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TRANSFER BETWEEN CONSUMMATORY AND ANTICIPATORY TASKS

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABBREVIATIONS

μl	microliter
ACC	anterior cingulate cortex
ACTH	adrenocorticotropic hormone
BNST	bed nucleus of the stria terminali
CDP	chlordiazepoxide
CeA	central nucleus of the amygdala
cm	centimeter
CR	continuous reinforcement
CS	conditioned stimulus
cSNC	consummatory successive negative contrast
dB	decibel
DPDPE	[d-pen2,d-pen5]encephalin
GABA	gamma-aminobutyric acid
h	hour
HPA	hypothalamic-pituitary-adrenal
ICR	immediate continuous reinforcement
Ip	intraperitoneal
iSNC	instrumental successive negative contrast
kcal/g	kiolocalorie per gram
M	mole
mg	milligram
min	minute

mPFC	medial prefrontal cortex
Nlx	naloxone
NMDA	n-methyl-d-aspartate
NST	nucleus of the solitary tract
PbN	parabrachial nucleus
PBS	phosphate buffer saline
PDR	partial delay of reinforcement
PDREE	partial delay of reinforcement extinction effect
PFC	prefrontal cortex
PR	partial reinforcement
PRAE	partial reinforcement acquisition effect
PREE	partial reinforcement acquisition effect
RHA	Roman High-Avoidance
RLA	Roman Low-Avoidance
s	second
Sal	saline
SEM	standard error of the mean
VLO	ventrolateral orbital cortex
VPM	ventral posteromedial nucleus of the thalamus

Incentive Relativity

Mammals demonstrate changes in behavior when an obtained reward deviates from the expected reward received under similar conditions. In Tinklepaugh's (1928) early research involving unexpected changes in incentive, a monkey was trained to select one of two cups. One cup hid a piece of either lettuce or banana while the other was empty. In this instance, the banana was the preferred of the two incentives, but, if the monkey was hungry, it would eat the lettuce. During training trials, the monkey could watch an experimenter place the food reward, banana or lettuce, under one of the two cups. The experimenter would then lower an opaque screen for a retention interval of a few seconds and, once the screen was raised, the monkey could choose between the two cups and consume the hidden food if the correct choice was made. During occasional test trials, the experimenter would place a banana under the cup, but would then switch the more preferred incentive, the banana, with the less preferred lettuce leaf while the screen was lowered. This switch was unknown to the monkey. When the screen was raised and the monkey could retrieve the food reward, discovering the lettuce had replaced the expected banana would often lead to searching under the cup, presumably for the missing banana. Occasionally, the monkey would shriek in apparent anger and leave the lettuce leaf uneaten. The rejection of the less preferred lettuce reward is best understood by assuming that the monkey had formed an expectation of a more preferred reward, the banana, and finding the less preferred reward, the piece of lettuce, had violated this expectation.

Elliot (1928) reported similar effects with rats trained in a complex maze. In this study, the two rewards were wet cereal, the preferred incentive, and sunflower seeds, less preferred (but still acceptable) incentive. Rats were first trained to complete a maze with either the wet cereal reward or sunflower seeds placed in the goal box. Acquisition was faster with the wet cereal than

with the sunflower seeds. The wet cereal animals were then unexpectedly downshifted to receive the less favorable sunflower seeds in the goal box. During subsequent trials, downshifted animals took longer to complete the maze and made more errors compared to animals that had always received the sunflower seed reward. Elliot (1928, p. 29) concluded that the animals "had learned to expect a specific reward," and attributed the increase in running time and errors to searching for the missing reward.

Tinklepaugh's and Elliot's experiments involved changes in the qualitative value of rewards, but changes in the quantitative value of rewards produce similar effects on behavior. Crespi (1942) manipulated the magnitude of rewards (grams of food) in a runway procedure. In this study, rats exhibited significant reductions in running speeds when downshifted from a large reward to a small reward, compared to unshifted controls. Conversely, when animals were shifted from a small reward to a large reward, they appeared to show faster running speeds compared to their preshift running speed (although Crespi did not include an unshifted large reward control group in this study). Crespi referred to these effects as "depression" and "elation," respectively, and proposed that these behavioral changes were due to emotional responses triggered by violations of reward expectancies.

These findings suggested the Thorndikian view (Thorndike, 1911), that reward magnitude directly affects associative strength without itself being represented (i.e., stimulus-response theory), was insufficient to explain the observed behavioral changes. Such Thorndikian view suggested a gradual adjustment of behavior to the reward downshift, rather that the exaggerated "depression effect" observed in these experiments. Instead, these results prompted the idea that reward magnitude influences incentive motivation, affecting behavior independently of learning (Flaherty, 1996), and that the value of a current incentive needed to be viewed in

relation to the value of expected incentives (Crespi, 1942). Crespi's early research later led to Flahtery's (1996) definition of incentive relativity, which suggested an animal's behavior with a given reward is based on the animal's prior experience with different rewards of differing amount or qualities and the animal's comparison between the different rewards. The notion of incentive relativity suggests that incentives are not simply valued in terms of their own properties (their absolute value), but also in relation to the value of other incentives (Flaherty, Krauss, Rowan, & Gibson, 1994).

The terms "positive contrast" and "negative contrast" were first coined by Zeaman (1949) in reference to the behavioral changes that occurred when increasing and decreasing, respectively, the magnitude of a cheese reinforcer in his runway experiments. When a cheese reinforcer was reduced from 2.4 g to 0.6 g for traveling down a runway, Zeaman found that animals took significantly longer to reach the goal compared to animals that had previously reached asymptotic latencies while rewarded with 0.6 g of cheese per trial (negative contrast). Likewise, when animals were upshifted from a small reward to a larger reward, they took significantly less time to reach the goal compared to the asymptotic latencies of animals that previously received the large reward (positive contrast). Here the term "contrast" refers to the comparison of reward values, and "positive" and "negative" refer to the direction of the shift in reward value (whether the change was upward or downward). Bower's (1961) later research added the terms "successive" and "simultaneous" into the contrast repertoire. Successive contrast refers to instances in which different incentives are presented across two separate phases of training; this procedure usually involves only a single shift, as in the rat studies described thus far. In simultaneous contrast, animals receive both reward values within the same session, but in different contexts. Bower trained rats to run toward a large reward in a black runway and toward

a small reward in a white alley, thus causing the formation of reward size expectancies in the two contexts (large in black and small in white). He then compared the latencies to reach the goal for each context against animals that received the same reward (large or small) regardless of context, and found that animals that had been trained to discriminate between the two alleys ran faster in the alley associated with the large reward and slower in the alley associated with the small reward compared to the respective control groups. These effects are known as positive and negative simultaneous contrast, respectively.

Elliot (1928), Crespi (1942), and Zeaman (1949) measured the behavior of animals that were moving toward and searching for the incentive, and are thus referred to as instrumental successive negative contrast (iSNC). Vogel, Mikulka, and Spear (1968) devised a model of SNC based on consummatory behavior (cSNC). In this study, rats were given daily access to a 32% sucrose solution for 5-min trials for 11 days (preshift), and were then downshifted to a 4% solution for 6 trials (postshift). The downshift from a higher concentration of sucrose to a lower concentration produced significantly fewer licks than control animals that received only 4% sucrose throughout the study. The reduction of the licking response was acute on the first trial of downshift, but over subsequent trials, the downshifted animals began to show a recovery of their previous consummatory behavior, until, eventually, they did not differ from the unshifted control group. Figure 1a illustrates the cSNC effect.

Flaherty (1996) described the downshift phase as occurring in two stages (see Figure 1b). Stage 1 occurs on the first downshift trial, when the animal detects the change in incentive value, rejects the new incentive, and engages in searching behavior to either find the missing, preferred incentive or to escape/avoid the less desirable incentive. Stage 2 occurs during the subsequent daily trials following the initial downshift. During Stage 2, an animal experiences a conflict

between the tendency to approach the new incentive because deprivation gives it some value, and to avoid the new incentive because it is less than the expected one.

Amsel's (1992) model offers a more detailed account of the processes that characterize Flaherty's (1996) multistage model (see Wood, Daniel, & Papini, 2005). First, in a typical cSNC experiment, the animal forms an expectation of 32% sucrose when in the training context. Second, when first presented with the less preferred downshifted solution, the animal detects the discrepancy between the expected 32% solution and the obtained 4% solution. This requires recognizing that the current solution is different from the memory of the solution received in the past. Third, the animal reacts to the less preferred solution by rejecting it and this leads to an emotional response (i.e., frustration).

In addition to Flaherty's (1996) multistage theory and Amsel's (1992) model, Papini (2003) proposed that during a downshift experience, two different types of learning and memory formation are taking place. When the animal first detects the change in incentive value that occurs on the first trial (or session) of downshift, the negative discrepancy between expected and received rewards results in the development of an emotional memory. This process is called egocentric learning because it encodes the animal's negative reaction to the reward downshift. But additionally, every interaction with the new, downshifted reward results in a memory update of the reward representation. This process is referred to as allocentric learning because it encodes information about the rewarding stimulus.

These theoretical developments (e.g., multistage model, frustration theory, and egocentric/allocentric memory) are a tool to interpret the effects of various types of environmental and neurobiological manipulations on SNC effects. I start with a description of the neurobiological basis of the cSNC effect.

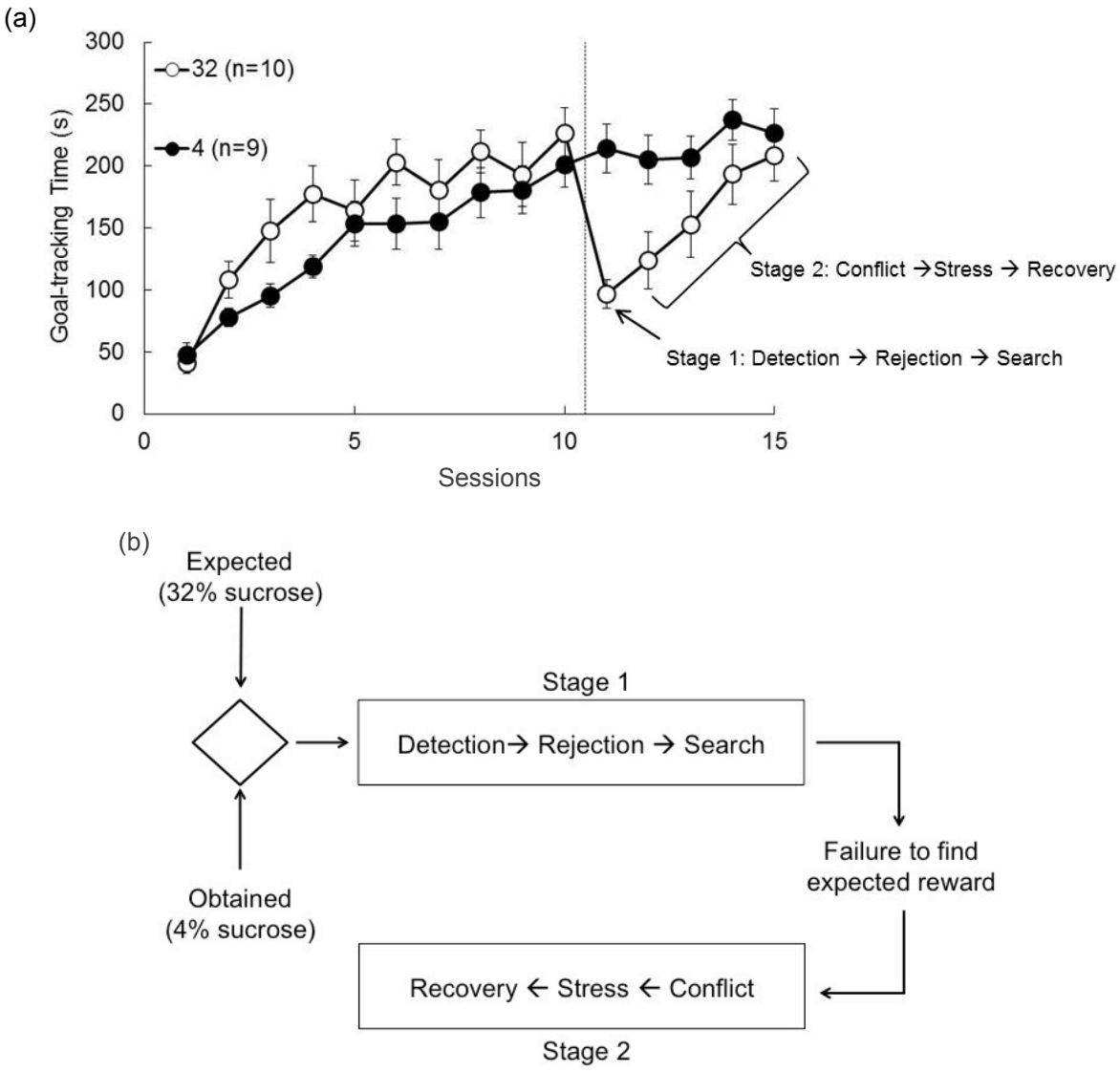

Figure 1: (a) Example of cSNC obtained by averaging the performance of animals from an experiment where both groups were treated with saline injections immediately following Session 11 and after a 3 h delay (date from Ortega et al., 2014). The dependent variable is the cumulative time in contact with the sipper tube, goal-tracking time, expressed in seconds (error bars are ± SEM). (b) A schematic representation of Flaherty's (1996) multistage model of cSNC. The main components are the comparison of expected and obtained rewards (represented by the diamond shape) and the two stages that follow.

Factors Affecting Incentive Downshift

Psychopharmacology

Pharmacological manipulations have been extensively used to examine the neural basis underlying cSNC. The main conclusion from these studies is that some drugs have session-selective effects, that is, they affect cSNC when administered before one specific session. It was the session selectivity of some drugs (e.g., benzodiazepine anxiolytics) that led Flaherty (1996) to suggest the multistage model for incentive downshift (Figure 1). Some of the drugs that have been found to modulate incentive downshift and tap on relatively selective classes of receptors are: hormones, anxiolytics, opioids, and the memory enhancer D-cycloserine.

Stress hormones. Corticosterone and the adrenocorticotropic hormone (ACTH) are stress hormones of interest when examining the cSNC paradigm. Corticosterone has been widely associated with both acute and chronic stress responses (e.g., McEwen, 2007). It is produced in the adrenal cortex, a component of the hypothalamic-pituitary-adrenal (HPA) axis (Herman, 2009). The release of corticosterone is controlled by ACTH, which is produced in the anterior pituitary gland, which, in turn, is modulated by the hypothalamus. The HPA axis is a key mechanism that allows for behavioral and physiological adjustments in response to relatively intense environmental challenges (Pecoraro & Dallman, 2009). Stress hormones have a variety of effects, including acting on membrane receptors in the pyramidal cells of the hippocampus in the areas of CA1 and CA2 and on the granule cells of the dentate gyrus, neurons of the central nucleus of the amygdala, cerebellar Purkinje neurons, cortical pyramidal neurons, and parvocellar neurons of the hypothalamic paraventricular nucleus (Rossie, Jaychandran, & Meisel, 2006).

Two avenues of research provide evidence for stress hormones being involved in cSNC. The first line of evidence involves hormone levels as a dependent variable. Several researchers (Flaherty, Becker, & Pohorecky, 1985; Mitchell & Flaherty, 1998; Pecoraro, de Jong, & Dallman, 2009) reported that plasma levels of corticosterone and ACTH were higher in rats undergoing cSNC compared to animals in the unshifted control group after Session 11 and before and after Session 12. Flaherty and colleagues' (1985) earlier work suggested that corticosterone was selectively released on Session 12, but not on Session 11. However, Pecoraro et al.'s (2009) more recent work provided evidence that corticosterone levels peak after the first downshift session and then decrease after the second downshift session. There were some procedural differences that may account for the discrepancy in results obtained between these studies.

Flaherty and colleagues (1985) and Mitchell and Flaherty (1998) conducted the cSNC testing in a separate apparatus rather than in the animals' home cage, as did Pecoraro et al. (2009). Previous research (Daniel, Wood, Pellegrini, Norris, & Papini, 2008) suggests that cSNC boxes may have served as a predictor for the delivery of 32% sucrose and therefore may have weakened the HPA axis outflow, for the first session of downshift, and then became a predictor of a less valuable incentive, the 4% sucrose, thus enhancing the HPA axis outflow for the second session of downshift. Pecoraro et al. (2009) tested the predictive context hypothesis in two ways: (1) by testing the animals in their home cages vs. a separate cSNC apparatus, and (2) by using distinctive contexts which predicted whether or not sucrose would be delivered. Both tests yielded the same results: ACTH and corticosterone levels were higher on the first downshift session and decreased after the second downshift session. Moreover, although the external context can be manipulated to yield a cSNC effect, contextual control over licking is rather weak

(Daniel et al., 2008). Also, Pecoraro et al. (2009) employed a 12-session preshift period with 5.5-min sessions as opposed to a 10-session preshift and 5-min sessions used in the other studies (Flaherty et al., 1985; Mitchell & Flaherty, 1998). Perhaps the prolonged preshift period provided a more stressful downshift experience in the Pecoraro et al. (2009) study. Therefore, it is not yet possible to determine whether corticosterone and ACTH release during cSNC is session selective, but it is clearly released during an incentive downshift experience. Such release also has implications for the rate of recovery from cSNC, as shown by the studies reviewed next.

The second line of evidence linking corticosterone to cSNC involved its administration immediately after Session 11 (i.e., as an independent variable). Corticosterone receptors are found in high densities in the limbic system (see above) as well as in the medial prefrontal cortex (mPFC; Sousa, Cerqueira, & Almeida, 2002), and while acute exposure to corticosterone can aid in learning, chronic or repeated exposure to corticosterone can lead to profound maladaptive behavior and memory impairment (Cai, Blundell, Han, Greene, & Powell, 2006). The experiments reviewed here involved acute corticosterone administration and, thus, were concerned with the memory-enhancing effects of this hormone.

Postsession 11 (i.e., acute) administration of corticosterone resulted in prolonged consummatory suppression in later sessions (Bentosela, Ruetti, Muzio, Mustaca, & Papini, 2006). Interestingly, this effect was observed in successive, but not anticipatory contrast; after a large, 32-to-4% sucrose downshift, but not a small, 8-to-4% sucrose downshift; and it could not be explained in terms of conditioned taste aversion (Ruetti, Justel, Mustaca, & Papini, 2009). Importantly, Postsession 11 administration of corticosterone affected the behavior of downshifted animals, but not the behavior of unshifted controls. These results suggest that corticosterone facilitates the encoding of an emotional memory of the frustrative reaction

(Ruetti et al., 2009), as it is known to do in other aversive situations (McGaugh, 2000; Roozendaal, 2000). Thus, the spontaneous release of stress hormones after the initial downshift event may function to enhance memory retrieval in subsequent sessions.

Testosterone. Testosterone is an androgen steroidal hormone secreted primarily in the testes (the testicles of males and the ovaries of females), and secreted in small amounts by the adrenal glands (Mooradian, Morley, & Korenman, 1987). Sexual behavior elicits an anxiolytic-like effect in the cSNC situation. Copulatory experience 20 h and immediately before an unexpected downshift, 32-to-4% sucrose, attenuated the cSNC effect (Freidin, Kamentexky, & Mustaca, 2005). Because copulatory experience is known to enhance testosterone release, Justel and colleagues (2012a) explored the hypothesis that testosterone has anxiolytic-like properties in the cSNC situation. In this study, animals were systemically pretreated with testosterone six days prior to the start of testing and then again before the first session of downshift and through the subsequent sessions following the downshift (Sessions 11-15). The results demonstrated that animals treated with testosterone showed a reduced cSNC effect on the first downshift session (Session 11) and a shorter recovery period compared to control animals. Interestingly, testosterone's attenuating effect appears to be limited to cSNC. When animals were treated similarly in a cANC paradigm, a situation known to be insensitive to the effect of anxiolytics (Flaherty, 1996), testosterone had no effect on behavior.

A second study conducted by Justel and colleagues (2012b), investigated the effects of testosterone on gonadectomized animals. In this study, gonadectomized animals were trained in a typical cSNC paradigm and testosterone (or a vehicle) was administered before Session 5 and continued until Session 15. Results were similar to those previously reported. Gonadectomized animals that had been treated with testosterone demonstrated a reduced cSNC effect and had a

faster recovery, relative to vehicle controls. These results are similar to those to be discussed next for benzodiazepine anxiolytics.

Anxiolytics. Two classes of anxiolytics proved effective in reducing cSNC: benzodiazepine anxiolytics and ethanol. Both act on GABA (gamma-aminobutyric acid) receptors located throughout the brain. GABA receptors are found in high concentration in the cerebral cortex, hippocampus, thalamus, basal ganglia, cerebellum, and brainstem (Young & Chu, 1990). There are two subtypes of GABA receptors: $GABA_A$ and $GABA_B$. Benzodiazepines and ethanol are allosteric neuromodulators that enhance the $GABA_A$ receptor activation when GABA is simultaneously bound to the receptor.

Neither benzodiazepines nor ethanol affect cSNC when administered before the first downshift session (usually Session 11), but they both reduce the cSNC effect when administered before the second downshift session (Session 12; Flaherty, 1996). These results suggested that the GABAergic system is activated during Flaherty's (1996) Stage 2 (see Figure 1b). To explain the session selectivity of benzodiazepine anxiolytics, Flaherty (1996) hypothesized that after the cSNC effect occurs, an endogenous recovery process is triggered involving $GABA_A$ receptors. To test whether the benzodiazepine chlordiazepoxide (CDP) is ineffective on the first downshift session because the GABA circuit has not yet been activated, Flaherty (1996) injected muscimol, a direct GABA agonist, into the lateral ventricles of rats before Session 11, followed by a systemic injection of CDP. Animals that received both muscimol and CDP treatments showed no signs of the cSNC effect on Session 11, whereas animals that received only CDP showed significant signs of the cSNC effect on that session. These results are consistent with the hypothesis that GABAergic activity needs to be present in order for the benzodiazepine anxiolytics to reduce the cSNC effect.

