MICROSTRUCTURE OF APPROACH-AVOIDANCE CONFLICT IN THE SUCCESSIVE NEGATIVE CONTRAST PARADIGM

by

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Learning

The study of how animals learn from their interactions with the environment is a fundamental aspect of psychology. The first major theories of learning were articulated in the early 20th century and influenced the way psychological phenomena are viewed. Psychologists like E. L. Thorndike and J. B. Watson formulated purely reflexive and S-R learning theories, in which learning is the result of associations made between a stimulus (S) and a response (R) (Watson, 1917). According to this view, the reward (S^R) for producing the response is important as a catalyst for the S-R connection, but is not itself encoded. Thorndike's (1911) law of effect addressed the idea suggested by empirical evidence that behaviors that lead to positive outcomes increase in occurrence, and conversely, behaviors paired with negative outcomes decrease in occurrence. To explain these findings theoretically, the law of effect states that different amounts of reward (positive outcomes) lead to different "habit strengths." These habit strengths represent the force of the associative bond between a stimulus and its corresponding response (i.e., the S-R association). Larger rewards create stronger habit strength than smaller rewards and therefore better facilitate learning. Smaller rewards or nonreward weakens the associative strength, resulting in fewer occurrences of the behavior in question.

The law of effect and S-R learning theory provide a theoretical basis for the study of behavior founded upon empirical data. These theories provide a plausible explanation for differential acquisition with different levels of reward and for nonparadoxical extinction effects. This is accomplished without describing a formation of expectancies. It is important to note that this view, while logically sound and well supported, has its limitations. The popular idea among psychologists at the time was to develop a behavioral theory that was independent of mentalistic variables (i.e., expectation), that

would be virtually impossible to measure empirically. The law of effect seems to hold true as long as reinforcer magnitudes remain stable; but when reward magnitude becomes dynamic, Thorndikian theory alone is not enough to explain changes in behavior.

Incentive Contrast

The idea that animals are capable of forming expectations of rewards and exhibit changes in behavior when those expected rewards are supplanted with novel rewards has been explored for over seven decades. Tinklepaugh (1928) conducted an experiment to show that monkeys can develop expectations. A monkey was trained to look for either a banana or a piece of lettuce under one of two cups. Monkeys prefer bananas to lettuce, but will eat the lettuce if they are hungry. In a typical trial, the monkey saw the banana (or lettuce) placed under one of two cups, then a blind was lowered during a retention interval lasting a few seconds. Finally, the screen was lifted and the monkey could make a choice between cups and consume the reward. In some occasional trials, the monkey was shown the banana, the blind was lowered, and the banana was then replaced with a piece of lettuce while the monkey could not see it. Once the blind was lifted, the monkey was allowed to choose a cup. Upon looking under the cup and finding lettuce instead of the expected banana, the monkey examined the cup carefully and looked around as if searching for the missing banana. She occasionally turned toward the observers in the room and shrieked in apparent anger. In these trials, the lettuce was usually left uneaten. The rejection of the lettuce is best understood by assuming that an expectation of "banana" had been formed, such that the finding of lettuce violated this expectation. Associated with the violation of the expectation of a banana with a less desirable food is an apparent emotional response: frustration.

In the same lab, around the same time, Elliott (1928) conducted a similar study with rats in an instrumental conditioning situation. Rats were trained to navigate a complex maze for bran mash and then shifted to a sunflower seed reward. Shifted animals ran more slowly for the sunflower seed than rats trained always with sunflower seeds. They also entered more blind alleys, suggesting that animals were searching for the missing reward. Again, the rats appeared to not only develop an expectation for the reward, but the shift to a less desirable reward elicited significant changes in behavior. To Tinklepaugh and Elliott, "incentive contrast" involved not only the strengthening of S-R connections via a reward, but also the development of a representation of that particular reward. Tinklepaugh (1928, p. 234) referred to these "representative factors" as "ideational in function," and also standing for "qualitative and quantitative aspects of those [reward] objects." Elliott (1928, p. 29) attributed the errors made by his rats in the maze to "searching for the accustomed (and more desirable) food." He concluded, "Rats running the maze…were learning to expect a specific reward rather than mere satisfaction of hunger."

