS and an aversive US. It could be argued that pairing the CDR and shock in Experiment 1a and 1b did not serve to devalue the CDR itself, but instead established the CDR as an aversive CS for shock. Pearce & Dickinson (1975) reported additional evidence supporting this possibility, such that aversive USs of high intensity can block the dual activation of the appetitive system following counterconditioning. In that sense, because we used a strong shock (1 ma for 4 sec) for our devaluation treatment, the subsequent suppression of responding observed in the reevaluation test could be attributed to a higher activation of the negative system, from the intense shock, which overrode the activation of the positive system by the CDR's prior association with food (Pearce & Dickinson, 1975).

The results from the current experiment inform this prediction. We only observed suppression of responding in the Paired Reexposure and Two Paired groups. If the devaluation treatment served to establish the CDR as an aversive CS for shock, then rats in the Paired without Reexposure group should have also suppressed responding in both the reevaluation and reacquisition tests. However, it could be the case that counterconditioned stimuli also require reexposure. Further, traditional studies of counterconditioning involve multiple pairings of the aversive and appetitive US (Pearce & Dickinson, 1975). By this logic, the Two Paired group should have demonstrated more suppression than either of the Paired groups, but there were in fact no differences in responding between the Paired Reexposure and Two Paired groups. Finally, counterconditioning is not supported by the results of our study given the rapid recovery of responding typically demonstrated in counterconditioning studies (Cuenya et al., 2015; Pearce & Dickinson, 1975). The counterconditioning literature does suggest some additional research which may elucidate the nature of the devalued CDR. For example, if the CDR is both an appetitive and aversive CS then manipulation of contextual cues or other variables (e.g.,

reinstatement) would be expected to selectively activate different behavioral effects of the CDR. If the CDR has experienced a hedonic shift, these procedures would be expected to have very little effect.

The results of Experiment 1b indicated that devaluation of a CDR with a painful shock did not result in response suppression until the rats were reexposed to the conditioned reinforcer. Our demonstrated reexposure effect indicates that our devaluation treatment resulted in a change of the affective properties of the CDR from appetitive to aversive. To our knowledge, this is the first demonstration of reexposure effect with a CDR, and with a devaluation treatment that involved a painful stimulus rather than nausea. Our findings are in contrast to the assertion that hedonic shift can only occur with nausea-inducing illness. A painful shock resulted in the activation of a motivational system which updated the affective value of the CDR. Because our aversive stimulus was not nausea, the shock could not have activated the gut-defense system (Garcia, 1989; Provenza, 1995). Thus, the gut-defense system is not the only motivational system which results in the affective processing of stimuli. It is possible that activation of the skin-defense system results in affective processing of distal cues in much the same way that the gut-system does with taste cues. It is also possible that affective processing occurs via activation of general appetitive and aversive systems which generate different responses based on the type of stimulus presented. Overall, our results provide support for the generality of hedonic shift theory beyond procedures which produce conditioned taste aversions.

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PRESENTATIONS

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Elliott, C. R. E., Cleland, L. M., Willie, C., White, J. P., & Leising, K. J. (2018). *Emotion Labeling with Visual Stimuli: The Effects of Physiological Responses on Conditioning*. Poster presented at the Comparative Cognition Society Spring Conference, Melbourne, FL.

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ABSTRACT

OUTCOME DEVALUATION OF A CONDITIONED REINFORCER: HEDONIC SHIFT VS. SIGNALING PERSPECTIVES

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Outcome devaluation occurs when an appetitive stimulus (e.g., food) is paired with a painful stimulus (e.g., shock), and results in a suppression of responses elicited by the appetitive stimulus (Adams & Dickinson, 1981). Hedonic shift theory states that response suppression occurs from a change in the affective value of the outcome from appetitive to aversive. Subsequent response suppression is not observed until the outcome is contacted again. Contrarily, signaling theory states that the affective value of the outcome does not change, but instead the outcome acts as a predictor for illness, and reexposure is not needed for the suppression of the response (Balleine & Dickinson, 1991). The current study investigated whether a conditioned reinforcer, initially paired with food and subsequently paired with a painful shock, would exhibit the same devaluation and reexposure effects. Rats reexposed to the conditioned reinforcer subsequently pressed the lever less than rats that were not reexposed. These results reveal that a conditioned reinforcer can be devalued, and that hedonic shift occurs beyond conditioned taste aversion procedures.