Flaherty and colleagues further explored the GABAergic activation hypothesis in terms of presession CDP administration. In one study, the duration of the first postshift session was extended from the typical 5 min to a 20 min session (Flahtery, Grigson, & Rowan, 1986). Results revealed that while CDP did not affect consummatory behavior during the first 5 min of the session, it did reduce cSNC during the second 5 min period. In turn, this suggests that after the first 5 min of access to the downshifted solution, the GABAergic system is activated and thus the administration of CDP helps to modulate the negative effects of cSNC. Additionally, in order to further investigate the effects of presession CDP administration, animals were exposed to a series of eight downshifts throughout cSNC training. Results revealed that presession CDP administration was ineffective during the first three downshifts, but became increasingly effective at reducing cSNC for the fourth downshifts and then eliminated cSNC following the fifth and subsequent downshifts (Flahtery, Clark, & Coppotelli, 1996)

Ortega, Glueck, Daniel, White, and Papini (2014) found, through a series of experiments, that CDP has a dual effect on cSNC depending on the timing of administration. When CDP is administered immediately after the first downshift session (Session 11), it enhanced the cSNC effect on subsequent sessions, whereas administration prior to the second downshift session (Session 12), as mentioned above, leads to a reduction of the cSNC effect. This dual effect of CDP raises several questions.

First, why did Presession 12 administration of CDP lead to a reduction of cSNC, whereas Postsession 11 CDP administrations enhance cSNC? One possible explanation was that the administration of CDP immediately following the first session of downshift inadvertently induced a conditioned taste aversion to the downshifted (4%) solution. However, no evidence supporting this hypothesis was found. Another explanation suggests that postsession CDP

administration was disrupting allocentric memory--the memory update process involving learning about the new, downshifted solution. This explanation is consistent with the selective effects of Postsession 11 CDP. Such treatment affects consummatory behavior only in the presence of a recent downshift experience. This was demonstrated by Ortega and colleagues when administered CDP in the absence of a downshift experience in animal exposed to 32% and 4% sucrose solution, and in animals that had CDP administration following a complete recovery from cSNC. These results suggest that $GABA_A$ receptors play a complex, time-dependent role in cSNC. Presession, CDP leads to anxiolytic effects without effecting memory and only affects consummatory behavior when the animal has had previous downshift experience (i.e., Session 12), but postsession CDP administration modulates memory consolidation. It was hypothesized that the administration of CDP after Session 11 interfered with the formation of the allocentric memory of the new downshift incentive, 4% solution (i.e., memory update).

D-cycloserine and other memory enhancers. N-methyl-D-aspartate (NMDA) receptors are generally thought of as the classic learning and memory receptors because of the way they are activated (Riedel, Platt, & Micheau, 2003). NMDA receptors are ionotropic channels with a voltage-dependent magnesium channel blocker. These receptors have a primary binding site for including glutamate, but also contain modulatory binding sites, such as a site for glycine. Channel opening requires the simultaneous binding of glutamate and intracellular depolarization to release the magnesium block. Calcium influx can initiate a cascade of intra-celluar signaling pathways involved in memory consolidation (Petrenko, Yamakura, Baba, & Shimoji, 2003).

Memory consolidation is a time-dependent process and can be best assessed by postsession pharmacological administration (McGaugh, 2002). Because drug administration occurs after training, the drug does not directly affect behavior during testing. Additionally,

subsequent behavioral testing typically occurs the day following drug administration, after the drug has been metabolized. Thus, the effects of the drug can be assumed to be related to memory consolidation, rather than to motivation, motor control, or attention.

Norris, Ortega, and Papini (2011) tested the memory enhancing effects of D-cycloserine in the cSNC paradigm and found that when it was administered after Session 11, it enhanced the aversive memory of the downshifted reward and retarded the typical recovery process from the downshift. Similar results were found when D-cycloserine was administered prior to Session 11. Interestingly, the effect was specific to the aversive downshift memory, as it did not disrupt consummatory behavior in the unshifted control animals. Moreover, D-cycloserine's effect on cSNC could not be explained in terms of conditioned taste aversion.

Norepinephrine is also thought to have a role in the modulation of aversive memories via the amygdala (McGaugh, Ferry, Vardarjanova, & Roozendall, 2000). Unlike norepinephrine's apparent role in aversive memory modulation, Flaherty's (1996) review of some published and unpublished findings suggested that cSNC is resistant to adrenergic manipulation. There was no detectable effect on cSNC when either α- or β-adrenergic receptors were antagonized. This suggests a difference in the neurochemical mechanisms of aversive procedures such as passive avoidance and cSNC. The aversive memory consolidation following passive avoidance learning is modulated by the manipulation of norepinephrine levels, via epinephrine administration, and by postsession administration of opioids (Izquierdo & Dias, 1983, 1985). There is no evidence that either of these drug classes modulate cSNC (for opioids, see: Daniel, Ortega, & Papini, 2009; for catecholamines, see: Flaherty, 1996).

Based on previous research on passive avoidance (Taylor, 1990) and on iSNC (Salinas, 1997), it was predicted that cholinergic neurotransmission would be involved in the memory

consolidation of reward loss, which occurs during cSNC. Bentosela, D'Ambros, Altamirano, Muzio, Baratti, and Mustaca (2005) administered a cholinergic antagonist (atropine) and an acetylcholinesterase inhibitor (physostigmine) immediately after the first downshift session (Session 11) and immediately after the last preshift session (Session 10), in different experiments. They reported no detectable effects of any of these treatments on subsequent postshift sessions. Thus, there is no evidence that cholinergic neurotransmission is involved in memory consolidation processes in the cSNC situation.

Opioids. Opioids are neuroactive peptides that bind to four G-protein coupled receptor types: mu, delta, kappa, and ORL-1 (Papini & Ortega, 2011). These receptors are widely, but differentially distributed in the mammalian brain (Mansour, Fox, Akil, & Watson, 1995; Sim-Selley, Vogt, Childers, & Vogt, 2003).

Nonspecific opioid receptor agonists and antagonist have been found to modulate both stages of Flaherty's (1996) model. Specifically, cSNC was attenuated when morphine, a nonselective opioid-receptor agonist (with somewhat greater affinity for mu receptors), was administered prior to Sessions 11 or 12 in the downshifted animals only (Rowan & Flaherty, 1987). However, this effect was only observable when used in low to moderate doses (0.5 to 8.0 mg/kg); at larger doses (16 mg/kg) morphine also depressed consummatory performance in unshifted control animals. Additionally, the attenuating effect of morphine was eliminated when the nonselective competitive opioid antagonist naloxone (also exhibiting greater affinity for the mu receptor) was coadministered, thereby blocking opioid receptors. Interestingly, Rowan and Flaherty (1987) reported no discernible effects of naloxone when administered alone. However, it was later discovered that naloxone did affect contrast when administered at a higher dose (Pellegrini, Wood, Daniel, & Papini, 2005). Moreover, rats that showed a slower rate of recovery

from reward downshift also demonstrated a higher sensitivity to naloxone administration before an activity test compared to animals that experienced a faster rate of recovery.

Papini (2009) hypothesized that the results of blocking opioid receptors could be attributed to four potential processes: (1) modulation of the downshift experience via an amplification of the rejection process or by reducing the incentive value of sucrose; (2) disruption of downshift detection process; (3) enhanced consolidation of the memory of the downshift event; and (4) induction of a conditioned taste aversion to the downshifted solution. Daniel, Ortega, and Papini (2009) tested the detection, memory consolidation, and taste aversion hypotheses with the following conclusions.

Previous research revealed that sucrose solutions with equal discrepancy ratios yield similar levels of consummatory suppression during cSNC, despite differences in the absolute values of concentrations involved in downshift (Papini & Pellegrini, 2006). For example, consummatory behavior was roughly equivalent after 32-to-4% sucrose or 16-to-2% sucrose downshift, both involving an 8-to-1 change in sucrose concentration. However, when naloxone was administered prior to the first downshift session, it shifted the comparison from a ratio-based to a difference-based comparison. Thus the drug effect was more pronounced the larger the difference between sucrose concentrations (i.e., 32-4 > 16-2). These results suggest that opioid receptors modulate the comparison of current and expected incentives triggered by the incentive downshift. Thus, when the antagonist blocked the opioid receptors, the consummatory suppression was enhanced as a direct function of the absolute difference between the preshift and postshift solution concentrations.

Additionally, and as mentioned above, Daniel and colleagues (2009) found that the postsession administration of naloxone had no detectable effects on subsequent sessions, not

only in the cSNC situation, but also in appetitive extinction of lever-pressing behavior. These results provided no evidence that opioid receptors play a part in memory consolidation of the incentive downshift event. Daniel et al. (2009) also reported that naloxone administration failed to induce conditioned taste aversion to a novel 4% sucrose solution under conditions similar to those used in cSNC experiments, but without the downshift event. These results allowed for the tentative rejection of the memory consolidation and taste aversion hypotheses. More research is still needed to examine the role opioids potentially play in the amplification of the rejection and/or the reduction of the incentive value of sucrose.

There is evidence suggesting that specific opioid receptors are involved in the different stages of Flaherty's (1996) multistage theory. Wood, Daniel, and Papini (2005) administered the selective delta opioid receptor agonist [D-Pen2,D-Pen5]encephalin (DPDPE) prior to Sessions 11 or 12 in the cSNC paradigm. DPDPE reduced consummatory suppression followed administration prior to Session 11 (first downshift session), but had no effect when administered prior to Session 12 (second downshift session). To investigate the role of the delta opioid receptors further, naltrindole, a selective delta receptor antagonist, was administered prior to Sessions 11 and 12 with the expected result of enhancing the suppression of consummatory behavior on Session 11, but having no effect on Session 12 (Pellegrini et al., 2005). These results support the hypothesis that Stage 1 of Flaherty's theory of the rejection process selectively involves the delta opioid receptor. Thus far, DPDPE and naltrindole are the only pharmacological agents known to selectively modulate behavior during the first downshift experience (Pellegrini et al., 2005; Wood et al., 2005).

The second stage of Flaherty's theory can be pharmacologically manipulated by administering drugs immediately after Session 11 and prior to Session 12.

Wood, Norris, Daniel, and Papini (2008) reported that kappa opioid receptors are differentially involved in the modulation of Stage 2. When U-50,488H, a kappa opioid receptor agonist, was administered prior to Session 11 or 12, no drug effects were detected for Session 11, but a complex, dose-dependent effect occurred on Session 12. A low dose (1 mg/kg) attenuated cSNC while higher doses (3 and 10 mg/kg) enhanced cSNC. When a 3 mg/kg dose of U-50,488H was administered immediately after Session 11, cSNC was enhanced. However, when the low dose of 1 mg/kg was administered, no effect was observed. The enhancing effects of the 3 mg/kg dose of U-50, 488H were eventually explained as a drug-induced condition taste aversion to the 4% solution. These results suggested that kappa opioid receptors are involved in the conflict and recovery stage of cSNC, but only when agonized with low doses.

Brain Areas Involved in Incentive Downshift

Sucrose is detected by the taste receptors in the tongue and this information then travels along cranial nerves VII (facial), IX (glossopharyngeal), and X (vagus) to brainstem nuclei related to gustatory information and consummatory behavior (e.g., licking). The nucleus of the solitary tract (NST) is considered the first area in the brainstem to receive ascending projections from the periphery and the first area of central relay for taste information (Norgren, 1995). The parabrachial nucleus (PbN) receives ascending information from peripheral gustatory receptors, via the NST, and then sends signals via ascending fibers, which make synaptic connection in the bed nucleus of the stria terminalis (BNST).

Structures within the brainstem have been demonstrated to modulate cSNC. Rats that received bilateral electrolytic lesions to the PbN failed to demonstrate cSNC (Grigson, Spector, & Norgren, 1994). Variables that measured the licking behavior in animals during both preshift and postshift phases suggested the elimination of cSNC was not due to a disruption of

motivational, memory, or reward comparison factors. However, the decreased frequency of licking behaviors in lesioned animals compared to sham animals potentially suggests PbN might be involved in motor control. Additionally, abrupt suppression of responding to savory solutions following PbN lesions (e.g., Reilly & Trifunovic, 2000) may affect the interpretation of the role the PbN plays in cSNC. Rats with PbN lesions showed less consummatory behavior for the 32% solution during preshift, thus potentially affecting the comparison between pre- and postshift sucrose concentrations. The central nucleus of the amygdala (CeA), lateral hypothalamus, and gustatory cortex modulate the gustatory processing of sucrose solutions in the PbN (Lundy & Norgren, 2004). The PbN is heavily connected to the CeA, an area that seems to be vital for cSNC (Becker et al., 1984; more on this structure later). Grigson et al. (1994) suggested that a PbN lesion reduces the hedonic value of the preshift sucrose reward following a reward downshift; such hedonic value would depend on the interaction between the PbN and forebrain areas, such as the CeA.

Additionally, the PbN sends taste information to the ventral posteromedial nucleus of the thalamus (VPM), also known as the gustatory thalamus, which is considered the last central relay area of taste information before reaching the cortex (Norgren, 1995). Bilateral electrolytic lesions of the VPM eliminated cSNC (Reilly & Trifunovic, 1999), and this elimination did not seem to be related to the processing of the downshift memory or the absolute value of the sucrose rewards (Reilly & Trifunovic, 2000). Therefore, it seems plausible that VPM lesions led to a disruption of the reward comparison mechanism (memory of the preshift solution vs. postshift solution) triggered by the downshift event. Additionally, this comparator role of the VPM seems specific to sucrose solutions or to cSNC because chemical lesions of this area had no measurable effect on iSNC using food pellets as reward (Sastre & Reilly, 2006).

Lesions to the septal area yielded impairments in response inhibition (e.g., Dickinson, 1972; Donovick, 1968; McClearly, 1961); because cSNC involves a reduction in consummatory behavior, these results suggested that septal lesions should also attenuate the cSNC effect (Lombardi & Flaherty, 1978). Conversely, septal lesions also have been shown to enhance the rejection of bitter solutions, such as quinine solutions (Beatty & Schwartzbuam, 1967, 1968). To the extent that a downshifted sucrose solution is rejected, these results suggest that septal lesions might enhance the cSNC effect. Interestingly, Flaherty and Hamilton (1971) revealed that neither was the case, and it was hypothesized that, perhaps, these opposite effects cancel each other out. However, additional studies using similar lesions yielded a disruption of the cSNC effect, relative to sham controls, when a retention interval (4 days vs. 1 day) between the last preshift session (Session 10) and the first postshift session (Session 11) was introduced (Flaherty, Powell, & Hamilton, 1979). These results suggest the septal area may be critical in the reactivation of the memory of the preshift reward or in the mechanism involved in reward comparisons. The lack of an effect of septal lesion under typical cSNC parameters indicates that further research is needed to understand the role of this area.

Previous research involving inhibition deficits following hippocampal lesions, also suggested that cSNC would be similarly reduced, as in the case of septal lesions (Gray, 1982). The data for this particular brain area have yielded mixed results. Some research suggests that hippocampal lesions have no effect on cSNC (Kramarcy, Mikulka, & Freeman, 1973; Flaherty, Rowan, Emerich, & Walsh, 1989), while Murphy and Brown (1970) reported that hippocampal lesions eliminated cSNC. There are, however, some noteworthy procedural differences between these studies that could account for the discrepancies in the results. In the Murphy and Brown (1970) study, animals were subjected to several other behavioral tests (i.e., sucrose preference

test and two sodium depletion tests) prior to undergoing cSNC. Therefore, it is possible that this prior experience changed the animal's response to reward downshift in the cSNC situation. Likewise, Flaherty and colleagues (1989) implemented a 10 day preshift period rather than the 18 day preshift utilized by the other two studies; however, it is unlikely this was a pertinent factor given the similar the procedures and contradictory results reported by Murphy and Brown (1970) to those of Kramarcy and colleagues (1973).

There were also differences in the hippocampal areas targeted by the lesions. For instance, Murphy and Brown's (1970) aspiration lesions where larger and often extended to cortical tissue as well as the hippocampus, while still sparing the ventral tips of the hippocampus. However, Kramarcy et al. (1973) restricted their radio-frequency lesions to the dorsal hippocampus and had minimal cortical damage. Flaherty et al. (1989) used the neurotoxin colchicine to damage hippocampal granule cells. This procedure spared most of the cortex from damage. The conflicting results of these hippocampal lesion studies suggest that additional research is needed in order to better understand the role, or lack thereof, the hippocampus plays in cSNC.

When investigating emotional responses, the amygdala is one of the most studied structures. Previous research has revealed that lesions of the amygdala result in impairments in emotional learning (Cardinal, Parkinson, Hall, & Everitt, 2002). This coupled with the knowledge that the amygdala has high densities of opioid and GABA receptors (Mohler & Okada, 1977), and based on the effects that opioids and benzodiazepines have on cSNC (Flaherty, 1996; Papini, 2009) makes the amygdala a reasonable target for investigating its role in incentive downshift. Previous research has revealed ablation lesions to the basolateral amygdala significantly reduce the cSNC effect, whereas lesions to the corticomedial amygdala,

which included the CeA, eliminated cSNC (Becker, Jarvis, Wagner, & Flaherty, 1984). While these previous studies lend support to the hypothesis that the amygdala plays a prominent role in cSNC, the specific function has not been clearly identified based on the boundary conditions not being fully explored. Our lab has recently found (Kawasaki, Glueck, Annicchiarico, & Papini, in press) that reversible lidocaine lesions in the centromedial amygdala attenuated cSNC, while having no noticeable effects in unshifted controls. Additionally, this study showed that similar inactivation of the centromedial amygdala had no effect on anticipatory contrast, while increasing overall ambulatory behavior in an open field paradigm. These results confirm the previous view that the amygdala plays an important role in reward devaluation, specifically when the devaluation involves a negative emotional component. While cSNC is suspected of involving a negative emotional response (Papini, 2003, 2014; Papini, Fuchs, & Torres, 2015), supported by findings that consummatory suppression is accompanied by the release of stress hormones (Mitchell & Flaherty, 1998; Pecoraro et al., 2009) and endogenous opioids (Papini, 2009), anticipatory contrast does not seem to be accompanied by negative affect (Flaherty, 1996).

Additional support for the role of the amygdala in cSNC is provided by significant changes in cellular activation following an incentive downshift from 32% to 4% sucrose. Pecoraro and Dallman (2005) found increased c-Fos expression, a marker of cellular activity, following the first downshift session in the amygdala. Additionally, our lab more recently reported elevated levels of pCREB, a marker for neural plasticity (Kida & Serita, 2014), following the first session of downshift (Glueck, Dennis, Perotti, Torres, & Papini, 2015) in the central nucleus of the amygdala.

The role of the prefrontal cortex (PFC) in incentive downshift situations has also been examined. The PFC is a highly differentiated area with a variety of behaviorally relevant functions (Uylings, Groenewegenb, & Kolb, 2003). Chemical lesions to the insular cortex completely eliminated the cSNC effect, resulting in a gradual reduction of performance in downshifted animals until, eventually; consummatory behavior did not differ from that of the controls (Lin, Roman, & Reilly, 2009). Additionally, animals that received medial prefrontal cortex (mPFC) lesions performed similarly to unlesioned animals on the first session of downshift, but later showed greater sucrose consumption during the second half of an extended postshift phase (12 sessions; Pecoraro, de Jong, Ginsberg, & Dallman, 2008). However, there were no differences in a second reward downshift using the same animals. Unfortunately, no unshifted controls were included in this study, which makes it difficult to determine whether the effects of the mPFC lesions were related to the downshift event or to sucrose consumption in general. Interestingly, when an unshifted control group was included in the design (Ortega, Glueck, Uhelski, Fuchs, & Papini, 2013), there were no effects of mPFC lesions on cSNC, although lesioned animals in the unshifted control exposed only to 4% sucrose demonstrated reduced consummatory behavior throughout the experiment.

Additionally, Ortega and colleagues (2013) performed bilateral electrolytic lesions of either the ventrolateral orbital cortex (VLO) or the mPFC and exposed animals to two different incentive downshift situations: cSNC and partial reinforcement in an autoshaping situation. In this study, animals were first trained in a typical cSNC paradigm and then underwent autoshaping training under either a continuous or a partial reinforcement schedule. Animals with VLO lesions showed a significantly reduced cSNC effect on the first session of downshift (Session 11) during the last 100 s of the session. VLO lesions also eliminated the partial

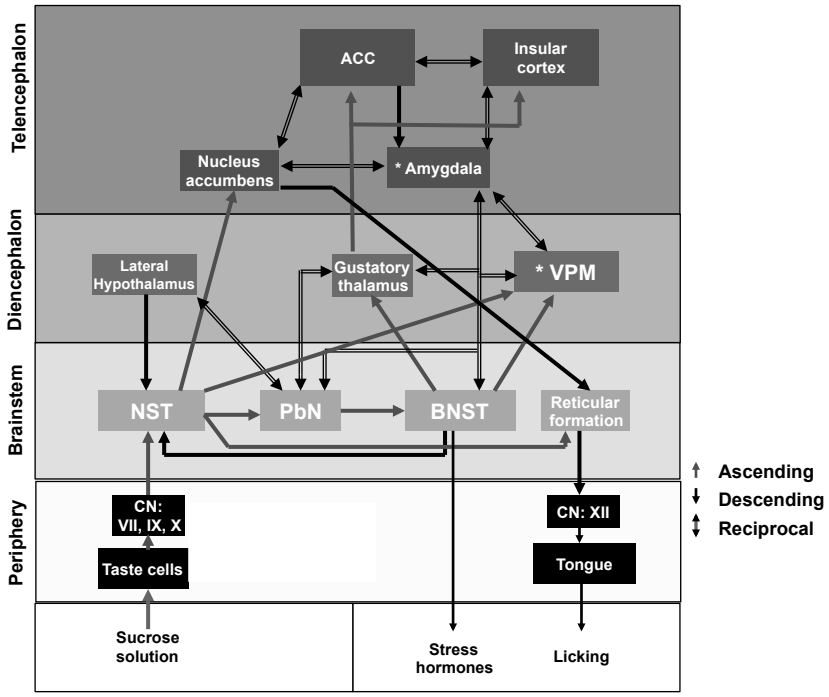

Figure 2. Brain areas involved in incentive downshift. Modified from Jones, Fontanini, and Katz (2006). *: Potential sites for reward comparisons (obtained vs. expected) in cSNC.

reinforcement acquisition effect (PRAE) during autoshaping training. The PRAE involves higher response level for the partial reinforcement condition than for the continuous reinforcement condition during acquisition sessions. These two effects of VLO lesions are consistent with a reduction in emotional activation.