The experiments of both Tinklepaugh and Elliott involved qualitative reward shifts, but the phenomenon was later shown in a situation involving a quantitative shift in reward. Crespi (1942) reported that rats in a runway showed a sudden decrement in running speed when shifted from a large to small reward, to a level below that of unshifted controls. When shifted from a small to a large reward, rats increased their speed above and beyond unshifted animals receiving the large reward. Crespi termed these effects "depression" and "elation," respectively, and assumed that they were due to emotional responses (frustration and joy). Clearly, S-R theory, which lacks an "expectation" component, was not capable of accounting for these behavioral changes

These findings prompted a move away from the Thorndikian idea that reward magnitude directly affects learning, and toward the notion that reward magnitude influences incentive motivation, which in turn, affects the behavior independently of learning. As Crespi (1942, p. 513) stated, "Incentive-value is profitably viewed as proportional to the distance between *level of expectation* (both of quality and quantity) and *level of attainment*." Thus, the emotional component is a change in motivation based on the difference between expectancy and the actual reward.

Zeaman (1949) coined the terms “positive contrast” and “negative contrast” in his experiments with rats and runways, using cheese as a reinforcer. Rats shifted from a 2.4 g cheese reinforcer for traversing a runway to 0.6 g increased their latency to the goal significantly above rats only given the 0.6 g reinforcer (negative contrast). He also found that rats shifted from the small to the large reinforcer decreased runway latency below unshifted large reward controls (positive contrast). The term “contrast” refers to the difference between the preshift and postshift rewards, and “positive” or “negative” refer to the direction of the shift. Later, the terms “successive” and “simultaneous” were also introduced; the former describes instances where the differing rewards are given one after another (as in all the studies cited so far), while the latter describes situations in which the experimental group receives both rewards throughout the experiment but in different contexts (Bower, 1961). Bower trained rats to expect a large reward in a black alley and a small reward in a white alley. These subjects were then compared to two groups which received only a large reward or only a small reward in both alleys. Rats taught to discriminate between the alleys ran slower for the small reward than rats that only received the smaller reward, and faster for the large reward than rats given only large

rewards. These effects are known, respectively, as simultaneous negative and positive contrast.

Vogel, Mikulka, and Spear (1968) devised an animal model for frustration based on consummatory behavior. Rats were given a 32% sucrose solution for 5 min daily for 11 trials, then shifted to a 4% solution for 6 trials. The shifted rats produced significantly fewer licking responses than controls that always received the 4% solution. Typically, the initial reduction in drinking behavior on the first day after the shift is very acute, but over subsequent trials the shifted group recovers to the same level of responding as the unshifted controls. This is called consummatory successive negative contrast (cSNC), to distinguish it from the experiments described by Elliott (1928) and Crespi (1942), in which the relevant behavior is instrumental (iSNC).

There are other types of contrast that must be distinguished from successive and simultaneous contrast. Behavioral contrast involves relative rates of responding and refers to the notion that performance of an instrumental response varies based on alternative rewards available in the same situation. Rates of responding to one component of a multiple schedule increase or decrease as the reinforcement schedule on another component decreases or increases, respectively (Reynolds, 1961). Anticipatory contrast refers to another form of behavioral suppression. Rats are given access to a less preferred reward and then given access to a more preferred reward immediately afterward. The lesser reward becomes a cue for predicting the greater reward. This anticipation of the greater reward results in suppression of responding to the smaller reward. Since the reward change is not surprising, it is unlikely that emotion plays a part in such a suppression. Chlordiazepoxide, a benzodiazepine anxiolytic, does not affect anticipatory

contrast (Flaherty & Rowan, 1988), indicating that the behavioral suppression in anticipatory contrast does not rely upon an emotional response.

These contrast effects can be explained with simple S-R theories, but they have several shortcomings. For example, Hull (1943) proposed that a compound stimulus was created by S combined with residual stimuli from the previous trials. When the reward is downshifted, the residual stimuli change, which in turn changes the compound stimulus, and results in a change in behavior. This interpretation is limited, however, since contrast effects can be obtained even when trials are spaced such that the residual stimuli dissipate (one trial per day; Weinstock, 1954).

Frustration Theory

Amsel (1992) developed a theory of frustration attributing the emotional reaction to the violation of a reward expectancy by the presentation of a smaller reward than expected. His qualitative model allows ordinal predictions to be made about processes that will arise before and after the reward downshift. First, experience with a relatively large reward creates an expectation of that reward. In the consummatory contrast setting, this is achieved through access to the large reward during preshift trials, where an association between some stimulus in the context (S) and the large reward allows S to control an approach response (R) and an expectation of the large reward (e_{large}; Figure 1a). Then, the subject unexpectedly receives a smaller reward during the postshift, generating a discrepancy between the expected and received rewards that results in an emotional reaction (Figure 1b). The emotional reaction is an unconditioned aversive internal state, termed primary frustration. Primary frustration is especially strong in the first shifted trial, when the animal has had no prior experience with the smaller reward. An association develops between the external cues (S) and the internal state of primary

frustration paired with them, through Pavlovian conditioning. This association induces an aversive anticipatory state, or an expectation of frustration, called secondary frustration (Figure 1c). At this point, therefore, S has the ability to control R_{app}, e_{Large}, and $e_{frustration}$. At the behavioral level, this multiple control of competing expectations can be seen as an approach-avoidance conflict (Miller, 1944). During postshift trials, the expectation of frustration also becomes counterconditioned to the smaller reward. In addition, a new expectation develops for the smaller reward, and the expectation for the large reward weakens (Figure 1d). Both of these factors contribute to the recovery of consummatory behavior to a level appropriate for the postshift incentive magnitude.

According to Amsel (1992), primary frustration has several properties. It invigorates behavior (e.g., lever pressing, Papini & Dudley, 1995), dramatically increasing response rates in animals when they encounter a surprising reward reduction (akin to pressing the button on a vending machine several times in rapid succession when it fails to deliver a beverage). Primary frustration is hedonically aversive, as animals will learn to escape from it if given the opportunity (Daly, 1974). It initiates search behavior (e.g. Flaherty, Troncoso, & Deschu 1979), as noted in the earliest reward shift experiments (see above). Primary frustration also maintains some stimulus properties on its own, retaining the ability to cue, for example, aggressive behaviors (Gallup, 1965), vocalizations, and increased locomotor activity (Papini & Dudley, 1997).

There are other additional consequences of surprising nonreward that occur in cSNC. For example, associated with reward downshift is the emission of an odor, which can actually serve as a signal to other rats (McHose & Ludvigson, 1966; Spear & Spitzner, 1966). Alone, this odor appears to be aversive, and can induce escape responses (Collerain & Ludvigson, 1972; Mellgren, Fouts, & Martin, 1973; Wasserman & Jensen,

1969); but can be counterconditioned or extinguished if no other aversive stimulus is associated (Collerain & Ludvigson, 1977).

Secondary frustration also has a distinct set of properties. Secondary frustration also invigorates behavior, as seen in animals partially reinforced during acquisition. These animals perform the instrumental response more vigorously than continuously reinforced animals. Goodrich (1959) trained rats to run an alley to receive rewards, either continuously or intermittently. Partially reinforced animals ran faster than continuously reinforced animals for the same reward. This partial reinforcement acquisition effect (PRAE) was most evident at the beginning of the alley and less evident nearer the goal. Secondary frustration is aversive as well, and animals will terminate a conditioned stimulus for nonreward if given the opportunity (Terrace, 1971). Flaherty, Becker, and Pohorecky (1985) reported elevated corticosterone release, an indicator of stress, in the second trial after shifting rats from 32% to 4% sucrose. In the first postshift trial, no corticosterone release was detected. This finding was replicated by Mitchell and Flaherty (1998). Secondary frustration also generates withdrawal from goal stimuli (Jones, 1970).