Finally, the anterior cingulate cortex (ACC) has previously been implicated in reward expectations and is known to reduce iSNC in a runway situation (Gurowitz, Rosen, & Tessel, 1970). Ortega and colleges (2011) examined the effects of bilateral electrolytic lesions of the ACC on cSNC. The lesions had no effect on the preshift performance, the unshifted control group, or on the first session of downshift (Session 11), but animals with ACC lesions demonstrated retarded recovery during subsequent sessions (Sessions 12-15). Interestingly,

further examination of the first 100 s of postshift sessions revealed that animals with ACC lesions demonstrated the cSNC effect earlier that sham-lesioned animals. Similar within-session analyses have been used to uncover subtle effects that are masked by pooled data for the entire trial (see Ortega, Uhelski, Fuchs, & Papini, 2011; Norris, Daniel, & Papini, 2008; Norris, Ortega, & Papini, 2009). These results suggest that the ACC is involved in learning about the newly downshifted reward, a learning that would aid in the recovery process by reducing or eliminating the negative discrepancy between expected and obtained incentive values.

Figure 2 summarizes the results reviewed in this section on the neurobiological basis of the cSNC effect.

Frustration Theory

As mentioned above, Amsel's (1992) frustration theory provides a detailed account of the mechanisms activated by the incentive downshift in the cSNC situation (Papini, 2003; Wood et al., 2005). Frustration theory is based on the notion that an aversive emotional reaction is triggered when an animal experiences a negative discrepancy between an expected reward and the presentation of a lesser reward, as in incentive downshift, or a nonreward, as in appetitive extinction. According to Amsel, this negative discrepancy triggers an unconditional, internal emotional state, called *primary frustration*. An association then develops between external cues and the animal's internal state of primary frustration. The product of this association is the aversive anticipatory state of *secondary frustration*.

Primary frustration is assumed to have several properties. First, the unconditional reaction to a frustrating event is drive inducing and typically leads to a temporary increase in responding in both Pavolvian (Dudley & Papini, 1995; Papini & Dudley, 1997) and instrumental (Hall & Marr, 1969; Stout, Boughher, & Papini, 2003) situations. This energizing effect (called

the frustration effect) was illustrated in the instrumental procedures utilized in Hall and Marr's (1969) double runway study in which rats received different reward magnitudes depending on the alley runway they were being trained. The results revealed that rats ran faster after being downshift to a smaller reward compared to their running speeds in an unshifted control alley. Likewise, Dudley and Papini (1995) demonstrated the energizing property of primary frustration using a Pavlovian procedure in which rats were exposed to lever-food pairings proceeded immediately before by either light-food or food-only trials in different groups. In this study, animals lever pressed at higher rates when lever-food trials were preceded occasionally by light-only trials (greater surprise because of the light signal previously paired with the reward) than when lever-food trials were preceded by food omission (less surprising because there was no specific signal for the reward). That is, rats lever pressed more after nonreinforced trials in the group in which the light signaled food presentation than in the group in which food was unsignaled (i.e., food omission was more surprising in the former than in the latter group). Using this procedure, previous research reported similar results after the surprising omission of a sucrose solution and after a reward reduction (5-to-1 pellet downshift), rather than reward omission (Dudley & Papini, 1995). Similar effects were observed immediately after reward omissions in an instrumental situation (Stout et al., 2003). In both situations, Pavlovian and instrumental, an increase in the length of the interval between the omission and the opportunity to respond led to a reduction of the frustration effect, suggesting that the frustration effect is short lived.

Secondary frustration results when stimuli associated with primary frustration begin to trigger an expectation of frustration (Amsel, 1992). The anticipatory effect results from an association between the stimuli that previously predicted a high value reward being paired with

the internal state of primary frustration. As the animal learns about its own emotional response to the downshifted incentive, its egocentric memory is updated and the animal comes to anticipate the aversive emotional state of secondary frustration. Eventually the cues become ambiguous by activating the conflicting expectations of reward and frustration. This discrepancy results in an approach-avoidance conflict. The animal is motivated to both avoid the frustrating experience and approach the reward. Secondary frustration may also lead to a persistence of behavior when paired with reward. The pairing of secondary frustration and reward leads to the development of tolerance to frustration through the process of *counterconditioning*. Counterconditioning may lead to a hedonic shift of secondary frustration from an aversive to an appetitive state. As counterconditioning occurs there is a hypothesized reduction of the approach-avoidance conflict, which interferes with the drinking behavior. However, as the animal's allocentric memory of the new incentive is updated, the discrepancy between the expected and obtained incentive is reduced and primary frustration is weakened, therein promoting the consummatory behavior. This, in turn, results in an increase in behavioral persistence (i.e., goal approach) as the disruptive effects of secondary frustration are reduced. This is best illustrated in terms of the partial reinforcement extinction effect (PREE). Animals that were previously trained under a partial reinforcement schedule demonstrate greater resistance to extinction, illustrated by persistence in lever-pressing behavior, compared to animals trained under a continuous reinforcement schedule (e.g., Boughner & Papini, 2006).

Frustration Theory and cSNC

Amsel's (1992) frustration theory has been applied to cSNC in the following manner (see Papini, 2003; Wood, Daniel, & Papini, 2005). Frustration theory assumes during the preshift phase of cSNC (Session 1-10 in a typical cSNC experiment), animals form an expectation of

obtaining the 32% sucrose solution when drinking in the context of the cSNC box. The context of the cSNC box (whether this is the box itself, the front wall of the box with the hole for the sipper, fluid in the mouth, or some combination), in turn, triggers the drinking response. On the first downshift session (Session 11), when the animal detects the surprisingly reduced reward, the discrepancy between the expected 32% to the actual 4% solution is detected. This detection is followed by an unconditional, internal, aversive state of primary frustration, presumably leading to rejection of the downshifted solution and search for the missing reward. An association then develops between external cues of the cSNC context and the internal state of primary frustration leading to the aversive anticipatory state of secondary frustration (egocentric learning). At this point, the cSNC context has the ability to trigger both approach and avoidance of the sipper tube. Through subsequent pairings of secondary frustration and the less valued 4% sucrose incentive, two dissociable processes are induced that contribute to recovery from reward downshift. First, the appetitive reinforcement while under the state of frustration (primary, secondary, or both) leads to the counterconditioning of frustration, which reduces the avoidance/rejection component of the conflict, thus promoting recovery from cSNC. This counterconditioning mechanism is central to the type of transsituational transfer of tolerance to frustration that was investigated in the present dissertation. Second, experiencing the new 4% sucrose solution triggers new learning. Through this process of memory update (allocentric learning), the reward expectation is adjusted to the new incentive value. Both conflict reduction via counterconditioning and the update of the expectation of the old incentive (32% sucrose) to the new one (4% sucrose) contribute to the recovery of consummatory behavior during subsequent postshift sessions (see Figure 3). The memory update process was inferred from the effects of memory interfering manipulations that prolonged the cSNC effect, including lesions of the ACC (Ortega et al., 2011)

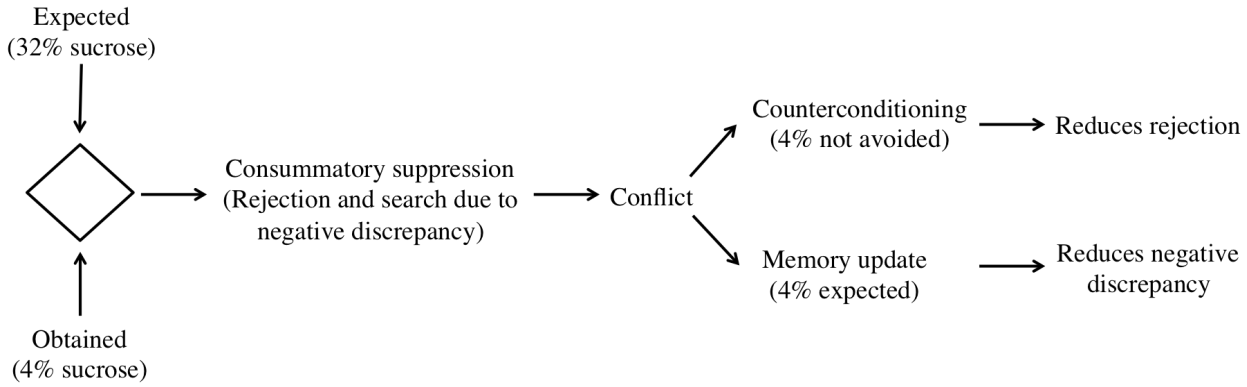

Figure 3. Amsel's (1992) frustration theory applied to cSNC. Recovery from the downshift is explained as resulting from two potentially distinguishable processes, one reducing rejection (counterconditioning) and the other reducing the negative discrepancy (memory update during allocentric learning).

and postsession 11 administration of CDP (Ortega et al., 2014). How could the second factor, counterconditioning, be demonstrated?

Transfer of Tolerance to Frustration

According to Amsel's (1992) frustration theory, once an animal undergoes counterconditioning of secondary frustration then any situation that induces an internal state of secondary frustration, regardless of the context in which it is induced, should support approach behavior. This associative triggering of an approach response is the basis of the transsituational transfer of tolerance to frustration. A counterintuitive prediction of Amsel's (1992) theory suggests that such a transfer of tolerance to frustration would occur in novel contexts even if no counterconditioning had occurred in that novel context, provided secondary frustration were induced.

Early research conducted by Theios (1962) and Jenkins (1962) revealed that animals that had previously undergone partial reinforcement (PR) training, demonstrated transfer that carried

through a block of continuous reinforcement (CR) training and into extinction trials. In both instances, the effects of PR training survived the intervening experience with CR training to emerge during extinction, causing increased persistence relative to groups always given CR training. Donin, Surridge, and Amsel (1967) explored a similar transfer effect by first training animals under either partial delay of reinforcement (PDR), another training procedure proven to produce resistance to extinction, or immediate continuous reinforcement (ICR). In PDR training there is a 50% mixture of two types of trials, one ending in immediate reinforcement and another ending in delayed reinforcement (i.e., interpolating a few seconds between the occurrence of the response and the presentation of the reward). Animals were then given a 90 day break or "vacation" from training, followed by a block of ICR training and finally extinction. The results revealed that animals that received PDR training demonstrated a resistance to extinction (i.e., a partial delay of reinforcement extinction effect, PDREE) compared to animal that had been previously trained with ICR. Additional research investigated the durability of transfer by first training animals under CR vs. PR (or PDR vs. ICR) schedules, extinguishing the behavior, retraining the animals under a CR schedule (reacquisition), and then running the animals through a second series of extinction sessions. Results revealed that the PREE (or the PDREE) was still present even after the first round of extinction training and CR reacquisition training (see Wong, Lee, & Novier, 1971; Traupmann, Wong, & Amsel, 1971; Amsel, Wong, & Traupmann, 1971).

Previous research investigating the transfer of tolerance to frustration has revealed that extensive exposure to surprising nonreward reduces subsequent behavioral reactions to other frustrating events, presumably through counterconditioning (Pellegrini et al., 2004; Ross, 1964). Pellegrini and colleagues (2004) found that prior exposure to PR training attenuated cSNC and facilitated the recovery process. In this study, rats were trained either under CR or PR with two

sucrose solutions: 32% or 4%, in a typical cSNC paradigm for 20 daily sessions. The PR in this experiment differed from previous experiments in that during nonreinforced trials animals were presented with distilled water rather than nonreward, additionally, animals received only one trial per day as opposed to multiple discrete trials per session. Animals in the CR condition were presented with either 32% or 4% solution (depending on group assignment) in every preshift session; the PR groups were presented with their respective solution in half the sessions (reinforced sessions) and with distilled water in the remaining 10 sessions (nonreinforced sessions). For the postshift sessions, all animals received 4% sucrose solution. Results revealed that animals in the downshift PR condition demonstrated reduced cSNC compared to the downshift CR condition. Likewise, downshifted PR animals showed faster recovery of consummatory behavior compared to that of downshifted CR animals. Amsel's (1992) frustration theory suggests that this attenuation and faster recovery from the reward downshift after PR training is the result of the counterconditioning of secondary frustration that occurred during the rewarded preshift sessions.

Additionally, this effect of PR on cSNC was eliminated when nonreinforced preshift sessions were preceded by the administration of the benzodiazepine anxiolytic CDP (Pellegrini et al., 2004), and modulated by the delta opioid receptor agonist DPDPE administered before nonreinforced preshift sessions (Wood, Daniel, & Papini, 2005). Thus, counterconditioning can be influenced via pharmacological manipulation during PR training.

Ross (1964) conducted an experiment to test whether the counterconditioing that occurs during PR in one context could be transferred to another context, even after animals had more recently undergone CR training in the second context (Table 1). In addition to changing the context, Ross' experiment involved changes in the deprivation state (food vs. water) and in the responses

required across the first and second training phases. Thus, this design pushed the idea of transfer to an extreme by varying the external (context), internal (deprivation), and behavioral (responses) components across two different phases of training. Of specific interest here is the hypothesis that "compatible" responses (e.g., running and jumping) should lead to positive transfer, whereas "incompatible" responses (e.g., running and climbing) should produce negative transfer. Positive transfer refers to increased persistence in extinction during the second task after PR training in the first task. By contrast, negative transfer refers to rapid extinction in the second task after PR training in the first task. The assumption was that counterconditioning in the first task would tend to elicit the same response during extinction in the second task, thus either retarding or accelerating extinction depending on the degree of compatibility between responses. Could extinction of the second response reflect the history of counterconditioning even after all these changes across phases? To test this hypothesis, rats were first deprived of food and trained to run, jump, or climb to obtain food as the reward at the end of a short, black, wide box under 50% PR or CR (a total of 6 groups). After completion of the first acquisition phase, animals were then deprived of water and trained to run down a long, white, narrow runway under a CR schedule to obtain water as the reward. The same response was required of all animals: running. Following this second acquisition phase, animals underwent extinction in the runway, where they had only experienced CR for water and based on the running response. Thus, from the first to the second phase, animals were trained in different apparatus (white box vs. black runway), under different deprivation conditions (food deprived vs. water deprived), with different rewards (food vs. water), and with variations in the response requirements (run, jump, or climb vs. run).

The results of the second acquisition phase revealed that the animals' prior schedule of training in the box had no effect on acquisition behavior in the runway. As predicted, however, animals

Table 1

Table describing Ross' (1964) experiment

	Phase 1: Acquisition 1	**Phase 2: Acquisition 2**	**Phase 3: Extinction**
Apparatus→	(A) Short, black wide box	(B) Long, white narrow runway	(B) Long, white narrow runway
Motivation →	Hunger	Thirst	Thirst
Incentive →	Food pellets	Water	None
Response and Schedule →	Jumping CR Jumping PR	Running CR	Running EXT
Response and Schedule →	Climbing CR Climbing PR	Running CR	Running EXT
Response and Schedule →	Running CR Running PR	Running CR	Running EXT

Note. A total of six groups participated in this experiment (three responses and two schedules of reinforcement in Phase 1). The letter in parentheses refers to the apparatus used for training. CR: continuous reinforcement. PR: partial reinforcement. EXT: extinction training.

that learned to jump or run in the box under PR demonstrated greater persistence in the extinction of running in the runway compared to CR animals. In contrast, rats that learned to climb in the box under PR showed faster extinction of running in the runway than CR animals. These results are shown in Figure 4. Frustration theory (Amsel, 1992) argues that these transfer

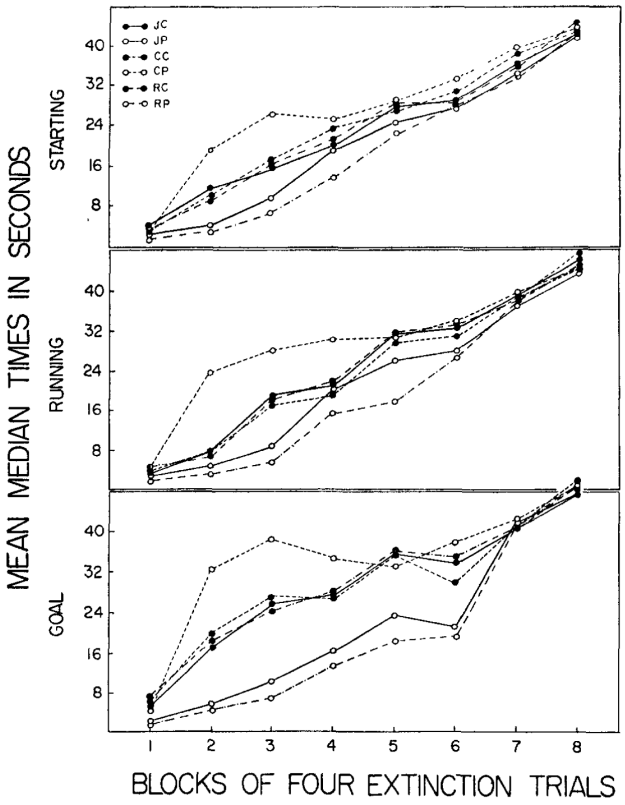

Figure 4. From Ross (1964, Figure 3): Starting, running and goal performance during extinction training (Phase 3). Notice that groups that had received continuous reinforcement (C) training in Phase 1 were not affected by the transfer manipulation. However, groups that had received partial reinforcement (P) in Phase 1 were affected as a function of the response type (e.g., jump, J; climb, C; run, R). See Table 1 for a description of the design.

effects after previous exposure to PR, even under different conditions, are the result of the counterconditioning of anticipatory frustration that occurred during the first acquisition phase of training. Such counterconditioning was then reactivated by the induction of frustration during extinction, in the second phase of training. Thus, the theory suggests that the previous counterconditioning of frustration allows for transfer across situations, internal states, and

behaviors. Whether the animal is inoculated against the disrupting effects of other frustrating events depends on the topography of the response associated to secondary frustration: Compatible responses lead to positive transfer, whereas incompatible responses lead to negative transfer.

Additionally, Cuenya and colleagues (under review) investigated the role of transfer across SNC tasks, cSNC and iSNC, in inbred Roman strains of rats. Roman rats have been selectively bred since the 1960s to exhibit either fast (Roman high-avoidance strain, RHA) or slow (Roman low-avoidance strain, RLA) avoidance learning in the two-way active avoidance situation. Strains also differ in a variety of nonselected traits. For example, RLA rats exhibit higher levels of anxiety than RHA rats in a wide range of situations (see Driscoll, Fernández-Teruel, Corda, Giorgi, & Steimer, 2009; Steimer & Driscoll, 2005; Torres & Sabariego, 2014), including cSNC and iSNC tasks (Gómez, Escarabajal, de la Torre, Tobeña, Fernández-Teruel, & Torres, 2009; Rosas, Callejas-Aguilera, Escarabajal, Gómez, de la Torre, Agüero, Tobeña, Fernández-Teruel, & Torres, 2007; Torres, Cándido, Escarabajal, de la Torre, Maldonado, Tobeña, & Fernández-Teruel, 2005). Because RLA animals demonstrate an increased sensitivity to incentive downshift, illustrated by a greater suppression of consummatory behavior in cSNC situation and by increased latency to approach the goal in iSNC tasks compared to RHA animals, it was hypothesized that only the RLA would demonstrate positive transfer, that is, an attenuation of the SNC effect in a second SNC task after having experienced an incentive downshift.

To explore the effects of transfer, animals were first trained in either a cSNC or an iSNC task, and then exposed to the opposite SNC in a counterbalanced order for the second phase of the experiment. Comparisons were then made between the behavior of animals that had first

experienced cSNC during Phase 1 and animals that had experienced cSNC during Phase 2, and vice versa for the iSNC tasks, for both RLA and RHA animals. These results revealed that while RHA animals exhibited both effects with an equal duration whether in Phase 1 (no prior experience) or in Phase 2 (exposure to the alternative task), thus yielding no evidence of transfer, prior experience affected the performance of RLA rats in both tasks. Thus, in RLA rats, exposure to one SNC task during Phase 1 either shortened or eliminated the other SNC task during Phase 2. Therefore, RLA rats showed evidence of positive transfer and the effects were symmetrical (i.e., from iSNC to cSNC and vice versa).

The results of Cuenya et al.'s (under review) suggest that consummatory and running responses share a significant degree of compatibility since the transfer was positive. Most of the research reviewed thus far has explored the transfer hypothesis utilizing anticipatory tasks (e.g., Amsel, 1992; Ross, 1964). Unlike in previous experiments, the research conducted in Cuenya et al. (under review) investigated the transfer of tolerance to frustration using a mixture of anticipatory (iSNC) and consummatory (cSNC) tasks. Papini and Pellegrini (2006) suggested that different memory processes are involved in anticipatory and consummatory contrast tasks.

During cSNC, the animal confronts the downshift solution and must decide whether it is the same or different from the memory of the preshift solution. Thus, this is a memory recognition task, according to which, during the downshift, the animal detects the current solution and this reactivates the memory of the training solution. A comparison is then made between the remembered solution and the current one, and this mismatch (i.e., recognition failure) between expected and obtained solutions leads to consummatory suppression. However, during an anticipatory task (iSNC) the animal must retrieve the emotion induced by reward loss based on a signal. This is, therefore, a cued-recall task. Therefore, the findings in this study

provide additional evidence that positive transfer is possible across two SNC tasks, despite the fact that cSNC and iSNC differ in terms of incentives (liquid sucrose vs. food pellet), response (consummatory vs. anticipatory), context (conditioning box vs. runway), types of response topography (licking vs. running), reward magnitude manipulation (qualitative vs. quantitative), and spatial demands (near vs. far goal).