Based on Amsel's (1992) theory, it could be argued that in cSNC, the suppression of consummatory performance in the first shifted trial is controlled predominantly by primary frustration, whereas the suppression that occurs in the following trials (e.g., during the recovery of performance) is controlled by a mixture of primary and secondary frustration. The next section provides evidence consistent with this claim.

Factors Affecting SNC

There are many factors that can affect size of cSNC. For instance, level of food deprivation can profoundly change the contrast effect. Nondeprived animals shifted from 32% sucrose to 4% do not seem to recover from contrast (Grigson, Spector, & Norgren

1992; Riley & Dunlap, 1979). Presumably, nondeprived subjects have less need to consume any reward at all, and can avoid the smaller reward altogether. Highly deprived animals have more necessity in consuming the calories in the smaller reward, even though it may be less desired, and will therefore recover more quickly. However, experiments attempting to show the effect of deprivation levels side-by-side have indicated that lower deprivation levels make contrast less likely to occur. Several studies have revealed situations in which a high deprivation group exhibited contrast (iSNC and cSNC), whereas a low deprivation group showed no contrast (e.g., Cleland, Williams, & DiLollo, 1969; Flaherty & Kelly, 1973). It is possible that deprivation may serve as a catalyst in situations that normally yield very little contrast.

Another factor influencing contrast size is the disparity between rewards. In the iSNC situation, the larger the difference between the large and small reward, the larger the size of contrast (e.g., DiLollo & Beez, 1966; Gonzalez, Gleitman, & Bitterman, 1962). Even Crespi (1942) reported that rats shifted from 256 to 16 units of reward showed greater disruption of behavior than those shifted from 64 to 16. In fact, recent studies by Papini and Pellegrini (2005) using a cSNC situation indicated that the size of the behavioral suppression after a downshift is a constant proportion of the ratio between the concentration of the pre- and postshift rewards. For example, animals shifted from 32% sucrose to 8% would exhibit the same magnitude of contrast as animals shifted from 16% to 4%—a 4:1 ratio holds in both cases.

The intertrial interval (ITI) can also affect the SNC effect. Contrast effects achieved with an ITI of just a few minutes are much larger than contrast effects with an ITI of 24 h (Capaldi, 1972). Similarly, the retention interval between the subject's last experience with the preshift reward and the introduction of the postshift reward can

reduce contrast. Vogel, Mikulka, and Spear (1968) reported clear contrast when shifting subjects to 4% sucrose up to 10 days after the last 32% preshift trial. At 17 days, the effect waned to marginal significance, and after 32 days had completely disappeared. Flaherty and Lombardi (1977) gave rats a chance to discriminate between the preshift and postshift solutions, and then gave 10 days access to the 32% solution before a 10-day retention interval. This prior experience enhanced the degree of contrast, compared to the animals that did not receive prior discriminative training.

Prior experience can affect contrast in a variety of ways. Experience with the smaller reward before administration of the contrast training can reduce or eliminate contrast (Capaldi, 1972). The partial reinforcement extinction effect (PREE) refers to partially reinforced animals showing greater persistence when shifted to extinction than continuously reinforced counterparts, presumably due to counterconditioning of an expectation of nonreward (Amsel, 1992). Likewise, partial reinforcement during preshift training produces less contrast than continuous reinforcement in both iSNC and cSNC procedures (Mikulka, Lehr, & Pavlik, 1967; Pellegrini, Mustaca, Muzio, & Papini, 2004). With regard to Amsel's theory, this reduction of cSNC could be viewed as a consequence of the counterconditioning of frustration prior to the shift (Figure 1d). Each nonrewarded trial is like a shift to extinction, creating a level of frustration, which is paired with reward on the next reinforced trial. Eventually, secondary frustration becomes a signal for reward, and it encourages the instrumental or consummatory response, thus attenuating the SNC effect.

Pharmacological studies of SNC have resulted in some interesting findings. If primary frustration and secondary frustration are controlled by different mechanisms, they should be dissociable. Furthermore, on the previously mentioned assumption that

consummatory suppression is mainly dependent on primary frustration in the first postshift trial, but on secondary frustration in subsequent postshift trials, one would predict differential effects of drugs on these trials. For example, it has been shown that anxiolytic drugs can reduce the amount of contrast on the second, but not the first, postshift trial (e.g., Becker, 1986; Flaherty, Grigson, Demetrikopoulos, Weaver, Krauss, & Rowan, 1990; Flaherty, & Rowan, 1989). The benzodiazepine chlordiazepoxide (CDP) and midazolam both reduce contrast only on the second postshift trial (Becker, 1986; Flaherty, Lombardi, Wrightson, & Deptula, 1980). Several experiments demonstrate that benzodiazepines do affect behavior on the first trial when the trial is longer (Flaherty, Grigson, & Rowan, 1986) or the animal is repeatedly shifted (Flaherty, Clarke, & Coppotelli, 1996). Anxiolytics affect behavior only after some experience with the new, downgraded solution. Secondary frustration is a likely candidate on which benzodiazepines may be selectively taking effect.

Rowan and Flaherty (1987) conducted a series of experiments in which deprived rats were given access to either 32% or 4% sucrose for 5 min per trial for 10 trials; then, all rats were given 4% in 3 postshift trials and the number of licks recorded. An injection of morphine sulfate was given 20 min prior to testing on the second (Experiment 1) or first (Experiment 2) postshift trials. In both experiments, the contrast was significantly reduced for both 4.0 and 8.0 mg/kg morphine doses. Morphine is a nonselective opioid agonist, with an affinity for the μ, κ, and δ-opioid receptors. It is therefore unclear exactly how morphine acts to reduce contrast.

The effects of morphine were antagonized by pretreatment with naloxone, a nonselective opioid antagonist. Naloxone (0.5 mg/kg) was given before administration of an ineffective (1.0 mg/kg) or effective (4.0 mg/kg) dose of morphine on the second

postshift day. Naloxone had no effect on the ineffective morphine dose, but it reversed the effects of the 4.0 mg/kg dose of morphine on cSNC. Naloxone alone, however, did not produce a significant effect on cSNC at doses of 0.25, 0.5, and 1.0 mg/kg. Since no effect of naloxone was found, these experiments failed to support the idea that the opioid system is normally engaged in cSNC. However, the consummatory contrast procedure is susceptible to floor effects, given that response suppression is the measure of contrast. To avoid the masking of a possible opioid antagonist-induced increase in contrast size by a floor effect, conditions that normally produce very little contrast (i.e., little suppression) may be used.

Wood, Daniel, and Papini (2005) found that DPDPE, a δ-receptor agonist, reduces contrast on the first, but not the second postshift trial. After 10 trials (one trial per day) of preshift training with either 32% or 4% sucrose, rats were shifted to 4% for five trials. An injection of either 24 μg/kg DPDPE or vehicle was administered 6 min prior to testing on either the first or second postshift trial. Shifted animals given vehicle on the first shifted trial showed significant contrast, whereas those given DPDPE did not. However, subjects that received DPDPE on the second shifted trial were not different from animals given vehicle; DPDPE had no effect on contrast. This was the first compound discovered to reduce contrast selectively on the first postshift day, completing the dissociation of primary and secondary frustration with drugs such as the benzodiazepines and DPDPE.

Frustration shares similarities with another form of anxiety: fear. Gray (1987) suggested that fear and frustration are analogous, since they share many behavioral effects, depend upon the same brain structures, and are affected by the same drugs in similar ways. For example, the partial punishment extinction effect (PPEE) is very similar to the partial reinforcement extinction effect (PREE). In the PPEE, animals are