Problems with transfer. The research conducted by Cuenya and colleagues (under review) and Ross (1964) supports Amsel's (1992) transfer hypothesis that predicts once an animal has experienced counterconditioning to frustration in one task, then an approach response would be triggered when the animal experiences frustration again, regardless of the task, and even if counterconditioning was never experienced in the new context. However, there is at least one piece of unpublished research that yielded results that are only partially consistent with Amsel's hypothesis.

Glueck et al. (2013) exposed animals to two incentive downshifts situations. In the first experiment, animals were run through a typical cSNC (see Figure 5a), with 10 preshift sessions and 4 postshift sessions. Following the completion of the cSNC task, animals were trained in a one-way avoidance task. For this phase of the experiment, animals that had previously experienced the downshift during cSNC, were once again exposed to downshift and the unshifted control animals, again, served as the unshifted controls. Animals were placed in a one-way avoidance chamber, consisting of two equal compartments (a black-danger and white-safe compartment). Throughout each of the four preshift sessions, animals were placed in the danger compartment, where a tone signaled the delivery of an electric shock (1 mA) that continued until the animal either moved to the safe compartment or until 30-s had elapsed. Animals in the downshifted condition were then left in the safety compartment for 40 s in each preshift trial,

before being returned to their home cages. However, they were eventually downshifted to 3 s in the safe compartment after each trial, during postshift sessions, and their performance was compared to that of unshifted controls always left 3 s in the safe compartment after each trial. Learning in the one-way avoidance task was assessed by measuring the number of trials to 5 successive avoidance responses (preshift criterion) and the number of trials to 5, 8, and 10 successive avoidance responses (postshift successive criteria).

In the one-way avoidance task, animals that are downshifted from a 40-s to a 3-s safety period require significantly more trials to reach the successive criteria during postshift sessions, compared to animals that continuously experience a 3-s duration in the safety box (see Figure 5c; Candido, Maldonado, Megias, & Catena, 1992). An interpretation of this SNC effect in the one-way situation based on frustration theory suggests that shortening the safety period is analogous to reducing reward magnitude in a food-reinforced situation. In the typical situation, approach to the safe compartment after the downshift would be disrupted by anticipatory frustration. If transfer of tolerance to frustration were to occur, then one would expect the downshifted animals in both tasks to demonstrate similar responding to the unshifted control group, during the second phase.

Animals that had previously experienced a downshift in the cSNC paradigm (Figure 5a), exhibited similar responding to that of the unshifted control animals in the one-way avoidance task in the second phase (Figure 5b) thus, previous downshift experience had produced counterconditioning of secondary frustration, leading to positive transfer in the downshift phase of the one-way avoidance task. Counterconditioning of approach in one situation (drinking) facilitated approach in the other (crossing to the safe compartment).

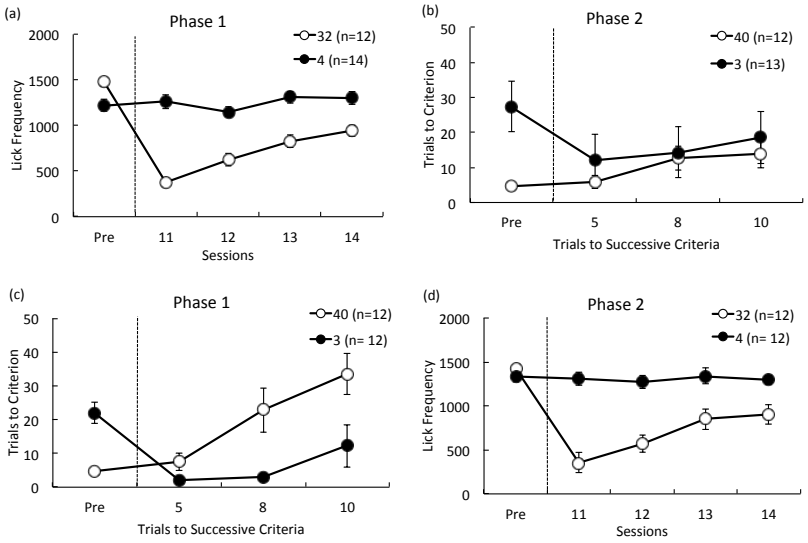

Figure 5. From Glueck et al. (2013): cSNC (*a*) followed by one-way avoidance (*b*) and the reverse, one-way avoidance (*c*) to cSNC (*d*). The dependent measure in Figure 5a and 5d is the average number of licks for each group of animals (32% and 4%) during the final preshift session and during the subsequent postshift sessions (Sessions 11-14) (error bars are ± SEMs). The dependent measure in Figure 5b and 5c is the number of trials needed to reach the successive criteria during the preshift phase (5 consecutive avoidance responses) and during the postshift phase (5, 8, and 10 consecutive avoidance responses) (error bars are ± SEMs). Animals in the downshift (40 s) condition had previously experienced a downshift from 32% sucrose solution to 4% sucrose in a cSNC paradigm, and animals in the unshifted control group (3 s) served as the unshifted (4% sucrose) controls during cSNC.

The second portion of this experiment reversed the order of the behavioral tasks, such that animals first underwent a downshift (40-3 s in the safety compartment) during the one-way avoidance task (Figure 5c) followed by cSNC (Figure 2d). In this experiment, positive transfer

would be demonstrated if animals that had previously been downshifted during the one-way avoidance task demonstrated reduced cSNC (consummatory suppression) on the first session of downshift (Session 11), followed by an attenuated recovery during the subsequent postshift sessions (Sessions 12-14). However, unlike with the opposite sequence (cSNC followed by one-way avoidance), there was no evidence of transfer during the cSNC phase (Figure 5d). Animals previously downshifted in the one-way avoidance situation demonstrated a significant consummatory suppression compared to that of the unshifted controls and their performance was indistinguishable from that of a group given cSNC training in Phase 1 (compare Figures 5a and 5d).

These results provided partial confirmation for Amsel's (1992) transfer hypothesis. Transfer of tolerance to frustration, or greater persistence, was observed in the one-way avoidance task after animals had undergone a consummatory downshift. However, contrary to Amsel's (1992) predictions, the transfer of tolerance to frustration was not bidirectional, as illustrated by the lack of transfer from one-way avoidance downshift to the cSNC situation. Amsel's (1992) transfer hypothesis predicts that if transfer of tolerance to frustration occurs in one direction (i.e., paradigm A to paradigm B), then it should also occur when reversing the order (i.e., paradigm B to paradigm A). Other researchers had found that transfer of tolerance to frustration persisted across different behaviors, incentives, motivational states (Ross, 1964) and even across long periods (Chen & Amsel, 1975). However, the symmetry issue has not been studied before even though Amsel's (1992) theory makes a clear prediction. The aim of the current research was to explore the degree of symmetry in transfer between two types of task involving reward downshifts: cSNC and lever pressing in the autoshaping situation.

Current Research

The purpose of the current research was to explore the transfer of tolerance to frustration across situations. The general strategy was to determine whether exposure to one task involving reward downshift in Phase 1 would affect the performance of animals in a second, different task also involving reward downshift in Phase 2. In most of the experiments described below, one was the cSNC task and the other was lever pressing in the autoshaping procedure. The theoretical framework behind these experiments involves the assumption that both tasks induce the development of anticipatory frustration (a conditioned state with negative emotional content), which, when paired with some amount of reward, supports the development of counterconditioning. Such counterconditioning is assumed to become associated to specific responses, thus leading to either positive or negative transfer effects depending on the extent to which the responses are compatible.

Experiment 1: Transfer from cSNC to Autoshaping Extinction

Perhaps the asymmetric results described above reflect a peculiar feature of the one-way avoidance situation, which may not lead to significant amounts of counterconditioning of approach behavior. In the one-way avoidance situation it is unclear what would be the rewarding event responsible for counterconditioning of the response of approaching the safe compartment. The first experiment investigated the transfer hypothesis (Amsel, 1992) by exposing animals to an incentive downshift in a typical cSNC paradigm (see Table 2) followed by autoshaping acquisition training under continuous reinforcement (CR) and extinction.

Based on Amsel's (1992) transfer hypothesis and Ross' (1964) previous findings, we predicted that downshifted and unshifted animals in the cSNC situation would not differ in lever-

pressing responding during CR training in autoshaping. Recall that in the Ross' (1964) study there were no differences in responding during the second acquisition phase, under CR training.

However, and also based on Ross' (1964) results, I hypothesized that animals with prior downshift experience, and the subsequent counterconditioning that presumably occurs during recovery from cSNC, would demonstrate a significant difference in extinction behavior in autoshaping compared to that of unshifted control animals, even though both groups received the same acquisition training. Because the "compatibility" between consummatory and lever pressing behavior was not known, no prediction was made as to the direction of transfer. If animals with prior downshift experience demonstrated significantly greater sensitivity to extinction training (faster extinction) compared to that of the unshifted controls, it would suggest an "incompatibility" between the consummatory and lever pressing behavior. This result would be described as negative transfer. However, if animals with prior downshift experience demonstrated greater resistance to extinction (slower extinction) compared to unshifted controls, this would suggest a "compatibility" between consummatory and lever pressing behavior. This outcome would be described as positive transfer.

Method

Subjects. Eighteen female Wistar rats, approximately 90 days old, deprived to 81-84% of their ad libitum weight, served as subjects for Experiment 1. Rats were kept within 81-84% deprivation levels by providing the appropriate amount of food each day, at least 15 min after the end of the daily training session. Animals were housed under a 12 h light/12 h dark cycle in a room that controlled for noise, and was keep at a constant temperature (22–23 $^{\circ}$C), and humidity (40-65%).

Apparatus. cSNC training took place in eight conditioning boxes (MED Associates, St. Albans, VT) constructed of aluminum and Plexiglas, and measuring 29.4 × 28.9 × 24.7 cm (L × H × W). The floor was made of steel rods 0.5 cm in diameter and 1.2 cm apart (from center to center) running perpendicular to the feeder wall. A tray filled with corncob bedding was placed below the floor to collect fecal pellets and urine. Against the feeder wall were two elliptical holes 1 × 1 cm (W × H), 3.5 cm from the floor, separated by 6.5 cm. A sipper tube, 1 cm in diameter, was inserted through the middle hole (the lateral hole for a second sipper tube was not used in this experiment). When fully inserted, the sipper tubes were flush against the outer wall of the apparatus, such that the rats could only reach the tubes with their tongues. A computer located in an adjacent room controlled the presentation and retraction of the sipper tube, and detected contact with the sipper tube via a circuit involving the steel rods in the floor. Such circuit was used to record lick frequency (the absolute number of licks made by each animal during each session) for each box. Each conditioning box was in a sound-attenuating chamber that contained a house light, a speaker that delivered white noise, and a fan for ventilation. Together, the speaker and fan produced noise with an intensity of 80.1 dB (SPL, Scale C).

Four standard operant chambers (MED Associates, St. Albans, VT) each enclosed in a sound-attenuating chamber were used during the autoshaping acquisition and extinction phase of this experiment. Each box was 20.1 x 28 x 20.5 cm (W x L x H), with a grid floor consisting of stainless steel bars 0.4 cm in diameter and spaced 1.6 cm apart (from center to center). Underneath the grid floor was a pan filled with corncob bedding. The food cup was located on the front wall of the chamber, 2 cm above the floor. Two retractable levers were located 1 cm to the right and left of the feeder, and 6 cm above the floor. Only one lever, located to the left of the magazine hole, was used in this experiment. This lever was 4.8 cm wide and when fully inserted

protruded 1.9 cm into the chamber. It took 0.2 s for the lever to be fully inserted or retracted. Pellet dispensers delivered 45-mg food pellets (Bio-Serv, Frenchtown, NJ). Each food pellet contained protein (18.8%), fat (5.0%), carbohydrate (61.5%), fiber (4.6%), ash (4.4%), and moisture (5.0%), and provided 3.68 kcal/g. The sound-attenuating chambers were equipped with a light (GE 1820) that provided diffuse illumination, a speaker that administered white noise, and a fan for air circulation. Background masking noise (speaker and fan) registered 80.1 dB (SPL, Scale C).

Procedure. Once animals had reached their deprivation weight (at approximately 96 days of age), they were matched for weight and randomly assigned to one of two sucrose solution groups: 32%, or 4%. During the preshift phase of this study, animals received 10 daily sessions of access to a 32% sucrose solution (w/w, 32 g sucrose for every 68 g of distilled water) or 4% sucrose solution (w/w, 4 g sucrose for every 96 g of distilled water), depending on the contrast condition. This was followed by 5 daily sessions in which all animals received 4% sucrose solution (postshift). Each session lasted 5 min from the first detected contact with the drinking spout. The amount of time the animal was in contact with the sipper tube (goal tracking time) was the dependent variable. Sessions were administered around the same time each day, although the order of running was varied across sessions. Goal tracking times were automatically recorded by a computer in a room adjacent to testing.

Following the final cSNC session, animals began autoshaping acquisition training. During the autoshaping acquisition training of this experiment, all animals were trained under a CR (100%) reinforcement schedule for 10 daily sessions (consisting of 10 trials per session, totaling 100 trials). In each trial, the lever was presented for 10 s. Trials were separated by variable intervals averaging 90 s (range: 60-120 s). During acquisition, each lever presentation

Table 2

Design of Experiment 1

Group	**Phase 1: cSNC**	**Phase 2: autoshaping**
32	(10) 32% → (5) 4%	(10) CR → (10) EXT
4	(10) 4% → (5) 4%	(10) CR → (10) EXT

Note. The number in parentheses refers to the number of daily sessions. 32% and 4%: sucrose concentrations. CR: continuous reinforcement acquisition training in which each trial involved a response-independent pairing of a lever presentation and food delivery. EXT: extinction training in which the lever was presented without the food.

response-independent pairing of a lever presentation and food delivery. EXT: extinction training in which the lever was presented without the food. ended with the delivery of five 45-mg precision food pellets for both groups of animals. Pellets were delivered at a rate of one every 0.2 s. A computer controlled the administration of events and recorded the number of lever-pressing responses. Although rats did not have to press the lever to obtain food, they nonetheless came to approach and make contact with the lever (a phenomenon called "autoshaping").

Once the acquisition phase was completed, all animals underwent extinction training for 10 daily sessions (consisting of 10 trials per session; totaling 100 trials). Animals did not receive any reinforcement during extinction sessions. The design is described in Table 2.

The results of all the experiments presented in this dissertation were analyzed using mixed-model analyses of variance (ANOVA) with sessions as the repeated-measure factor, and an α =0.05 level. LSD pairwise comparisons were used to determine the source of interactions. All statistical analyses were computed using the SPSS software (v. 23).

Results

cSNC. During the preshift phase, animals learned to drink sucrose solution at similar rates whether having access to 32% or 4%. A Contrast (32, 4) x Session (1-10) ANOVA yielded a significant main effect of Session, $F(9, 144) = 11.78$, $p < 0.001$. All other effects were not significant, Fs < 1.

The results of the final preshift and 5 postshift sessions of cSNC are illustrated in Figure 6a. Following downshift on Session 11, animals in the 32% group demonstrated a reduction in consummatory behavior (lick frequency) compared to that of the unshifted control group. A Contrast (32, 4) x Session (11-15) x ANOVA yielded a significant interaction, $F(4, 64) = 5.72$, $p < 0.01$. Additionally, there was a significant main effect of Session (11-15), $F(4, 64) = 8.80$, $p < 0.001$, and for Contrast, $F(1,16) = 7.25$, $p < 0.05$. The source of the significant interaction was determined by a post hoc LSD test. On the first two sessions of downshift (Session 11 & 12), the 32% animals licked significantly less compared to the unshifted 4% controls, Fs(1, 16) > 10.99, ps < 0.05.

Autoshaping acquisition. Autoshaping acquisition sessions (1-10) lever pressing responses per minute averages for animals with prior experience with 32% or 4% sucrose solutions during cSNC training are shown in Figure 6b. During the autoshaping acquisition phase, both sucrose solutions resulted in similar lever pressing behavior. A Contrast (32,4) x Session (1-10) ANOVA yielded a significant main effect of session, $F(9, 144) = 5.96$, $p < 0.001$. All other effects were not significant, Fs < 1.

Autoshaping extinction. Autoshaping extinction sessions (11-20) lever pressing responses per minute averages for animals with prior experience with 32% or 4% sucrose solutions during cSNC training are shown in Figure 6b. Extinction training resulting in animals

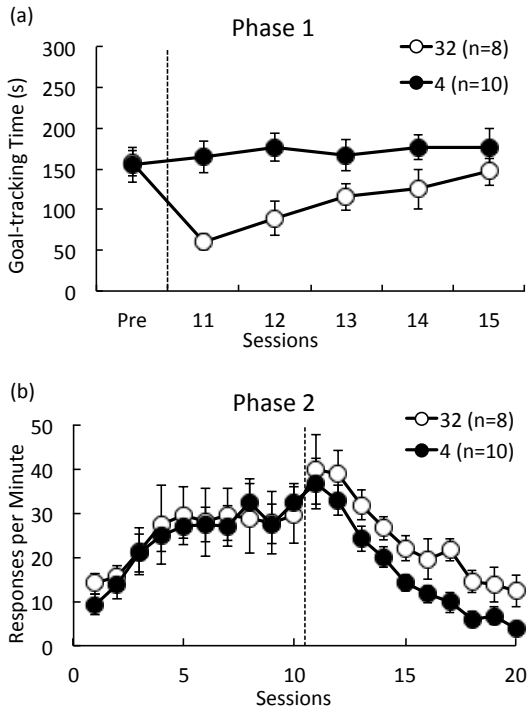

Figure 6. cSNC (*a*) followed by autoshaping acquisition and extinction (*b*). The dependent measure in Figure 6a is the group average for the cumulative time in contact with the sipper tube, goal-tracking time, for the last preshift session (Session 10) and the postshift sessions (Sessions 11-15) during cSNC, and is expressed in seconds (error bars are ±SEMs). The dependent measure in Figure 6b is the group average of lever pressing responses per minute for animals that experienced a downshift (32) during the cSNC phase and for the unshifted (4) control animals (error bars are ± SEMs). The dotted line depicts the division between acquisition (Sessions 1-10) and extinction (Sessions 11-20) training. Each autoshaping session consisted of 10 trials and animals ran one session per day.

with prior downshift experience (32) demonstrating great resistance to extinction compared with unshifted controls (4). A Contrast (32, 4) x Session (11-20) ANOVA yielded significant main effects of session, $F(9, 144) = 22.50$, $p < 0.001$, and contrast, $F(1, 16) = 9.05$, $p < 0.01$. The interaction was not significant, Fs < 1.

Discussion

These results are consistent with Ross' (1964) findings and with Amsel's (1992) frustration theory: (1) The behavior of animals with previous downshifted experience did not differ from that of unshifted controls during autoshaping acquisition, but (2) Animals with previous downshift experience in the cSNC situation demonstrated a greater resistance to extinction compared to that of the unshifted controls.

These results imply positive transfer between these two tasks. Thus, pairings of a frustration state with 4% sucrose during recovery from reward downshift would countercondition anticipatory frustration. When frustration is again induced during extinction, even though the CR schedule should not support counterconditioning, animals displayed increased resistance to extinction. The implication is that counterconditioning acquired in one situation (cSNC) transferred positively to another situation (autoshaping extinction).

The results from cSNC to autoshaping extinction were consistent with the results obtained in the transition from cSNC to one-way avoidance contrast (Glueck et al., 2013). However, it should be noted that prior counterconditioning through incentive downshift experience was able to induce an attenuation of SNC (positive transfer) in one-way avoidance, but the reversal of the tasks did not result in symmetric transfer. Therefore the aim of Experiment 2 was to explore whether reversing the tasks used in Experiment 1 would also produce evidence of transfer.

Experiment 2: From Autoshaping Acquisition under PR vs. CR to cSNC

In designing the opposite order (i.e., from autoshaping to cSNC), I opted to induce counterconditioning via PR training. Extinction can be used to induce frustration, but because it does not involve reward, it cannot support counterconditioning. To determine whether PR training affected behavior, a CR group was introduced during the first phase. Therefore, animals were first trained under either CR (100%) or PR (50%) in an autoshaping task and then run through a typical cSNC task. Amsel's (1992) transfer hypothesis predicts that animals that experienced counterconditioning during the PR training in the autoshaping phase should demonstrate transfer during the downshift phase of cSNC. If the transfer were positive (as in Experiment 1), then prior PR training should reduce the size of the cSNC effect. However, if the transfer were negative, then the cSNC effect should be enhanced.

Method

Subjects. Forty female Wistar rats served as subjects for Experiment 2. Animals were of similar age, and were maintained and deprived as in Experiment 1.

Apparatus. The same conditioning and consummatory boxes described in Experiment 1 were used in Experiment 2.

Procedure. Once animals had reached their deprivation weight (at approximately 96 days of age), they were matched for weight and randomly assigned to one of two training groups based on autoshaping reinforcement schedules: CR: 100% reinforcement, or PR: 50% reinforcement. There were 10 sessions of acquisition, at 1 session/day, with each session consisting of 10 trials. In each trial, the lever was presented for 10 s. Trials were separated by variable intervals averaging 90 s (range: 60-120 s). During acquisition, each lever presentation ended with the delivery of five 45-mg precision food pellets for the CR group, but only a random

Table 3

Design of Experiment 2

Group	**Phase 1: autoshaping**	**Phase 2: cSNC**
CR/32	(10) CR	(10) 32% → (5) 4%
PR/32	(10) PR	(10) 32% → (5) 4%
CR/4	(10) CR	(10) 4% → (5) 4%
PR/4	(10) PR	(10) 4% → (5) 4%

Note. Autoshaping involved pairings of a lever and food pellets. The number in parentheses refers to the number of daily sessions. CR: continuous reinforcement. PR: 50% partial reinforcement. 32% and 4%: sucrose concentrations.

reinforcement. 32% and 4%: sucrose concentrations.50% of the trials ended with food delivery for the PR group. During nonreinforced trials, pellets were not administered. All other aspects were the same as described in Experiment 1.

cSNC training started a day after the last autoshaping session. Animals were assigned to groups such that lever-pressing responses were similar across schedules: CR/32, CR/4, PR/32, PR/4. cSNC training was the same as in Experiment 1. The design is described in Table 3.