trained to collect a reward, but in some of the trials, an aversive shock is given together with the reward. The shock creates conditioned fear, which, as training continues, is in some trials paired with the reward. This type of pairing tends to reduce the disrupting effects of fear (in the PPEE situation), just as it tends to reduce the disrupting effects of anticipatory frustration (in the PREE situation; see above). As a result, when shifted to extinction, these animals are more persistent in performing the conditioned behavior than those that received only food in acquisition. The shock itself becomes a cue for reward, and is therefore counterconditioned in a similar manner to what happens in the PREE and in the SNC after partial reinforcement (see references above). Anxiolytic drugs increase suppression of the conditioned behavior. Administration of CDP has been shown to increase persistence during extinction in continuously reinforced animals (Fowler, 1974), while resulting in faster extinction for PREE rats (Demarest & MacKinnon, 1978). CDP, therefore, appears to be reducing the conditioned anxiety generated by reward loss. The faster extinction in PREE animals treated with CDP is very much like the faster recovery seen when secondary frustration (also conditioned anxiety generated by the reaction to reward loss) is reduced by anxiolytics.

Gray's (1987) comparisons were between fear, a conditioned expectation of pain, and secondary frustration, a conditioned expectation of primary frustration. The idea can be taken a step further. In the experiments reviewed by Gray (1987) as background for his fear=frustration hypothesis, fear was generally induced by the administration of electric shock to the animal’s feet, a stimulus that causes peripheral pain. The extension, then, takes the form of relating the two unconditioned events that support both fear and secondary frustration. Thus, if fear=secondary frustration, then pain=primary frustration. If these analogies are correct, they explain why some opioids (e.g., DPDPE), which are

notorious for their effects on pain (for a review, see McNally & Akil, 2002), affect cSNC selectively on the first postshift trial.

Anxiety and Conflict

Conflict occurs when there is competition between incompatible responses (Miller, 1944), such as when a behavior is rewarded and punished at the same time. Anxiety can be a result of such a conflict.

Anxiety can be a concept difficult to operationalize, but there are a variety of ways in which it can be studied. Since anxiety induces changes in behavior, anxiety levels can be inferred by examining behavioral changes in tests that invoke anxiety. Table 1 lists a variety of tests that have been used to assess anxiety (modified from Flaherty, 1991). The table classifies procedures according to how anxiety is induced, such as presenting aversive stimuli, removing appetitive stimuli, or exploiting "innate" tendencies. Each of these procedures has been divided between tests that involve or do not involve conflict. A few of these tests are described below as examples.

The defensive burying test exploits an "innate" tendency of rodents to cover a noxious or threatening stimulus with bedding material (De Boer & Koolhaas, 2003). A wall-mounted electric shock prod is placed in a familiar cage a few centimeters above the floor. Any contact with the prod results in shock to the animal. After the first contact with the prod, the animal's behavior is recorded for 10-15 min. Rodents tend to use their paws and snout to fling bedding over the shock prod to conceal it. Since the behavior does not involve competing responses, conflict does not seem to play a major role.

In contrast, the elevated plus maze, which has become a common test to measure anxiety, exploits innate tendencies in exploratory behavior to create conflict. The apparatus consists of two runways elevated some distance above the floor which cross in

the middle, creating four arms and a central platform. One of the runways (two opposing arms) has high walls, while the other runway is an open platform. The assumption is that closed arms offer protection, while open arms are perceived as being more dangerous. Anxiety is induced because the approach tendency to explore the open runways conflicts with the tendency to avoid open alleys. Anxiety is evidenced by elevated corticosterone concentrations, more fecal boli, and an increase of freezing responses when subjects are confined to open arms (Pellow, Chopin, File, & Briley, 1985). Rats prefer to spend less time in the open arms; and exploratory behavior favors the closed arms. Anxiogenic drugs, such as pentylenetetrazole and yohimbine, increase aversion to the open arms, while anxiolytics, such as chlordiazepoxide and diazepam, promote open-arm exploration. These results provide pharmacological validation for the elevated plus maze as a test of anxiety (Pellow et al., 1985). Anxiety is assessed by examining open arm entries and time spent in these arms. Usually, this is expressed as a percentage of total entries or of total time spent in the maze. Closed arm entries are used as a measure of locomotor activity. The elevated plus maze appears to be a reasonable test for anxiety, but there are several variables that must be carefully examined, such as platform construction, pretest handling, and scoring of behavior (see Hogg, 1996, for a review). Interestingly, the percent drop in lick rate in cSNC has a significant positive correlation with open arm entries and total entries in the elevated plus maze, which is consistent with the idea that primary frustration does not involve anxiety, since high anxiety animals display fewer open arm entries (Flaherty, Greenwood, Martin, & Leszczuk, 1998).