Results

Autoshaping acquisition. Session averages for schedules (CR, PR) during acquisition are shown in Figure 7a for the lever pressing responses per minute for the 10 acquisition sessions.

During the autoshaping acquisition phase, both schedules of reinforcement resulted in animals acquiring lever pressing behavior. Animals in the PR condition pressed the lever more frequently starting on Session 4 and continuing throughout the remainder of training compare to

the CR condition. This is referred to as the partial reinforcement acquisition effect (PRAE). A Schedule (CR, PR) x Session (1-10) ANOVA yielded a significant interaction, $F(9, 342) = 4.38$, $p < 0.001$. Additionally, there were significant main effects of Session, $F(9, 342) = 46.97$, $p < 0.001$, and Schedule, $F(1, 38) = 10.93$, $p < 0.01$. The emergence of the PRAE in the lever pressing behavior shows that he PR manipulation affected behavior and suggested that counterconditioning had occurred during autoshaping acquisition to potentially induce transfer in the cSNC phase.

The source of the interaction was determined with post hoc LSD tests. Animals trained under the PR schedule demonstrated significantly greater lever pressing responding starting on Session 5 and persisting until the final session of acquisition (Session 10) compared to animals trained under the CR schedule, Fs$(1, 38) > 8.09$, ps < 0.01.

cSNC. During the preshift phase, animals learned to drink sucrose solution whether having access to 32% or 4%. A Contrast (32, 4) x Schedule (CR, PR) x Session (1-10) ANOVA yielded a significant Session by Contrast interaction, $F(9, 324) = 5.12$, $p < 0.001$, and a significant Schedule by cSNC interaction, $F(1, 36) = 4.90$, $p < 0.05$. Additionally, there was a significant main effect of Session, $F(9, 324) = 44.71$, $p < 0.001$. All other effects were not significant, Fs < 1.28, ps > 0.25.

The sources of the significant interactions were determined by post hoc LSD tests. On Session 2, animals that had received 32% sucrose goal tracked significantly more than animals that had received 4% sucrose, $F(1,36) = 16.48$, $p > 0.001$. A similar test revealed that animals with prior PR experience received 32% sucrose solution (PR/32) goal tracked significantly less than animals that received 4% solution (PR/4), $F(1,36) = 4.73$, $p > 0.05$.

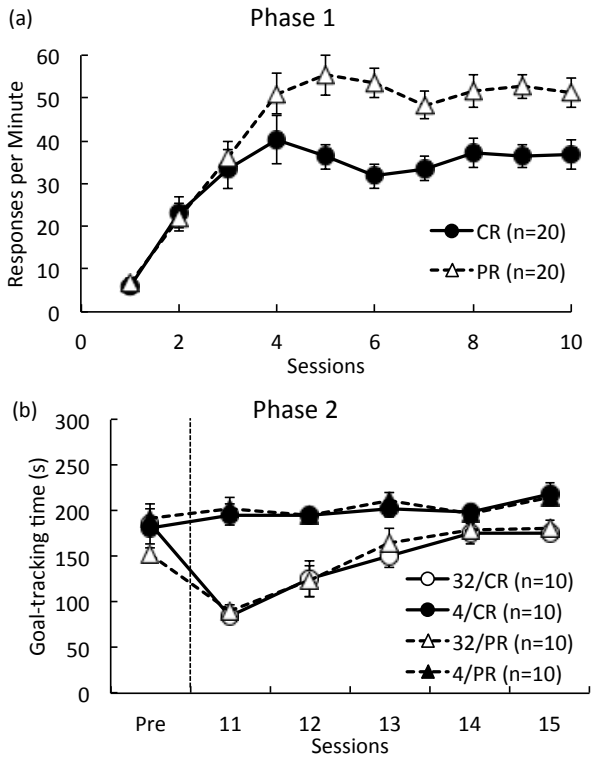

Figure 7. Autoshaping acquisition (*a*) followed by cSNC (*b*). The dependent measure in Figure 7a is the group average of responses per minute for animals that experienced CR or PR training during autoshaping acquisition (error bars are ±SEMs). The dependent measure in Figure 7b is the group average goal-tracking time for the last preshift session (Session 10) and the postshift sessions (Sessions 11-15) during cSNC (error bars are ±SEMs). Animals in the CR conditions (32-4/CR, 4-4/CR) received CR training and animals in the PR conditions (32-4/PR, 4-4/PR) received 50% PR training during the autoshaping acquisition phase.

Of specific interest in this phase was whether animals that were previously trained under the PR schedule would demonstrate transfer following an incentive downshift (Sessions 11-15). The average amount of time the animals spent in contact with the sipper tube (goal tracking time) results for the final preshift session (Session 10) and subsequent postshift sessions (Sessions 11-

15) are illustrated in Figure 7b. A Contrast (32, 4) x Schedule (CR, PR) x Session (11-15) ANOVA yielded a significant Contrast by Session interaction, $F(4, 144) = 18.37$, $p < 0.001$, and significant main effects of Session, $F(4, 144) = 28.32$, $p < 0.001$, and Contrast, $F(1, 36) = 49.45$, $p < 0.001$. All other effects were not significant, Fs < 1. The source of the significant interaction was determined by post hoc LSD test. On Sessions 11-15, downshifted animals (CR/32, PR/32) demonstrated a significantly less goal tracking time compared to that of the unshifted control groups (CR/4, PR/4), Fs $(1, 36) > 5.35$, ps < 0.05.

Discussion

Animals with prior counterconditioning experienced in the form of PR training during autoshaping demonstrated no significant difference in consummatory behavior following an incentive downshift in cSNC, compared to that of the unshifted controls (Figure 7b). The lack of transfer cannot be attributed to a failure of PR training to affect behavior because a clear PRAE was observed in Phase 1 (Figure 7a). These results are more consistent with the previous transfer experiments in the one-way avoidance situation (Glueck et al., 2013), than with the transfer effects between SNC task (Cuenya et al., under review). It appears that, at least in some cases, the cSNC effect is not as easily influenced by prior counterconditioning experience as it is able to influence behavior in subsequent situations involving downshifts in incentive conditions. The results of Experiments 1 and 2 provide a partial confirmation of Amsel's (1992) transfer hypothesis. These experiments revealed an asymmetric transfer when cSNC was involved. Whereas prior cSNC experience affected subsequent training in either one-way avoidance or autoshaping, the opposite was not true. Behavior in the cSNC situation was not influenced by prior incentive downshift experience. I was interested in further investigating this lack of evidence for transfer from autoshaping to cSNC. One potential hypothesis suggests that 100

trials of PR training produced an insufficient amount of counterconditioning for transfer to occur. Therefore, Experiment 3 sought to investigate whether tripling the amount of counterconditioning opportunities would be sufficient to produce enough counterconditioning to induce transfer.

Experiment 3: From Extended Autoshaping Acquisition to cSNC

One potential explanation for the lack of transfer seen in cSNC is that there was insufficient counterconditioning that occurred during Phase 1 in Experiment 2 and in the one-way avoidance to cSNC experiment (Glueck et al., 2013). Therefore, in order to test this hypothesis, I increased the number of trials per 10 daily sessions to 30 (compared to 10 in Experiment 2) tripling the total number of acquisition trials to 300 in Experiment 3, thereby increasing the opportunities for counterconditioning to occur.

Method

Subjects. Forty female Wistar rats served as subjects for Experiment 3. Animals were a similar age and maintained and deprived the same as in Experiment 1.

Apparatus. The same conditioning and consummatory boxes described in Experiment 1 were used in Experiment 3.

Procedure. Once animals had reached their deprivation weight (at approximately 96 days of age), they were matched for weight and randomly assigned to either CR: 100% reinforcement, or PR: 50% reinforcement, for autoshaping acquisition training. The procedure was identical to that previously described in Experiment 2, with the exception for the number of trials per session. There were 10 sessions of acquisition, at 1 session/day, with each session consisting of 30 trials, for a total of 300 acquisition trials. All other aspects of autoshaping acquisition and cSNC training were as described in Experiment 2 (see Table 4).

Table 4

Design of Experiment 3

Group	Phase 1: autoshaping	Phase 2: cSNC
CR/32	(10) CR	(10) 32% → (5) 4%
PR/32	(10) PR	(10) 32% → (5) 4%
CR/4	(10) CR	(10) 4% → (5) 4%
PR/4	(10) PR	(10) 4% → (5) 4%

Note. Autoshaping involved pairings of a lever and food pellets. The number in parentheses refers to the number of daily sessions. CR: continuous reinforcement. PR: 50% partial reinforcement. 32% and 4%: sucrose concentrations.

Results

Autoshaping acquisition. Session averages for schedules (CR, PR) during acquisition are shown in Figure 8a for the lever pressing responses per minute for the 10 acquisition sessions. During the autoshaping acquisition phase, both schedules of reinforcement resulted in animals acquiring lever pressing behavior. Animals in the PR condition demonstrated the PRAE starting on Session 3 and continuing throughout the remainder of training. A Schedule (CR, PR) x Session (1-10) ANOVA yielded a significant interaction, $F(9, 342) = 4.06, p < 0.001$.

Additionally, there were significant main effects of Session, $F(9, 342) = 12.43, p < 0.001$, and Schedule, $F(1, 38) = 10.76, p < 0.01$. The emergence of the PRAE in the lever pressing behavior shows that he PR manipulation affected behavior and suggested that counterconditioning had occurred during autoshaping acquisition to potentially induce transfer in the cSNC phase.

The source of the interaction was determined with post hoc LSD tests. Animals trained under the PR schedule demonstrated significantly greater lever pressing responding starting on Session 3 and persisting until the final session of acquisition (Session 10) compared to animals trained under the CR schedule, Fs(1, 38) > 6.70, ps < 0.05.

cSNC. During the preshift phase, animals learned to drink sucrose solution from the sipper regardless of whether they were given access to 32% or 4%. A Schedule (CR, PR) x Contrast (32, 4) x Session (1-10) ANOVA yielded a significant Session by Contrast interaction, $F(9, 324) = 4.15$, $p < 0.001$, and significant main effect of Session, $F(9, 324) = 43.98$, $p < 0.001$, and Contrast, $F(1, 36) = 6.71$, $p < 0.05$. All other effects were not significant, Fs < 2.13, ps > 0.15. The source of the significant interaction was determined by post hoc LSD tests. On Sessions 3, 5, 6, 9, and 10 animals that had received 32% sucrose goal tracked significantly less than animals that had received 4% sucrose, Fs(1, 36) > 5.36, $p < 0.05$.

Of specific interest in this phase was whether animals that were previously trained under the PR schedule would demonstrate transfer following an incentive downshift (Sessions 11-15). The average amount of time the animals spent in contact with the sipper tube (goal tracking time) results for the final preshift session (Session 10) and subsequent postshift sessions (Sessions 11-15) are illustrated in Figure 8b. A Schedule (CR, PR) x Contrast (32, 4) x Session (11-15) ANOVA yielded a significant Contrast by Session interaction, $F(4, 144) = 12.91$, $p < 0.001$, and significant main effects of Session, $F(4, 144) = 19.29$, $p < 0.001$, and Contrast, $F(1, 36) = 45.06$, $p < 0.001$. All other effects were not significant, Fs < 1.46, ps > 0.22.

The source of the significant interaction was determined by post hoc LSD test. On Sessions 11-15, downshifted animals (CR/32, PR/32) demonstrated a significantly less goal

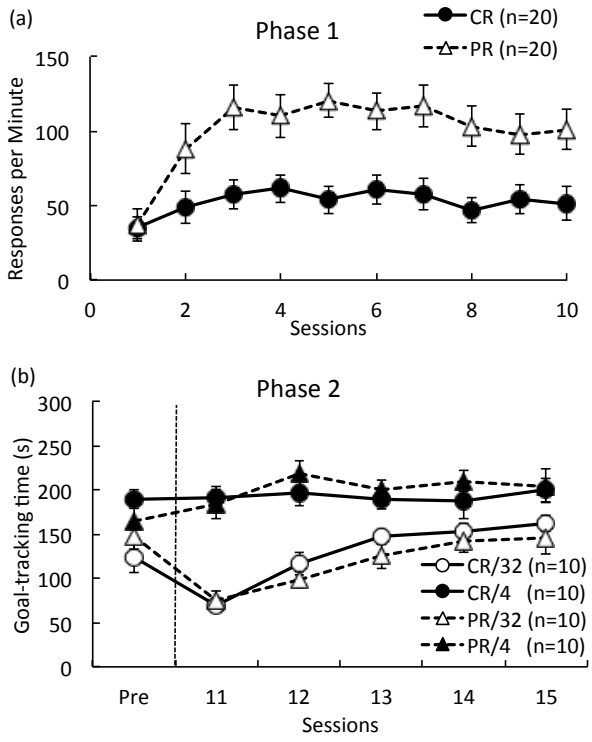

Figure 8. Autoshaping acquisition (300 trials) (*a*) followed by cSNC (*b*). The dependent measures are the same as in *Figure 7*.

tracking time compared to that of the unshifted control groups (CR/4, PR/4), *F*s (1, 36) > 9.29, *p*s < 0.01.

Discussion

Increasing the total number of acquisition trials from 100 to 300 produced a strong PRAE that appeared earlier than in Experiment 1. However, increasing the number of acquisition trials did not induce transfer in the cSNC situation. In view of subsequent results (see Experiment 7), I note that there was a nonsignificant trend towards negative transfer in the PR/32 animals. Downshifted animals demonstrated similar consummatory suppression on the first downshift session (Session 11) followed by similar recovery rates, regardless of prior counterconditioning experience.

The results of Experiment 3 suggest the lack of transfer from autoshaping to cSNC seen in Experiment 2 was probably not due to insufficient counterconditioning during the autoshaping phase. Another possibility is that the lack of transfer from autoshaping to cSNC could be due to a relatively weaker strength of counterconditioning in the autoshaping situation. One way to enhance the overall aversiveness of the reward loss experienced during nonreinforced trials is through pharmacological manipulation. Experiment 4 focused on this manipulation as a means of inducing transfer.

Experiment 4: From PR Acquisition with Naloxone vs. Saline to cSNC.

Another way to strengthen the counterconditioning experience to increase the intensity of the reward loss event is through pharmacological administration. Provided that animals eventually develop approach behavior, a stronger aversive experience should induce a stronger counterconditioned response (Amsel, 1992; Daly & Daly, 1982). Previous research has revealed the nonselective opioid antagonist naloxone enhances the incentive loss experience in cSNC (Daniel et al., 2009; Pellegrini et al., 2005) and accelerates appetitive extinction in an instrumental, lever-pressing situation (Norris, Perez-Acosta, Ortega, & Papini, 2009). Thus, I hypothesized that naloxone should enhance the aversiveness of reward omission in the autoshaping situation. In Experiment 4, animals were administered naloxone prior to each daily autoshaping acquisition session as a means of intensifying the aversiveness of nonreward.

Method

Subjects. Thirty-nine female Wistar rats served as subjects for Experiment 4. Animals were of similar age and maintain and deprived the same as outlined in Experiment 1.

Apparatus. The same conditioning and consummatory boxes described in Experiment 1 were used in Experiment 4.

Table 5

Design of Experiment 4.

Group	Phase 1: autoshaping	Phase 2: cSNC
Nlx/32	(10) Nlx/PR	(10) 32% → (5) 4%
Sal/32	(10) Sal/PR	(10) 32% → (5) 4%
Nlx/4	(10) Nlx/PR	(10) 4% → (5) 4%
Sal/4	(10) Sal/PR	(10) 4% → (5) 4%

Note. The number in parentheses refers to the number of daily sessions. Nlx: naloxone (2 mg/kg, ip). Sal: saline (equal volume). 32% and 4%: sucrose concentrations. All animals received 50% PR training during autoshaping acquisition (Phase 1) involving pairings of a lever and food pellets.

Procedure. Once animals reached their deprivation weight, they were matched for weight and randomly assigned to either receive naloxone (Nlx, 2 mg/kg, ip) or saline (Sal, equal volume) 15 min prior to the start of each daily session. Autoshaping acquisition training procedure was identical to that of Experiment 2 except that all animals in Experiment 4 received PR (50%) training. This was done because I was specifically interested in examining whether enhancing the counterconditioning experience through naloxone treatment would yield to the detection of transfer.

The cSNC training procedure was the same as in Experiment 2 (see Table 5).

Results

Autoshaping acquisition. Session averages for drug conditions (Nlx, Sal) during acquisition are shown in Figure 9a for the lever pressing responses per minute for the 10

acquisition sessions. During the autoshaping acquisition phase, both drug conditions resulted in animals acquiring lever pressing behavior. A Drug (Nlx, Sal) x Session (1-10) ANOVA yielded a significant interaction, $F(9, 333) = 1.95, p < 0.05$. Additionally, there was a significant main effect of Session, $F(9, 333) = 50.17, p < 0.001$, and marginally significant main effect of Drug, $F(1, 37) = 4.04, p = 0.05$.

The source of the interaction was determined with post hoc LSD tests. Animals treated with naloxone prior to acquisition training demonstrated significantly less responding on Sessions 3 and 4 compared to animals treated with saline, Fs$(1, 37) > 7.19$, ps < 0.05.

cSNC. During the preshift phase, animals learned to drink sucrose solution at similar rates whether having access to 32% or 4%. A Drug (Nlx, Sal) x Contrast (32, 4) x Session (1-10) ANOVA yielded significant main effects of Session, $F(9, 315) = 40.39, p < 0.001$, and Contrast, $F(1, 36) = 31.54, p < 0.001$. All other effects were not significant, Fs < 1.20, ps > 0.30.

Of specific interest in this phase was whether animals that were previously treated with naloxone prior to each autoshaping acquisition session would demonstrate transfer following an incentive downshift (Sessions 11-15). The average amount of time the animals spent in contact with the sipper tube (goal tracking time) results for the final preshift session (Session 10) and subsequent postshift sessions (Sessions 11-15) are illustrated in Figure 9b. A Drug (Nlx, Sal) x Contrast (32, 4) x Session (11-15) ANOVA yielded a significant Contrast by Session interaction, $F(4, 140) = 7.23, p < 0.001$, and significant main effects of Session, $F(4, 140) = 20.81, p < 0.001$, and Contrast, $F(1, 35) = 42.32, p < 0.001$. All other effects were not significant, Fs < 1.05, ps > 0.31.

The source of the significant interaction was determined by post hoc LSD test. On Sessions 11-15, downshifted animals (Nlx/32, Sal/32) demonstrated a significantly less goal

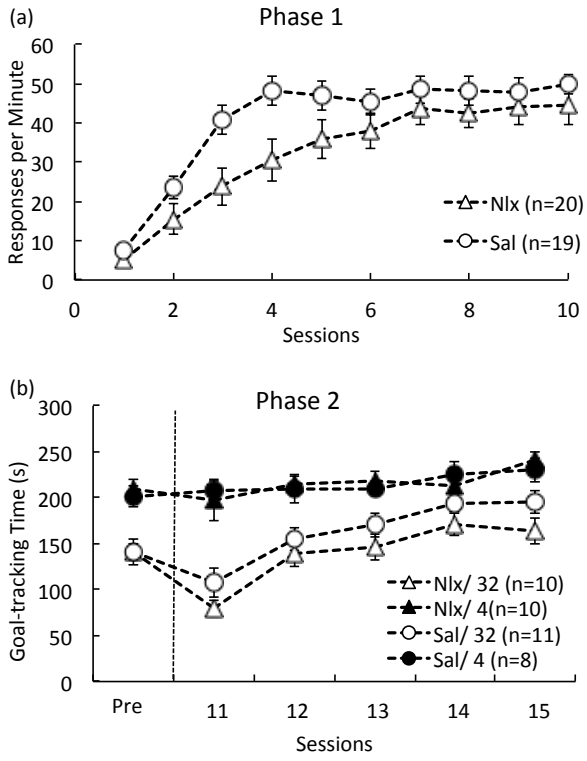

Figure 9. Autoshaping acquisition (PR with naloxone) (*a*) followed by cSNC (*b*). The dependent measures are the same as in *Figure 7*. Animals received ip naloxone (Nlx, 2 mg/kg, ip) or saline (Sal, equal volume) injections 20 min prior to the start of each PR-acquisition session (Session 1-10).

tracking time compared to that of the unshifted control groups (Nlx/4, Sal/4), Fs $(1, 35) > 7.08$, ps < 0.05.

Discussion

As expected, naloxone (Nlx) disrupted lever-pressing responses early in training, relative to Saline (Sal) controls, but eventually yielded the same terminal level of performance. The hypothesis was that counterconditioning should have been enhanced by naloxone, relative to the saline condition. Downshifted animals demonstrated similar cSNC and recovery in the second phase, regardless of drug administration during autoshaping acquisition. As in Experiment 3,

there was a nonsignificant trend for animals with the greater amount of counterconditioning to demonstrate slightly lower goal tracking behavior following an incentive downshift (Session 11) and through the subsequent recovery (Sessions 11-15).

The results from the transfer experiments involving cSNC suggest transfer is not as universal as Amsel (1992) originally hypothesized. Although there was a trend in two of the experiments (Figures 7 and 8) toward slower recovery from reward downshift in animals that had received the stronger counterconditioning training (either PR vs. CR or PR+naloxone vs. PR+saline), such a trend was not significant. I was interested in further exploring the parameters necessary to obtain a significant transfer from autoshaping to cSNC. I thought that perhaps the reason for these failures to see transfer of tolerance to frustration lie in the two paradigms (cSNC and autoshaping) and incentives (food pellets and sucrose) being too different to trigger a common memory of counterconditioning. Previous work suggests that even vast differences in training parameters do not prevent transfer (e.g., Ross, 1964). Similarly, Pellegrini and colleagues (2004) trained animals in the cSNC boxes and animals were subjected to the same reward (32% or 4% sucrose during reinforced sessions and distilled water during nonreinforced sessions of preshift, and then all animals received 4% solution during the downshift sessions). Therefore, even though Amsel (1992) predicted that the only similarity needed to induce transfer is the internal state of frustration, it is possible that external stimuli also participate in the transfer process. In such a case, it is plausible that there were not enough stimulus similarities in our previous procedures to trigger transfer. Experiment 5 sought to further explore the commonality of external stimuli hypothesis by equating the incentives used during autoshaping acquisition training and cSNC.

Experiment 5: From PR vs. CR Autoshaping with Sucrose pellets to cSNC with Sucrose Solutions

In Experiment 5, I explored the hypothesis that increasing common elements other than the internal state of frustration would induce a statistically detectable transfer from autoshaping to cSNC. I provided a commonality between the two paradigms by using sugar pellets in autoshaping (rather than food pellets, as in previous experiments) and sucrose solution in cSNC as the incentives in order to increase the stimulus similarity across phases.

Method

Subjects. Forty female Wistar rats served as subjects for Experiment 5. Animals were of similar age and maintain and deprived the same as outlined in Experiment 1.

Apparatus. The same conditioning and consummatory boxes described in Experiment 1 were used in Experiment 5.

Procedure. Once animals had reached their deprivation weight, they were matched for weight and randomly assigned to either CR: 100% reinforcement, or PR: 50% reinforcement, for autoshaping acquisition training. The procedure was identical to that previously described in Experiment 2, with the exception that sugar pellets were used as reinforcement rather than food pellets.

Each sugar pellet contained protein (0%), fat (0%), carbohydrate (89.5%), fiber (0%), ash (0%), and moisture (< 10%), and provided 3.58 kcal/g.

The cSNC training procedure was the same as in Experiment 2 (see Table 6).

Results

Autoshaping acquisition. Session averages for schedules (CR, PR) during acquisition are shown in Figure 10a for the lever pressing responses per minute for the 10 acquisition sessions.

Table 6

Design of Experiment 5

Group	**Phase 1: autoshaping**	**Phase 2: cSNC**
CR/32	(10) CR	(10) 32% → (5) 4%
PR/32	(10) PR	(10) 32% → (5) 4%
CR/4	(10) CR	(10) 4% → (5) 4%
PR/4	(10) PR	(10) 4% → (5) 4%

Note. Autoshaping involved pairings of a lever and sucrose pellets. The number in parentheses refers to the number of daily sessions. CR: continuous reinforcement. PR: 50% partial reinforcement. 32% and 4%: sucrose concentrations.

During the autoshaping acquisition phase, both schedules of reinforcement resulted in animals acquiring lever pressing behavior. The PRAE emerged later in training in this experiment, not reaching significance until Session 10. A Schedule (CR, PR) x Session (1-10) ANOVA yielded a significant interaction, $F(9, 342) = 2.34, p < 0.05$.

Additionally, there was a significant main effect of Session, $F(9, 342) = 50.89, p < 0.001$. The main effect of Schedule, $F(1, 38) = 2.58, p = 0.12$, failed to reach significance.

The source of the interaction was determined with post hoc LSD tests. Animals trained under the PR schedule demonstrated significantly greater lever pressing responding on Session 10 compared to animals trained under the CR schedule, $F(1, 38) = 5.00$, ps < 0.05.

cSNC. During the preshift phase, animals learned to drink sucrose solution whether having access to 32% or 4%. A Schedule (CR, PR) x Contrast (32, 4) x Session (1-10) ANOVA yielded a significant Contrast by Session interaction, $F(9, 324) = 4.12, p < 0.001$, and a

significant main effect of Session, $F(9, 324) = 29.53$, $p < 0.001$. All other effects were not significant, Fs < 1.30, ps > 0.23.

The sources of the significant interactions were determined by post hoc LSD tests. On Sessions 1 and 2, animals that received 32% sucrose (CR/32, PR/32) goal tracked significantly more than animals that received 4% sucrose, Fs$(1,36) = 15.98$, ps > 0.001, and on Session 7, animals that received 4% sucrose (CR/4, PR/4) goal tracked significantly more than animals in the 32% conditions (CR/32, PR/32), $F(1,36) = 7.28$, $p > 0.05$.

Of specific interest in this phase was whether animals that were previously trained under the PR schedule would demonstrate transfer following an incentive downshift (Sessions 11-15). The average amount of time the animals spent in contact with the sipper tube (goal tracking time) results for the final preshift session (Session 10) and subsequent postshift sessions (Sessions 11-15) are illustrated in Figure 10b. A Schedule (CR, PR) x Contrast (32, 4) x Session (11-15) ANOVA yielded a significant Contrast by Session interaction, $F(4, 144) = 21.66$, $p < 0.001$, and significant main effects of Session, $F(4, 144) = 32.84$, $p < 0.001$, and Contrast, $F(1, 36) = 23.53$, $p < 0.001$. All other effects were not significant, Fs < 1.32, ps > 0.27.

The source of the significant interaction was determined by post hoc LSD test. On Sessions 11-14, downshifted animals (CR/32, PR/32) demonstrated a significantly less goal tracking time compared to that of the unshifted control groups (CR/4, PR/4), Fs $(1, 36) > 7.17$, ps < 0.05.

Discussion

Providing greater commonality in the form of using a sweet incentive yielded interesting results. If all that was needed to detect transfer across these two situations (from autoshaping to cSNC) was a more similar incentive in the two tasks, then there should have been significant

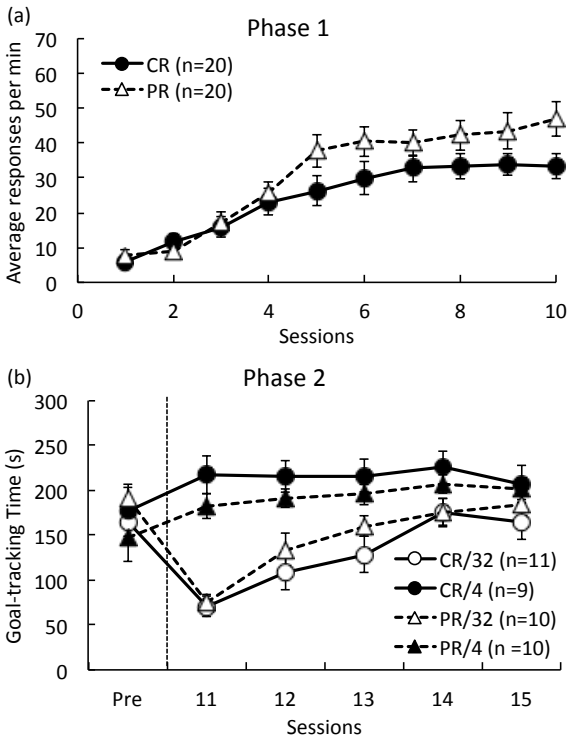

Figure 10. Autoshaping acquisition (with sugar pellets as the reinforcer) (*a*) followed by cSNC (*b*). The dependent measures are the same as in *Figure 7*.

evidence of transfer in Experiment 5. However, this was not the case. Even though there was evidence of a PRAE during autoshaping acquisition (although the effect was somewhat less dramatic than that obtained with food pellets; compare Figures 7a and 10a), the PR and CR groups did not significantly differ in lever pressing behavior until Session 10. Additionally, downshifted animals displayed similar reduction of consummatory behavior on the first session of downshift (Session 11) and similar recovery from the downshift experience during subsequent sessions in the cSNC situation (Figure 10b). There was a trend for PR animals to recover faster from the downshift than CR animals, but again this trend was not significant. These results are promising in that in Experiment 5, we first see the hint of positive transfer emerging in the form of the trend for the PR/32 animals to goal track slightly more than the CR/32 group. Therefore,

these results suggest that incorporating a greater similarity in incentives used in both paradigms can potentially produce evidence of positive transfer if the correct parameters can be identified.

The previous experiments (Experiments 1-5) involved procedural manipulations designed to enhance the counterconditioning experience in the autoshaping phase. However, it is possible that the lack of significant transfer seen in the previous experiments has nothing to do with the intensity of the counterconditioning, but instead with the parameters of the cSNC task. Perhaps modifying the cSNC task will enable the detection of transfer. Experiments 6 and 7 explored this hypothesis.

Experiment 6: From PR vs. CR Autoshaping to cSNC with Increased Number of Preshift Sessions

Frustration theory (1992) suggests that positive transfer from autoshaping to cSNC should reduce the cSNC effect. Therefore, it is plausible that the experiment conducted by Torres (unpublished) and the current Experiments 1-5 failed because the cSNC effect was rather weak. This would leave little room to see a reduction in the size of the cSNC effect required by a positive transfer scenario. Therefore, parameters that enhance the cSNC effect should improve the chances of detecting transfer from autoshaping. Previous research has revealed that extending the preshift phase from the typical 10 sessions to 20 sessions leads to a larger and longer-lasting cSNC effect (Pellegrini et al., 2004). Therefore, it was possible that by extending the preshift phase to 20 sessions, and in essence, enhancing cSNC, transfer from PR training in autoshaping would be detectable. Consequently, the aim of Experiment 6 was to extend the preshift phase in order to induce a larger cSNC effect in hopes of making inducing transfer.

Method

Subjects. Forty-one female Wistar rats served as subjects for Experiment 6. Animals were of similar age and maintain and deprived the same as outlined in Experiment 1.

Apparatus. The same conditioning and consummatory boxes described in Experiment 1 were used in Experiment 6.

Procedure. Once animals had reached their deprivation weight they were matched for weight and randomly assigned to one of two training groups based on autoshaping reinforcement schedules: CR: 100% reinforcement, or PR: 50% reinforcement. The autoshaping acquisition procedure was identical to that in Experiment 2 with the exception that there were 20 sessions of acquisition training.

Following the final autoshaping acquisition session, animals were assigned to cSNC groups such that lever-pressing responses were similar across schedules: CR/32, CR/4, PR/32, PR/4. The cSNC phase of this experiment was identical to Experiment 2 except that the preshift consisted of 20 daily sessions. Additionally, as a means of detecting transfer, the dependent measure in this experiment was the total number of licks the animal made during each session. The design is described in Table 7.

Results

Autoshaping acquisition. Session averages for schedules (CR, PR) during acquisition are shown in Figure 11a for the lever pressing responses per minute for the 10 acquisition sessions. During the autoshaping acquisition phase, both schedules of reinforcement resulted in animals acquiring lever pressing behavior. Animals in the PR condition pressed the lever more frequently starting on Session 4 and continuing throughout the remainder of training compare to the CR condition. This is referred to as the partial reinforcement acquisition effect (PRAE). A Schedule

Table 7

Design of Experiment 6

Group	Phase 1: autoshaping	Phase 2: cSNC
CR/32	(10) CR	(20) 32% → (5) 4%
PR/32	(10) PR	(20) 32% → (5) 4%
CR/4	(10) CR	(20) 4% → (5) 4%
PR/4	(10) PR	(20) 4% → (5) 4%

Note. Autoshaping training involved the presentation of a lever followed by food pellets. The number in parentheses refers to the number of daily sessions. CR: continuous reinforcement. PR: 50% partial reinforcement. 32% and 4%: sucrose concentrations.

(CR, PR) x Session (1-10) ANOVA yielded a significant interaction, $F(9, 351) = 4.31, p < 0.001$. Additionally, there were significant main effects of session, $F(9, 351) = 48.59, p < 0.001$, and schedule, $F(1, 39) = 9.62, p < 0.01$. The emergence of the PRAE in the lever pressing behavior shows that he PR manipulation affected behavior and suggested that counterconditioning had occurred during autoshaping acquisition to potentially induce transfer in the cSNC phase.

The source of the interaction was determined with post hoc LSD tests. Animals trained under the PR schedule demonstrated significantly greater lever pressing responding starting on Session 4 and persisting until the final session of acquisition (Session 10) compared to animals trained under the CR schedule, $Fs(1, 39) > 4.80$, $ps < 0.05$.

cSNC. During the preshift phase, animals learned to drink sucrose solution at similar rates whether having access to 32% or 4%. A Schedule (CR, PR) x Contrast (32, 4) x Session (1-20) ANOVA yielded a significant Contrast (32, 4) by Session (1-20) interaction, $F(19, 703) =$

2.67, $p < 0.001$, and a significant main effect of Session, $F(19, 703) = 30.71$, $p < 0.001$. All other effects were not significant, Fs < 1.01, ps > 0.45.

The source of the significant interaction was determined by post hoc LSD tests. On Sessions 1, and 7, animals that had received 32% sucrose licked significantly more than animals that had received 4% sucrose, Fs > 4.32, ps > 0.05. Additionally, on Session 14 and 17 animals in the 4% conditions licked significantly more than animals that had received 32% sucrose, Fs(1, 37) > 4.80, ps < 0.05.

Of specific interest in this phase was whether animals that were previously trained under the PR schedule would demonstrate transfer, illustrated by a significant difference in consummatory behavior following an incentive downshift after extended (20 sessions) preshift training. The average lick frequency (number of licks) results of the final preshift session and subsequent postshift sessions are illustrated in Figure 11b. A Schedule (CR, PR) x Contrast (32, 4) x Session (21-25) ANOVA yielded a significant Contrast by Session interaction, $F(4, 148) = 19.98$, $p < 0.001$, and significant main effects of Session, $F(4, 148) = 10.16$, $p < 0.001$, and Contrast, $F(1, 37) = 11.22$, $p < 0.01$. All other effects and interactions were not significant, Fs < 1.43, ps > 0.22.

The source of the significant interaction was determined by post hoc LSD test. On Sessions 21, 22, and 23, downshifted animals (CR/32, PR/32) demonstrated a significant decrease in licking behavior compared to that of the unshifted control groups (CR/4, PR/4), Fs (1, 37) > 6.35, ps < 0.05.

Discussion

It was hypothesized that a potential reason for not detecting significant positive transfer in previous studies (Experiment 2-5) was that the cSNC effect had been weak. Experiment 6

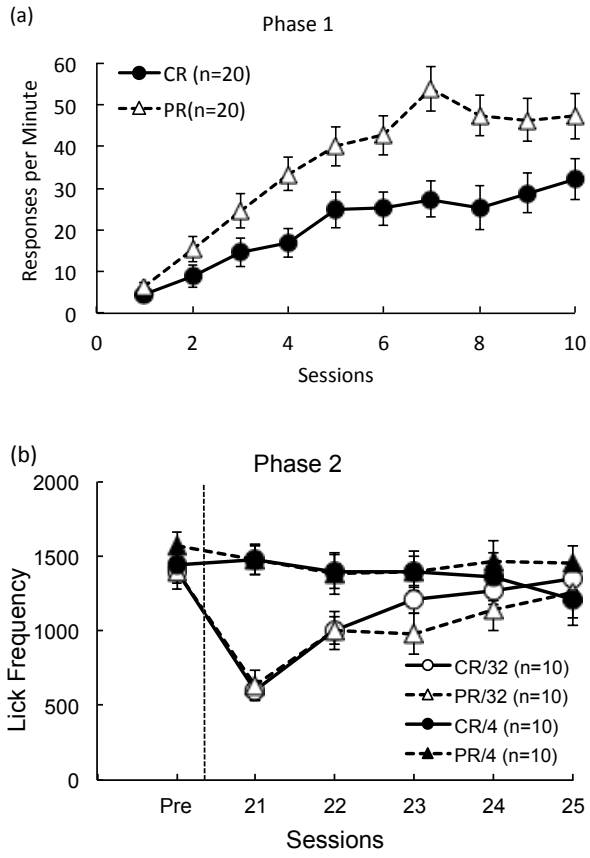

Figure 11. (a) Autoshaping acquisition followed by *(b)* cSNC with an extended preshift phase (20 sessions). . The dependent measure in Figure 11a is the dependent measures are the same as in *Figure 7a*. The dependent measure in Figure 11b is the group average number of licks in a 5-min session for the final preshift session (Session 20) and the postshift session (Session 21-25) during cSNC (error bars are ±SEMs). Animals in the CR conditions (CR/32, CR/4) received CR training and animals in the PR conditions (PR/32, PR/4) received 50% PR training during the autoshaping acquisition phase.

sought to enhance the cSNC effect by increasing the number of preshift sessions. By doubling the number of preshift sessions traditionally used in a typical cSNC paradigm, I hoped to

strengthen the cSNC effect in control downshifted animals, the CR/32 group, and thus make any behavioral differences easier to detect in the experimental condition, PR/32 group. I hypothesized that the PR/32 animals would show significantly different consummatory difference from that of the CR/32 condition and, thus, show transfer.

The results of this experiment provided no evidence of positive transfer. In fact, and as in Experiments 3 and 4, there was a nonsignificant trend toward negative transfer following an incentive downshift in cSNC. Ross (1964) demonstrated similar, but significant, results in his study in a group in which he suggested the behaviors trained during the first and second phase of acquisition training were competing responses and, thus, "incompatible" with each other, leading to a great sensitivity to frustration.

The possibility that transfer from autoshaping to cSNC is of a negative type seems difficult to reconcile with the clear evidence of positive transfer from cSNC to autoshaping extinction reported in Experiment 1. How would two behaviors be compatible in one direction (licking to lever pressing), but competing in the other (lever pressing to licking)? One obvious problem is that whereas Experiment 1 tested for transfer in extinction of lever pressing, subsequent experiments attempted to induce transfer via PR training. Thus, whereas the cSNC task was the same, the autoshaping task was not strictly the same across experiments. Despite the seemingly unlikely possibility that the degree of compatibility between two responses could depend on the direction of the transition from one to the other, I decided to test the possibility of negative transfer weakening the cSNC effect.

Experiment 7: From PR vs. CR Autoshaping to cSNC with Reduced Reward Discrepancy to CR Autoshaping Reacquisition and Extinction

If the transfer effect from lever pressing to licking is actually negative, then decreasing the size of the cSNC effect might minimize a floor effect and create room to observe enhanced consummatory suppression in Phase 2. Previous research revealed that decreasing the discrepancy ratio of the incentives used in both iSNC (DiLollo & Beez, 1966) and cSNC (Papini & Pellegrini, 2006) training leads to a weakening of the SNC effect. Additionally, decreasing the discrepancy in both cSNC and iSNC tasks has been shown to increase the task sensitivity to detect strain differences between Roman rat strains (Gómez et al., 2009; Rosas et al., 2007). It is possible that by reducing the discrepancy from the traditionally used 8:1 ratio (32% sucrose to 4% sucrose) to a 5.5:1 ratio (22% sucrose to 4% sucrose), as used in Gómez and colleagues (2009), might allow for the detection of transfer from autoshaping to cSNC.

Furthermore, several previous studies have found evidence of transfer following an initial bout of frustration followed by reacquisition under CR schedule with transfer appearing in extinction training (Mellgren, Hoffman, Nation, Williams, & Wrather, 1979; Ross, 1964; Traupmann, Wong, & Amsel, 1971; Wrather & Mellgren, 1980). Based on the success of previous studies, I decided to attempt to replicate these findings by introducing a 5-session autoshaping reacquisition phase followed by autoshaping extinction training in this experiment. Additionally, having reacquisition and extinction introduced in this experiment would allow me to test the degree of symmetry between these two situations within a single experiment. Therefore, the aim of Experiment 7 was to investigate whether a reduced reward discrepancy used in cSNC would enable the detection of negative transfer from autoshaping acquisition under PR, but of positive transfer in autoshaping extinction from previous PR and cSNC training.

Method

Subjects. Forty female Wistar rats, approximately 90 days old, deprived to 81-84% of their ad libitum weight, served as subjects. Animals were maintained and housed as described in Experiment 1.

Apparatus. The same conditioning and consummatory boxes described in Experiment 1 were used in Experiment 7.

Procedure. Once animals reached their deprivation weight (at approximately 96 days of age), they were matched for weight and randomly assigned into either CR (100%) or PR (50%) reinforcement schedules. The procedure was identical to that previously described in Experiment 2, with the exception of the total number of sessions. Animals underwent 20 session of acquisition training. The reason for extending the autoshaping acquisition phase in Experiment 7 was that at Session 9 of acquisition the animals in the PR group had yet to demonstrate the PRAE. It was decided then to extend the acquisition phase until the emergence of the PRAE before continuing to the cSNC phase.

Following the final day of autoshaping training, animals underwent cSNC training as previously described in Experiment 2, with the only difference being that downshifted animals received 10 daily sessions of access to a 22% sucrose solution (w/w, 22 g sucrose for every 78 g of distilled water) during preshift training. Additionally, the total lick frequency was recorded for each session.

Following the final session of cSNC, all animals were run through 5 sessions of CR, and ending with 5 sessions of extinction training. The reacquisition sessions were identical to those experienced by CR animals during the first acquisition phase, whereas, the each extinction trial ended with the retraction of the lever followed by no reinforcement delivery. Again, trials were

Table 8

Design of Experiment 7

Group	Phase 1: autoshaping	Phase 2: cSNC	Phase 3: autoshaping
CR/22	(20) CR	(10) 22% → (5) 4%	(5) CR → (5) Ext
PR/22	(20) PR	(10) 22% → (5) 4%	(5) CR → (5) Ext
CR/4	(20) CR	(10) 4% → (5) 4%	(5) CR → (5) Ext
PR/4	(20) PR	(10) 4% → (5) 4%	(5) CR → (5) Ext

Note. Autoshaping involved pairings of a lever and food pellets. The number in parentheses refers to the number of daily sessions. CR: continuous reinforcement. PR: 50% partial reinforcement. 22% and 4%: sucrose concentrations. Ext: autoshaping extinction sessions (i.e., lever-only trials).

separated by variable intervals averaging 90 s (range: 60-120 s). The design is described in Table 8.