Many animal models of anxiety involve the presentation of aversive reinforcers, usually pain from electric shock. For example, in the PPEE (cited in p. 13, above), conflict is generated by competition between conditioned fear generated by shock and

conditioned approach induced by reward. In punished drinking (a form of operant conflict), the subject is deprived of water and then given access to a drinking tube. After a certain time or number of licks, a period follows in which subsequent licks are shocked, then the cycle is repeated. The drives of thirst and fear compete, creating conflict. Anxiety suppresses drinking behavior during the shock period. Anxiolytics reduce the anxiety, resulting in more licks during the shock period. Therefore, the number of licks after the beginning of shocks can be used as a measure of the anxiolytic efficacy of a drug (Vogel, Beer, & Clody, 1971). Only in a few situations is reward loss used as a measure of anxiety, such as in appetitive extinction and in successive negative contrast.

Approach-Avoidance Conflict

As mentioned before, conflict occurs when there is competition between incompatible responses (Miller, 1944). For example, a situation in which the subject has strong tendencies to approach and avoid the same goal will result in conflict. Thus, the question is raised: How do these responses compete and what is the final outcome?

Approach-avoidance conflict can be described in terms of gradients (Miller, 1944). The approach gradient refers to the tendency to approach a goal paired with a positive outcome (e.g., food). The gradient becomes stronger in closer proximity to the goal. Similarly, the tendency to move away from or avoid a place or object paired with a negative outcome becomes stronger when in closer proximity to it; this is an avoidance gradient. There is evidence that the slope of avoidance gradients is steeper than that of approach gradients, since the strength of avoidance increases more rapidly than that of approach as the goal is nearer (Miller, 1944). Underlying drives (e.g., hunger, pain) control the strength of the entire gradient, shifting it up or down.

Each of these assumptions has received empirical support. Brown (1940) trained a group of food-deprived rats to traverse a runway for food and another group to receive a shock. By using a stationary harness tethered to a scale, he was able to measure the amount of push or pull each rat exerted when placed at different distances from the goal. The result was exactly as described above, with stronger tendencies nearer the goal in approach and avoidance, and the slope of the avoidance gradient being steeper than that of the approach gradient. Brown also showed that a reduction in deprivation, or hunger drive, caused a reduction in the entire approach gradient's height. Weaker shock, likewise, resulted in a generally lower avoidance gradient.

Figure 2 depicts approach and avoidance gradients as described by Miller (1944). Since the slopes of approach and avoidance gradients differ, they must cross at some point. When the approach tendency is stronger than the avoidance tendency, a subject will approach the goal. When the avoidance tendency is greater than the approach tendency, the subject will retreat from the goal. At the point of crossing, approach equals avoidance and the subject should come to a stop, as the conflicting tendencies to retreat and to come closer are in equilibrium. The equilibrium point changes as a function of the underlying drive strengths. For example, as hunger increases, the approach tendency will increase, causing the crossing point of the two gradients to shift toward the goal. If either of the drives is strong enough, they may be shifted such that they do not cross; an animal will either go toward the goal without hesitation, or stay as far away from the goal as possible.

These assumptions about the interaction between approach and avoidance have also been demonstrated experimentally. Miller, Brown, and Lipofsky (cited in Miller, 1944) trained hungry rats to traverse a runway for food, which was in a location indicated

by a light. While eating the food near the light, an electric shock was administered. The animals were then tested without shock or food, and their locomotor behavior was recorded. There were several groups, each receiving a different combination of food deprivation levels and shock intensities. Animals ran part of the way, and then, as predicted, stopped at a distance that was dependent upon the relative strength of the two drives.