Results

Autoshaping acquisition. Session averages for schedules (CR, PR) during acquisition are shown in Figure 12a for the lever pressing responses per minute for 20 acquisition sessions. A Schedule (CR, PR) x Session (1-20) ANOVA yielded a significant interaction, $F(19, 722) = 2.69$, $p < 0.001$. Additionally, there was a significant main effect of session, $F(19, 722) = 42.89$, $p < 0.001$, but not of schedule, $F(1,38) = 2.47$, $p > 0.05$.

The source of the interaction was determined with post hoc LSD tests. Animals trained under the PR schedule demonstrated significantly greater lever pressing responding on Sessions

13, 16, and 17, Fs$(1, 38) > 4.17$, ps < 0.05, with a marginally nonsignificant greater responding on Session 18, $F(1, 38) = 3.99$, $p = 0.053$), compared to animals trained under the CR schedule.

cSNC. During the preshift phase, animals learned to drink sucrose solutions. A Schedule (CR, PR) x Contrast (22, 4) x Session (1-10) ANOVA yielded a significant effect of Session, $F(9, 324) = 24.52$, $p < 0.001$. Additionally, there were significant interactions of Contrast by Session, $F(9, 324) = 4.14$, $p < 0.001$, and Schedule by Contrast, $F(1, 36) = 4.56$, $p < 0.05$. All other effects were not significant, Fs < 1.27, ps > 0.25.

The sources of the significant interactions were determined by post hoc LSD tests. On the first (Session 1) and second (Session 2) day of cSNC training, animals that received 22% sucrose, licked significantly more than animals that received 4% sucrose, Fs$(1, 36) > 7.39$, ps < 0.05. Additionally, on Session 5, animals that received 4% sucrose licked more than animals that received 22% sucrose, $F(1, 36) = 11.00$, $p < 0.01$. A similar analysis revealed that animals that had previously been trained under CR schedule drank marginally more 22% sucrose than 4% sucrose, $F(1, 36) = 3.50$, $p = 0.07$.

Of specific interest in this phase was whether animals with prior frustration experience (PR group) would demonstrate transfer, illustrated by a reduced cSNC effect, following a downshift with a reduced discrepancy ratio (22-4, or 5.5: 1) than what has been traditionally used (32-4, or 8:1). The results of the final preshift session (Session 10) and subsequent postshift sessions (Sessions 11-15) are illustrated in Figure 12b. A Schedule (CR, PR) x Contrast (22, 4) x Session (11-15) ANOVA yielded a significant Schedule by Contrast interaction, $F(1, 36) = 4.12$, $p = 0.05$???. Additionally, there was a significant main effect for Session, $F(4, 144) = 13.15$, $p < 0.001$, Contrast, $F(4, 144) = 6.91$, $p < 0.05$. All other effects were not significant, Fs < 1.67, ps > 0.16.

The source of the significant interaction was determined by post hoc LSD tests. The cSNC effect was eliminated in animals that had previously undergone CR training during Phase 1, but persisted in animals previously trained under a PR schedule. There was a significant reduction of consummatory behavior in the PR/22 animals during postshift sessions, $F(1, 36) = 10.85$, $p < 0.01$, compared to the PR/4 animals.

Autoshaping reacquisition. Session averages for the lever pressing responses per minute during the CR acquisition (Sessions 1-5), are shown in Figure 12d. Animals with prior PR and downshift training lever pressed more during the reacquisition phase than animals with prior CR experience. A Schedule (CR, PR) x Contrast (22, 4) x Session (1-5) ANOVA yielded a significant Session x Schedule interaction, $F(4, 144) = 2.54$, $p < 0.05$. All other effects and interactions were not significant, Fs < 2.28, ps > 0.06.

Autoshaping extinction. Session averages for the lever pressing responses per minute during the autoshaping extinction (Sessions 6-10), are shown in Figure 9d. All groups demonstrated an eventual decrease in responding across extinction sessions, but animals in the PR/22 condition demonstrate greater persistence in extinction compared to other groups. A Schedule (CR, PR) x Contrast (22, 4) x Session (6-10) ANOVA yielded a significant triple interaction, $F(4, 144) = 2.56$, $p < 0.05$, and a significant main effect for Sessions, $F(4, 144) = 11.86$, $p < 0.001$. All other effects and interactions were not significant, Fs < 3.67, ps > 0.06.

The source of the significant triple interaction was determined by post hoc LSD tests. Downshifted animals that had previously undergone PR training during Phase 1 (PR/22), demonstrated greater responding during the last 4 sessions of extinction training (Sessions 7-10), compared to animals that had received CR training during Phase 1 (CR/22), Fs > 4.21, ps < 0.05. A similar test revealed that PR animals with downshift experience (PR/22) lever pressed

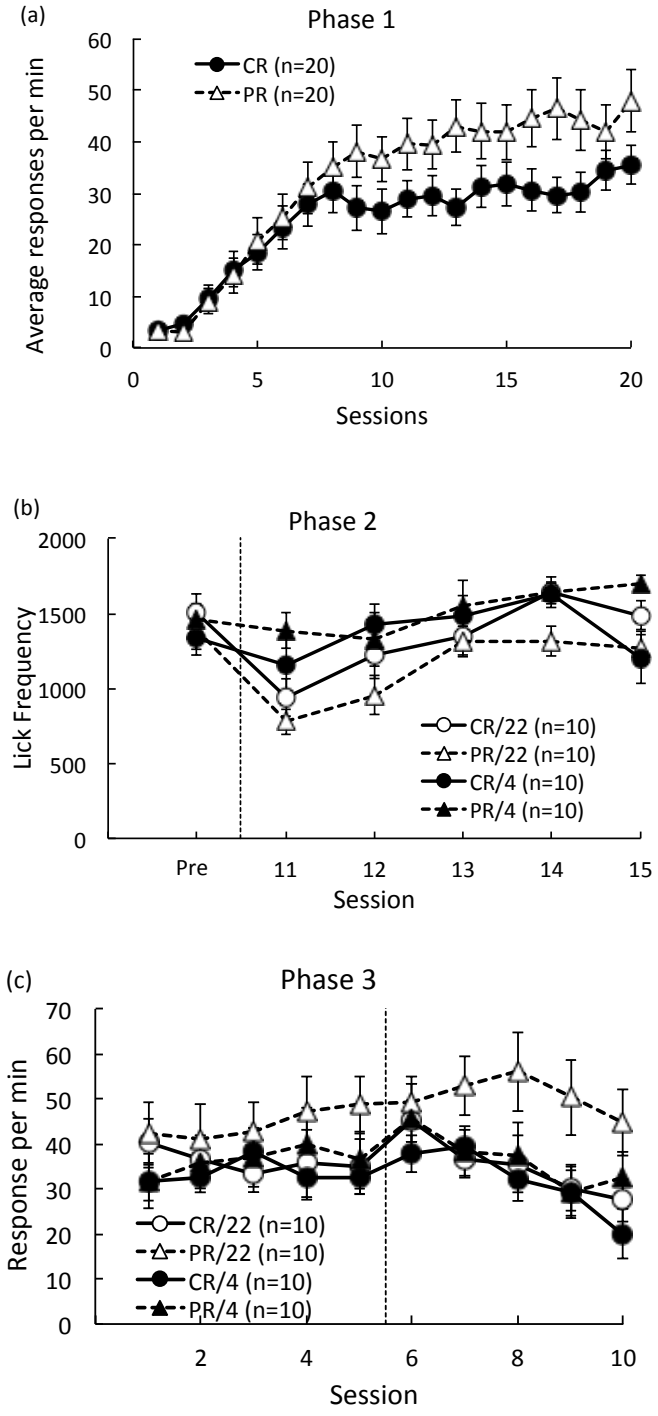

Figure 12. Autoshaping acquisition (*a)* followed by cSNC with a reduced discrepancy ratio (22-4) (*b*) followed by 5 session of CR reacquisition and autoshaping extinction (*c*). The dependent measures are the same as in Figure 11.

significantly more on Sessions 7 and 9, Fs > 4.19, ps < 0.05, compared to unshifted controls with prior PR training (PR/4).

Discussion

Experiment 7 yielded several interesting results. First, animals that had previously undergone PR training demonstrated greater sensitivity to incentive downshift (negative transfer) than animals that had undergone CR training in Phase 1. Phase 1 training did not consistently affect the performance of unshifted controls. These results are consistent with those of Experiment 3, 4, and 6. Apparently, using a smaller discrepancy ratio (22-to-4% sucrose, rather than 32-to-4% sucrose) facilitated the emergence of a negative transfer effect. Granted, in the case of CR animals, 4% control animals decreased licking on the critical downshift session (Session 11) and so while technically the CR/22 animals showed a decrease in licking, it is not lower than the CR/4 animals and, therefore, does not qualify as cSNC based on Flaherty's (1996) definition.

Second, the initial level of suppression is similar in both downshifted groups regardless of prior frustrative experience, but the speed of recovery between the two groups is different. While the CR/22 animals continued to drink at levels similar to their unshifted controls, the PR/22 animals drank consistently less than the PR/4 control group. Therefore, the results from Phase 2 suggest that weakening the cSNC effect by decreasing the discrepancy ratio yield evidence of negative transfer. Interestingly, a nonsignificant trend in the direction of negative transfer from autoshaping to cSNC was observed before (see, e.g., Figures 8, 9, and 11).

This finding is partially consistent with the results of autoshaping reacquisition and extinction. During Phase 3, I attempted to replicate Ross' (1964) findings by returning the animals to the same task where they had previously experienced autoshaping acquisition. I

hypothesized that animals that had previously undergone PR training during autoshaping acquisition and then experienced an incentive downshift during cSNC would demonstrate (1) highest level of lever pressing during reacquisition, because counterconditioning should promote approach behavior, and (2) the greatest resistance to extinction, followed next by animals from the PR/4 condition, then the CR/32 condition, and finally the CR/4 animals, which would extinguish lever pressing the fastest due to their lack of experience with frustration. This hypothesis was based, in part, on the results reported by Ross (1964) showing that animals with prior PR training in one context would demonstrate a resistance to extinction in a second context, even after a more recent reacquisition under CR training in the second context. Importantly, I hypothesized that increased experience with the counterconditioning of frustration would have a cumulative effect on the size of the transfer effect. Animals with the most amount of counterconditioning experience should be better able to cope or resist the negative behavioral effects of frustration compared to animals with lesser or no experience. Interestingly, this hypothesis was correct since PR/22 animals demonstrated the greatest resistance to extinction. However, I was incorrect in regards to the groups with "less" counterconditioning experience. The PR/4 (counterconditioning experiment in Phase 1) and the CR/22 animals (counterconditioning experiment in Phase 2) did not differ from the CR/4 animals that had never had any experience with frustration (i.e., CR training in Phase 1 and unshifted training in Phase 2).

This experiment is interesting in that it replicates the findings of positive transfer on autoshaping extinction observed in Experiment 1, where prior downshift experience led to increased resistance to autoshaping extinction and it allowed for the, up until this point, trend for prior counterconditioning experience in autoshaping acquisition to yield definitive negative

transfer (Phase 2). Here we have two tasks (autoshaping and cSNC), with two very different responses (lever pressing and licking), and two different paradigms (anticipatory and consummatory), that when reversed seemed to yield opposite transfer effects. These results raise an interesting question: Does the degree of compatibility between two responses depend on the sequence of their acquisition, rather than on their topography?

Recall that Ross (1964) found evidence of negative transfer when he trained two "incompatible" behaviors, defined purely in terms of their topography. Ross (1964) argued that climbing and running would cause a conflict of expression because their topography is incompatible, thus competing for expression. As a result, the elicitation of climbing during extinction would compete with the expression of running, thus resulting in accelerated extinction in a runway. My research takes Ross' previous work a step further in that I reversed the order of presentation of two potentially "incompatible" behaviors and found asymmetry in the type of transfer exhibited based on the order of presentation. Thus, whereas Ross (1964) studied transference from climbing to running, he did not test for transference from running to climbing. In fact, there seem to be no other experiments testing for symmetry of transfer across situations involving reward downshifts (Amsel, 1992), except for the unpublished research already cited (Cuenya et al., under review; Glueck et al., 2013). The current results yield consistent support for this hypothesis. Of the seven experiments presented so far, four (Experiment 3, 4, 6, and 7) have yielded either a nonsignificant trend for negative transfer or a significant negative transfer effect. Of the three remaining experiments, one (Experiment 1) involved going from cSNC to autoshaping extinction, one yielded inconclusive results with neither positive of or negative transfer trends (Experiment 2), and one yielded a trend toward positive transfer (Experiment 5). Additionally, Experiment 7 illustrated positive transfer during the third and final phase of

training (Phase 3), making it unique among the other experiments presented in that it demonstrated both negative and positive transfer within the same experiment.

Given the results of the previous seven experiments, I was curious to see if switching to two consummatory tasks, thereby training "compatible" behaviors (licking) and using taste as stimuli, would yield evidence of positive transfer to the cSNC task. Therefore, the aim of Experiment 8 was to explore the use of taste pathway to access frustration in both training tasks.

Experiments 8: From Taste Conditioning with Licking to cSNC with Licking

The previous seven experiments present in this document have involved exploring whether transfer would occur between two different tasks. The results revealed that while transfer will occur, it is often in the opposite direction, depending on the order of training of the two tasks. Given that cSNC can increase the animal's resistance to autoshaping extinction (see Figure 6), but counterconditioning during autoshaping acquisition causes increased sensitivity to an incentive downshift experience, suggests that these two responses (licking vs. level pressing) are incompatible behaviors and thus result in the asymmetric direction (positive vs. negative) of transfer. If this hypothesis is correct, then training animals with two tasks involving the same behavioral response (i.e., licking) could allow for the bidirectional transfer (in the same direction) predicted by Amsel's (1992) theory. To test this hypothesis, animals were trained through Pavlovian taste conditioning using two stimuli, lightly flavored strawberry milk and more heavily flavored chocolate milk, and cSNC.

Method

***Subjects*.** Twenty-seven female Wistar rats, approximately 90 days old, deprived to 81-84% of their ad libitum weight, served as subjects. Animals were maintained under the same condition previously stated in Experiment 1.

Apparatus. Pavlovian taste conditioning and cSNC training took place in the previously described cSNC boxes used in Experiment 1. One difference was that two sipper tubes were used during training in the Pavlovian taste conditioning task (Phase 1). As usual, one sipper tube was used during cSNC training (Phase 2; described in Experiment 1).

Procedure. Pavlovian taste conditioning began once animals reached their appropriate deprivation weight (at approximately 96 days of age). Rats were matched for weight and randomly assigned into one of 2 schedule groups: CR (100% reinforcement) or PR (50% reinforcement). Animals received the same incentives, lightly flavored strawberry milk (20 g of Strawberry Nesquick® dissolved in 2 L of fat free milk) as the first stimulus (S_1), and more heavily flavored chocolate milk (160 g of Chocolate Nesquick® dissolved in 2 L of fat free milk) as the second stimulus (S_2) throughout the CR or PR training. Rats received 10 daily acquisition sessions, consisting of 10 discrete trials, separated by variable intervals averaging 90 s (range: 60-120 s). Each trial began with the presentation of a bottle containing lightly flavored strawberry milk (S_1) for 15 s in the central sipper tube hole. If no response was detected after 10 s, the sipper tube was retracted and the animal received a score of 0 for the number of licks preformed during that stimulus presentation. A reinforced trial ended with the retraction of the strawberry milk sipper tube (S_1) and the presentation of a bottle containing heavily flavored chocolate milk (S_2) for 5 s through the lateral sipper tube hole. If no response was detected after 10 s, the sipper tube was retracted and the animal received a score of zero for the number of licks preformed during the stimulus presentation. A nonreinforced trial ended with the retraction of the strawberry sipper tube. During acquisition, each trial was reinforced for the CR group (100%), but only 50% of the trials were randomly reinforced for the PR group. A computer controlled the administration of events and recorded the number of licks to each sipper tube and for each trial.

Table 9

Design of Experiment 8

Group	**Phase 1: taste conditioning**	**Phase 2: cSNC**
CR/32	(10) CR	(10) 32% → (5) 4%
PR/32	(10) PR	(10) 32% → (5) 4%
CR/4	(10) CR	(10) 4% → (5) 4%
PR/4	(10) PR	(10) 4% → (5) 4%

Note. Taste conditioning involved pairings of strawberry flavor with chocolate flavor. The number in parentheses refers to the number of daily sessions. CR: continuous reinforcement. PR: 50% partial reinforcement. 32% and 4%: sucrose concentrations.

Following the final daily session of Pavlovian taste conditioning, animals underwent cSNC training in the same boxes, although the exact box an animal was tested in was varied to avoid potential confounds associated with the testing box itself. During this phase, animals only had access to one sipper tube presented through the central elliptical hole in the apparatus. Animals were assigned and trained under identical procedures as previously described in Experiment 2, with the only exception being that lick frequency was recorded. The design is described in Table 9.

Results

Taste conditioning. Session averages for the schedules during taste conditioning are shown in Figure 14 for the group averages lick frequency per minute for each session for presentation of strawberry milk (S_1, *a*) and chocolate milk (S_2, *b*). This measure provides a common base across groups, something especially important in the case of S2, since absolute

exposure was different for CR and PR animals. Both CR and PR animals readily consumed the lightly flavored strawberry milk (S_1) across sessions. A Schedule (CR, PR) x Session (1-10) ANOVA for S_1 yielded a significant main effect of Session, $F(9, 225) = 33.85$, $p < 0.001$. No other effects were significant for S_1, Fs < 1.

Animals in both CR and PR conditions acquired licking for heavily flavored chocolate milk, but PR animals licked more later in training than the CR animals (PRAE). A Schedule (CR, PR) x Session (1-10) ANOVA for S_2 yielded a significant interaction, $F(9, 225) = 3.21$, $p < 0.01$. Additionally there were significant main effects of session, $F(9, 225) = 23.09$, $p < 0.001$, and schedule, $F(1, 25) = 73.37$, $p < 0.001$. The source of the significant interaction was determined by post hoc LSD tests. Animals in the PR condition licked significantly more on Sessions 5-8, and 10, Fs$(1, 25) > 7.58$, $p < 0.05$, than animals in the CR condition. The emergence of the PRAE (higher rate of responding in PR than CR animals during taste conditioning training) in the licking behavior suggested that sufficient counterconditioning had occurred during the taste conditioning phase to potentially induce transfer in the cSNC phase.

cSNC. During the preshift phase, animals learned to drink sucrose solution across sessions. A Schedule (CR, PR) x Contrast (32, 4) x Session (1-10) ANOVA yielded a significant effect of session, $F(9, 207) = 2.64$, $p < 0.01$. Additionally, there was a significant Session (1-10) x Contrast (32, 4) interaction, $F(9, 207) = 3.54$, $p < 0.001$. All other effects were not significant, Fs < 3.53, ps > 0.08.

The source of the significant interaction was determined by post hoc LSD test. On Sessions 1 and 9 of cSNC preshift training, animals in the 32% sucrose conditions licked significantly more, Fs$(1, 23) > 7.56$, $p < 0.05$, than animals that received 4% sucrose.

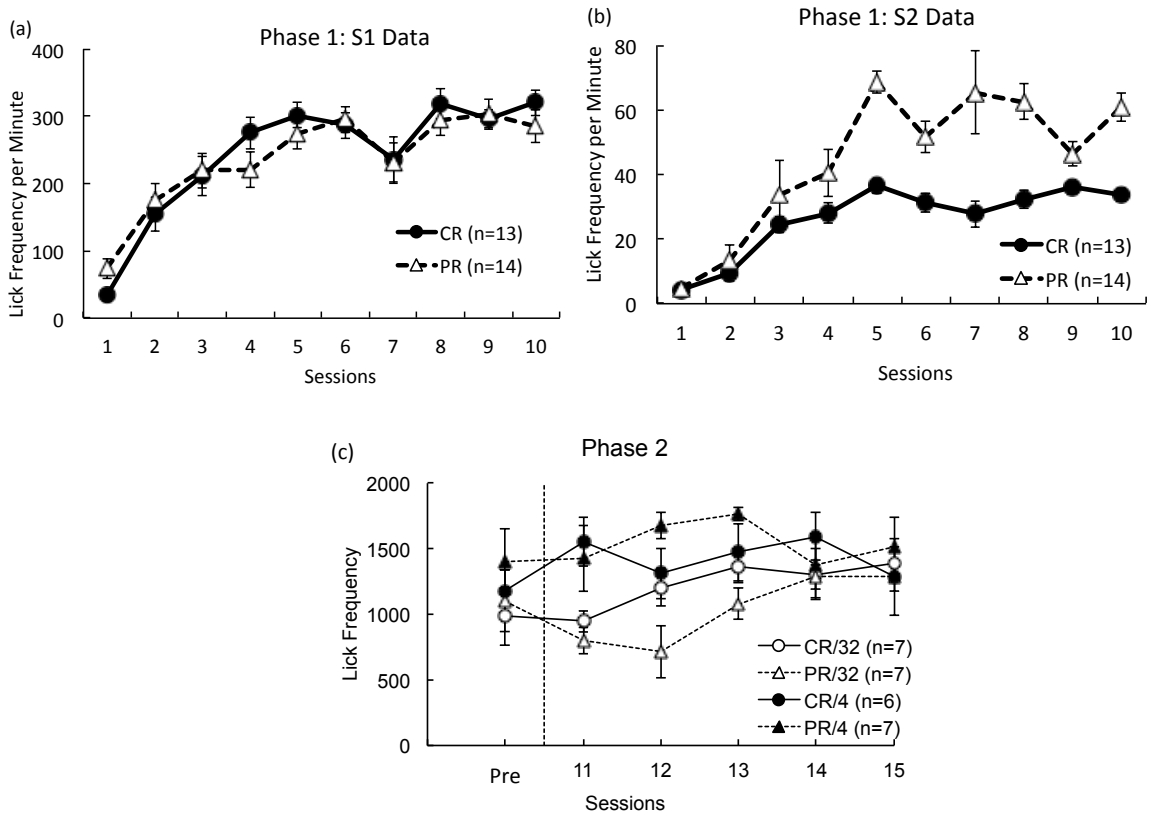

Figure 13. Taste conditioning for lightly flavored strawberry milk (S_1, *a)* and heavily flavored chocolate milk (S_2, *b*) followed by cSNC (*c*). The dependent measure in Figure 10a and 10b are the group averages of licks per minute for animals that experienced CR or PR training during taste conditioning (error bars are ±SEMs). The dependent measure in Figure 10c is the group average number of licks in a 5-min session for the final preshift session (Session 10) and the postshift session (Session 11-15) during cSNC (error bars are ±SEMs).

Additionally, on Session 5, animals in the 4% conditions licked significantly more, $F(1\ 23) = 8.05$, $p < 0.01$, than animals in the 32% sucrose conditions.

Of specific interest during Phase 2 was whether animals with prior frustration experience (PR group) during taste conditioning would demonstrate a reduced cSNC effect following a

downshift. The results of the final preshift session (Session 10) and subsequent postshift sessions (Session 11-15) are illustrated in Figure 14c. A Contrast (32, 4) x Schedule (CR, PR) x Session (11-15) ANOVA yielded a significant triple interaction, $F(4, 92) = 3.51, p = 0.01$. Additionally, there was a significant Contrast by Session interaction, $F(4, 92) = 4.26, p < 0.01$, significant main effects of Session, $F(4, 92) = 3.60, p < 0.01$, and Contrast, $F(1, 23) = 6.80, p < 0.05$. All other effects were not significant, Fs < 1.31, ps > 0.26.

The source of the significant triple interaction was determined with post hoc LSD tests. Both downshifted groups, CR/32 and PR/32, showed a significant decrease in consummatory behavior, compared to that of their unshifted controls, CR/4, $F(1, 23) = 6.18, p < 0.05$, PR/4, $F(1, 23) = 7.18, p < 0.05$, respectively, on the first session of downshift (Session 11). However, cSNC lasted for two sessions longer (Sessions 11-13) in the PR/32 group compared to the PR/4 group, Session 12, $F(1, 23) = 18.24, p < 0.001$, and Session 13, $F(1, 23) = 13.53, p = 0.001$. There were no significant differences between the two unshifted groups (CR/4, PR/4), Fs < 2.42, ps > 0.13.

Discussion

Using flavored stimuli in Pavlovian taste conditioning to induce transfer yielded interesting results. Although, animals trained under a PR schedule during the taste conditioning phase did demonstrate the PRAE during chocolate milk stimulus presentation, suggesting that sufficient counterconditioning had occurred, these animals later demonstrated an enhanced cSNC effect visible by a significant delay in recovery from cSNC compared the CR/32 condition. According to prior research in which animals received counterconditioning and transfer testing with the same behavior (e.g., running; Ross, 1964), one might have predicted that animals in the PR/32 conditioned would have demonstrated an attenuation of the cSNC effect during Phase 2

(i.e., positive transfer). According to Amsel (1992), the criterion was met for the transfer of tolerance to frustration during the initial acquisition phase, and therefore, the PR/32 animals should have demonstrated resistance to the cSNC effect. Instead, animals with prior frustration experience (PR/32) showed an enhanced cSNC effect, demonstrated by delayed recovery during subsequent sessions. These results cannot be explained in terms of response incompatibility since the target response was licking in both phases of the experiment. A feature of the procedure that is different is the location of the target response across phases, at least with respect to S2. Whereas during taste conditioning, the partially reinforced S2 stimulus was located on the right side of the front wall, the cSNC task was carried out by presenting a sipper tube in the center of the front wall. Interestingly, a similar incompatible location applies to the autoshaping vs. cSNC tasks. Although conducted in different boxes, levers were located on one side of the autoshaping boxes whereas the sipper tube is located in the center of the front wall in contrast boxes. Could it be possible that counterconditioning after training in the taste conditioning task (Experiment 8) or in autoshaping (Experiments 7) directed licking to one side of the box during reward downshift in the cSNC task, thus reducing licking to the centrally located sipper tube and yielding evidence of negative transfer? This remains to be evaluated.

General Discussion

According to Amsel's (1992) frustration theory, frustration counterconditioning training in one paradigm should affect behavior in a subsequent paradigm when frustration is induced, regardless of the task, context, or incentive. Prior frustration counterconditioning should either reduce the effects of frustration (positive transfer) or enhanced the effects of frustration (negative transfer) in the second task. This hypothesis was supported by the findings of several other

researchers (Cuenya et al., under review; Ross, 1964; Traupmann, Wong, & Amsel, 1971; Mellgren et al., 1979). However, the current research has demonstrated that transfer might not be as straightforward as Amsel (1992) originally believed.

Glueck et al. (2013) found that while positive transfer was readily apparent in training from cSNC to iSNC in the one-way avoidance situation, it was not observed in the opposite direction. The aim of the research presented here was to explore transfer effects across tasks involving consummatory behavior (the cSNC task) and tasks involving anticipatory behavior (autoshaping and taste conditioning). The first two experiments presented here explored whether transfer between cSNC and autoshaping could be induced. Experiment 1 exposed animals to an incentive downshift in cSNC and then, as in Ross' (1964) experiment, trained animals under CR acquisition in autoshaping followed by appetitive extinction. The results of Experiment 1 replicated and extended Ross' (1964) findings: (1) animals with previous downshifted experience did not differ behaviorally from unshifted controls during autoshaping acquisition, but (2) prior downshift animals demonstrated a greater resistance to extinction compared to that of the unshifted controls. These results were consistent with the results obtained in the transition from cSNC to one-way avoidance contrast (Glueck et al., 2013). In both cases, one can apply the same explanation based on frustration theory: having recovered from a task involving frustration, animals became more resistant to the disruptive effects of frustration in a second task—positive transfer.

For Experiment 2, the order of the tasks was reversed and counterconditioning in Phase 1 was induced via PR training. Here again the results were consistent with Glueck et al. (2013): no transfer was observed. The lack of transfer could not be attributed to a failure of PR training to affect behavior because a clear PRAE was observed in Phase 1. These results suggest that the

cSNC effect is not as easily influenced by prior counterconditioning experience, although it is able to influence behavior in subsequent situations involving downshifts in incentive conditions.

The results of Experiments 1 and 2 provided a partial confirmation of Amsel's (1992) transfer hypothesis. These experiments revealed an asymmetrical transfer when cSNC was involved. Whereas prior cSNC experience affected subsequent training in either one-way avoidance or autoshaping, and the effect was in the direction positive transfer, the opposite was not true. Behavior in the cSNC situation was not influenced by prior partial reinforcement experience. I was interested in further investigating this lack of evidence for transfer from autoshaping to cSNC. This led to subsequent experiments varying a number of parameters in either the autoshaping task (Experiments 3-5) or in the cSNC task (Experiments 6-7) in an attempt to determine whether the cSNC task could be modulated by prior reward downshift experience.

One potential hypothesis suggested that 100 trials of PR training produced an insufficient amount of counterconditioning for transfer to occur. Therefore, I hypothesized that tripling the amount of counterconditioning opportunities would be sufficient to produce enough counterconditioning to induce transfer to the cSNC task. In Experiment 3, I increased the number of trials from a total of 100 to a total of 300, and kept all other aspects of the training the same as in Experiment 2. This training produced a strong PRAE; however, increasing the number of acquisition trials only induced a nonsignificant trend toward negative transfer in the cSNC situation. This trend would become interesting only in light of subsequent findings in this series.

The results of Experiment 3 suggested the lack of transfer from autoshaping to cSNC was probably not due to insufficient counterconditioning during the autoshaping phase. Another possibility was that the lack of transfer from autoshaping to cSNC could have been due to a

relatively weaker strength of counterconditioning in the autoshaping situation. In Experiment 4, the intensity of the reward loss event was increased pharmacologically through the administration of naloxone prior to each acquisition session in an attempt to strengthen counterconditioning. Since I was specifically interested in intensifying the aversiveness of nonreward, animals were only trained under the PR schedule. Previous research had revealed the nonselective opioid antagonist naloxone enhances the incentive loss experience in cSNC (Daniel et al., 2009; Pellegrini et al., 2005;) and accelerates appetitive extinction in an instrumental, lever-pressing situation (Norris, Perez-Acosta, Ortega, & Papini, 2009). Thus, I hypothesized that naloxone should enhance the aversiveness of reward omission in the autoshaping situation. If the response was then allowed to recover from this initial disruption and since the magnitude of counterconditioning is assumed to be proportional to the strength of the frustration response (e.g., Daly & Daly, 1982), then one could assume that naloxone would strengthen counterconditioning and allow for the appearance of transfer following an incentive downshift event. However, as in Experiment 3, there was a nonsignificant trend toward negative transfer. That is, animals that had been treated with naloxone (Nlx/32) demonstrated greater sensitivity to cSNC than saline controls (Sal/32).

The results from the transfer experiments involving cSNC suggest transfer is not as universal as Amsel (1992) originally hypothesized. Although there was a trend in two of the experiments (Experiment 3 and 4) toward slower recovery from reward downshift in animals that had received the stronger counterconditioning training (PR vs. CR or PR+naloxone vs. PR+saline), such a trend was not significant. I was interested in further exploring the parameters necessary to obtain transfer from autoshaping to cSNC and I thought that perhaps the reason for negative transfer of tolerance to frustration lie in the general dissimilarity between two

paradigms used: cSNC and autoshaping. Despite previous work suggesting that even vast differences in training parameters do not prevent transfer (e.g., Ross, 1964), I hypothesized that increasing the similarity between the two tasks might bring about evidence of transfer. Accordingly, I substituted sucrose pellets for food pellets in the autoshaping situation, while preserving the use of sucrose solutions in the cSNC task.

If all that was needed to trigger transfer across these two situations (from autoshaping to cSNC) was a more similar incentive in the two tasks, then I should have seen significant differences in behavior in the animals exposed to PR training prior to the downshift experience. First, there was evidence of a PRAE during autoshaping acquisition, although the effect was somewhat less dramatic than that obtained with food pellets in previous experiments. Second, the downshifted animals displayed similar reduction of consummatory behavior on the first session of downshift (Session 11) and a nonsignificant trend for animals with prior counterconditioning experience in autoshaping (PR/32) to demonstrate faster recovery from cSNC, compared to the downshifted controls (CR/32). These results suggest that incorporating a greater similarity in incentives used in both paradigms produced a nonsignificant trend toward positive transfer.

Another potential explanation for the lack of significant transfer in Experiments 3-5 was, perhaps, the typical training parameters used in the cSNC task were insensitive to transfer. Experiments 6 and 7 were conducted to test this notion. In Experiment 6, the cSNC paradigm was enhanced by extending the preshift phase of cSNC from 10 sessions used in Experiment 2-5 to 20 sessions, a method that had proven successful in the past (Pellegrini et al., 2004). However, this method was ineffective in inducing a significant transfer, although, again, a nonsignificant trend toward negative transfer was observed in animals with prior PR and downshift experience.

In Experiment 7, rather than enhancing the cSNC effect through extensive preshift training, I sought to weaken the cSNC effect by decreasing the discrepancy ratio between the pre- and downshifted solutions. This method has proven effective in detecting strain difference between inbred Roman high- and low-avoidance rats (Gómez et al., 2009; Rosas et al., 2007). If the current situations tend to produce negative transfer, perhaps this trend can be enhanced by reducing the size of the cSNC effect. Additionally, as a means of replicating Ross' (1964) experiment, animals underwent autoshaping reacquisition under CR schedule and then were run through autoshaping extinction training. This method proved successful in producing significant transfer in both cSNC and autoshaping extinction.

Animals that had previously undergone PR training, during autoshaping acquisition, demonstrated greater sensitivity to incentive downshift (negative transfer) than animals that had undergone CR training in Phase 1, which is consistent with the nonsignificant trends observed in Experiment 3, 4, and 6. Apparently, using a smaller discrepancy ratio (5.5:1, rather than 8:1) facilitated the detection of a negative transfer effect that had been previously observed only as a nonsignificant trend. Additionally, I hypothesized that increased experience with frustration counterconditioning would have a cumulative effect on the size of the transfer effect seen in autoshaping extinction (Phase 3). Animals with the greatest amount of frustration counterconditioning experience were anticipated to demonstrate higher resistance to extinction than animals with lesser or no counterconditioning experience. Interestingly, animals that had prior counterconditioning experience during Phase 1 (PR in autoshaping) followed by incentive downshift during Phase 2 (cSNC), that is, Group PR/22, were the ones exhibiting the highest level of lever pressing behavior during Phase 3 (autoshaping extinction). However, I was incorrect in regards to the other two groups with "less" frustration counterconditioning

experience. Groups PR/4 and CR/22 had only exposure to counterconditioning either during Phase 1 (PR/4) or Phase 2 (CR/22) and their extinction performance in Phase 3 did not differ from that of control animals (CR/4) that had never had any experience with frustration. The lack of differentiation may reflect any one of a variety of factors, including interfering factors across phases, insufficient counterconditioning, or simply a lack of sensitivity in lever pressing as a dependent measure.

This experiment made two important contributions. First, it replicated the findings of positive transfer seen in Experiment 1, where prior downshift experience in the cSNC task led to increased resistance to autoshaping extinction (Phase 3 of Experiment 7). Second, it enhanced previously nonsignificant trends for prior counterconditioning experience in autoshaping acquisition to yield definitive evidence of negative transfer (Phase 2). The puzzling fact uncovered by these experiments is that these two tasks (autoshaping and cSNC), involving two different responses (anticipatory and consummatory), yielded positive transfer in one direction, but negative transfer when the sequence of phases was reversed.

The current research took Ross' (1964) work a step further in that I reversed the order of presentation of two potentially "incompatible" behaviors and found asymmetry in the type of transfer exhibited based on the order of presentation. I was interested in exploring these results further and was curious if the asymmetry in my studies was potentially related to Ross' (1964) competition between incompatible behaviors hypothesis. Ross hypothesized that by training two "incompatible" responses during different phases (climbing and running), a competition for expression occurred during extinction training, thus resulting in accelerated extinction (of running) during the second phase. The current results provide support for this hypothesis. Of the six experiments involving the same two tasks, in the same sequence (autoshaping to cSNC), four

(Experiment 3, 4, 6, and 7) yielded either a trend or a significant negative transfer effect.

It is possible that licking and lever pressing bear a complex relationship with each other uncovered here because of testing for transfer in both directions (i.e., from licking to lever pressing and vice versa). Ross' (1964) earlier work, transfer was tested in only one direction. In Phase 1, animals were trained to complete a runway by running, jumping, or climbing under either CR or PR schedules in order to gain entry to the goal box and the reinforcer within. The context, motivation, reinforcer, and behavior were then switched and all groups were trained under CR schedule to run toward the goal box before undergoing extinction training in the second context, during Phase 2. Animals that had been trained to run in both phases demonstrated increased resistance to extinction training (positive transfer). However, animals that were trained to climb under PR during the first phase demonstrated accelerated extinction (negative transfer). Ross (1964) suggested that running and climbing were "incompatible" behaviors and therefore produced competition between the two behaviors when frustration was encountered again during extinction training. Additionally, these animals tended to exhibit climbing behavior during extinction of the running response, more so than animals with prior climbing training under PR or with no previous climbing training. This "regression" response patterns have been previously observed in other experiments involving changes in training contexts and target responses (e.g., Boughner & Papini, 2006; Nation, Cooney, & Gartrell, 1979; Rashotte & Amsel, 1968).

Therefore, it is possible that one reason for the negative transfer observed in Experiment 7 is that the initial counterconditioning of lever pressing renders licking behavior incompatible. One way to answer this question would be to have video recordings monitoring alternative behaviors produced inside the conditioning boxes during transfer sessions. Therefore additional

research is needed in order to further investigate this hypothesis. However, another way to explore the trends for negative transfer is by equating the types of behaviors and stimuli used in training.

Given the results of the previous seven experiments, I was curious to see if switching to an anticipatory task also involving licking, thereby training presumably "compatible" behaviors (licking) in both phases, would yield evidence of positive, rather than negative, transfer. Using more similar rewards in Experiment 5 (sucrose pellets and solutions) yielded a nonsignificant trend toward positive transfer. Therefore, I hypothesized that by training the same response in both tasks would yield evidence of positive transfer. Experiment 8 was designed to explore this hypothesis using a Pavlovian taste conditioning procedure in Phase 1 followed by cSNC in Phase 2. Here, rather than having the animal being trained to respond to two different manipulanda in two different training contexts, animals licked sipper tubes in the consummatory boxes. Experiment 8 yielded similar results to those seen previously in Experiments 3, 4, 6, and 7, with animals with prior counterconditioning experience during PR taste conditioning training demonstrating negative transfer during reward downshift sessions (Group PR/32), compared to animals with CR taste conditioning experience (Group CR/32).

While these results are seemingly difficult to reconcile with Amsel's (1992) frustration theory, there is a potential explanation for negative transfer. As a means of distinguishing between the two tasks, I switched the bottle locations for which counterconditioning would occur. During Phase 1 (taste conditioning), the counterconditioned stimulus was presented through the lateral bottle, whereas during Phase 2 (cSNC) the medial bottle was used. Therefore, it is possible that the location of the bottle is a critical component of the counterconditioning process. If animals received counterconditioning of licking to the lateral bottle in Phase 1, then

the induction of frustration during the downshift sessions of Phase 2 could have directed behavior toward the lateral portion of the box, thereby resulting in reduced licking to the centrally located bottle and an enhanced cSNC effect in PR animals. A similar argument could be articulated with respect to autoshaping. In this task, the lever was always located in a lateral portion of the front wall. Although the boxes used in autoshaping and contrast tasks are different, they are generally very similar, a fact that could have supported substantial stimulus generalization across phases. Again, video recordings of the session could help clarify this issue by allowing a determination of possible changes in the spatial allocation of behavior across groups during the critical reward downshift sessions of the cSNC task. The spatial location of levers and sipper tubes could also be explicitly manipulated to test the spatial-location hypothesis.

Some of the hypotheses outlined in this dissertation still require further investigation before they can be definitively accepted or ruled out as possible explanations for the mixture of negative and positive transfer effects observed in these experiments. One implication of these results is that transfer effects are likely to be more related to response factors than to true tolerance to frustration. The responses reactivated during a frustrating event are a form of regression to behaviors previously linked to recovery from reward loss (Rashotte & Amsel, 1968). They represent previously effective coping strategies reactivated by current frustrating conditions and interacting with current coping responses. Whether one observes positive or negative transfer across situations may say little about the ability to overcome the negative emotion of frustration, and more about the resurgence of previously effective strategies.

The data presented in this paper suggest that transfer effects are more connected to the interaction between these coping responses, than to true tolerance to frustration. Amsel (1992)

believed that once an animal had become counterconditioned to the negative affective state of frustration, then it would be less prone to become frustrated in the future when encountering other frustrating situations. However, the current data suggests that a reduction in the response to frustration following Phase 2 does not necessarily reflect a reduction in the negative emotional state of frustration. Rather, the animal may feel just as frustrated, but its behavior may reflect what appears to be either less emotion (positive transfer) or stronger emotion (negative transfer) as a result of response/location biases induced by prior counterconditioning experience. That frustration may persist even after hundreds of frustrating events is suggested by the results of an experiment reported by Ludvigson and colleagues (1979) involving frustration odors. Rats trained in a PR schedule emit a distinct odor in trials when they received unexpected nonreward and other rats ("observers") can perceive such odors and respond accordingly. This experiment showed that following hundreds of trials of training under PR, rats still emitted frustration odors in every nonrewarded trial, as shown by the behavior of naïve "observer" rats introduced at various stages of training. Therefore, animals had not become tolerant to the negative effects of frustration even after repeated counterconditioning.

It is also important to note that in studies involving the investigation of emotion in nonhuman animals, researchers are not measuring the emotion itself, but rather the animal's behavioral response to the emotion. So while the previous (Amsel, 1992; Cuenya, under review; Glueck et al., 2013; Ludvigson et al., 1979; Ross, 1964) and current research explored the consequence of repeated exposures to frustration, it was really the behavioral responses of animals in reward loss situations that were being measured.

The results encourage the view that transfer across situation involving reward loss engages a complex interplay between coping responses that come from past frustrating experience and those currently being developed when confronted with new frustrating situations.

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ABSTRACT

COPING WITH FRUSTRATION:

TRANSFER BETWEEN CONSUMMATORY AND ANTICIPATORY TASKS

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The present experiments were designed to investigate transfer of tolerance to frustration between consummatory (cSNC) and anticipatory tasks (autoshaping and taste conditioning). The initial finding (Experiments 1-2) were consistent with the type of asymmetric transfer described by Glueck et al. (2013). In both cases, the cSNC task in Phase 1 influenced a subsequent task (one-way avoidance or autoshaping extinction), but it was not influenced by any of these tasks when cSNC occurred in Phase 2. Experiment 3-7, investigated the asymmetric transfer seen between autoshaping and cSNC. Experiments 3, explored whether the lack of transfer from autoshaping to cSNC was due to insufficient counterconditioning. In Experiment 3, the number of counterconditioning opportunities was tripled, and there was a nonsignificant trend towards negative transfer. Experiment 4 enhanced the counterconditioning experience during autoshaping acquisition through the administration of naloxone and, also, yielded a nonsignificant trend towards negative transfer. Experiment 5, explored whether equating the incentives used during both task (sucrose pellets in autoshaping and sucrose in cSNC), would yield evidence of transfer, and here there was a nonsignificant trend toward positive transfer. Experiment 6 and 7 explored whether modifying the cSNC parameters would yield significant transfer. In Experiment 6, the number of preshift sessions was doubled to enhance the cSNC effect; however, this manipulation

also yielded a nonsignificant trend toward negative transfer. For Experiment 7 the discrepancy ratio was reduced from an 8:1 to 5.5:1 ratio and then animals experienced a brief reacquisition under CR in autoshaping followed by appetitive extinction. This experiment yielded a significant negative transfer during cSNC for animals with prior PR and downshift experience, and then these same animals demonstrated a resistance to extinction training (positive transfer). The results of current research presented in this document indicate that transfer is not as universal as Amsel (1992) initially believed.