So far, Miller's (1944) model of conflict predicts that the subject will stop at the equilibrium point. In the studies outlined above, this seemed to be mostly, but not exactly, the case. As the subject approaches the goal, goal-associated stimuli and anticipatory responses facilitate the approach behavior. This causes approach behavior to continue past the equilibrium point, described by Miller (1944) as "psychological momentum." When the subject finally stops, the avoidance tendency is much stronger than approach, and a rapid retreat from the goal follows. Retreating induces internal cues that facilitate the retreat behavior, causing the subject to overshoot the equilibrium point once again. Together, these interactions result in an oscillation around the equilibrium point.

Measuring Conflict in the cSNC Situation

In terms of the cSNC effect, secondary frustration should interact with the 4% solution available on postshift trials to induce an approach-avoidance conflict. In turn, such a conflict should translate into the microstructure of consummatory behavior. However, very little research has focused on the microstructure of ingestive behavior in consummatory contrast. Grigson, Spector, and Norgren (1992) examined the microstructure of cSNC across trials, using deprived and nondeprived rats as subjects. Half of the subjects were deprived to 82% of their free-feeding weight, whereas the other

half was given food ad libitum. After 2 days of context exposure, the animals were allowed 5 min access to 1.0 *M* sucrose for 10 days, and then shifted to 0.1 *M* sucrose for 4 days. Unshifted control groups received 0.1 *M* sucrose throughout training. After the 4 postshift days, the deprivation conditions were reversed; those that were deprived were allowed to recover to their ad libitum weights, while their free-food counterparts were deprived to 82%. The reward downshift procedure was then repeated. The data collected included total licking per session, the number of "bursts" of licking (a series of licks with less than 0.5 s between licks), number of licks per burst, interburst interval, and interlick interval. All shifted animals (deprived and nondeprived) showed a decrement in total licks for 0.1 *M* sucrose compared to unshifted controls. Not surprisingly, this decrement persisted for nondeprived animals, whereas the deprived subjects recovered over the first two postshift days. Deprived shifted animals showed fewer licks per burst, and overall more bursts with longer intervals between bursts than unshifted controls. Similarly, nondeprived animals showed a reduction in licks/burst, and a greater interburst interval than unshifted nondeprived subjects, but failed to show an increase in the number of lick bursts.

The question remains, however: How does the microstructure of licking behavior change within a given trial? Is it possible to see oscillations in consummatory behavior similar to those observed in runway experiments? How is this measure affected by drugs that affect cSNC? The current proposal was designed to examine these questions using data gathered in previous experiments in our lab.

Establishing a New Measure of Conflict from Published Data

Traditional goal tracking and licking measures are not sensitive to within-trial measures of behavior that would be necessary to detect oscillations as described by

Miller (1944), and thus a new measure must be devised. This study provides an analysis of data collected from three experiments: Study A (Wood et al., 2004; Experiment 1), Study B (Pellegrini, et al., 2004, Experiment 1), and Study C (Pellegrini et al., 2004; Experiment 3). These experiments were conducted in the TCU lab as described in Table 2 and followed similar training procedures.

Procedures of Published Data

Subjects in all the experiments were naïve male and female rats, bred at the TCU vivarium. The animals were 90–110 days of age at the start of testing, and housed under a 12:12 h light:dark cycle (lights on at 07:00 h). Subjects were deprived to 81-84% of their free-feeding body weight via a daily feeding at least 15 min after the daily trial. Water was freely available in the home cages.

Four standard operant conditioning boxes were used, each 20.1 cm wide, 28 cm long, and 20.5 cm high. The floor of the boxes consisted of rows of stainless steel rods (0.4 cm diameter, 1.6 cm apart from center to center) parallel to the front wall of the box. A sipper tube, 6 mm in diameter, was inserted 1.5 cm into the box and retracted via a computer-controlled motor. Each conditioning box was surrounded by a sound attenuating chamber, equipped with a fan for air circulation and a speaker for background noise (80.1dB SPL, scale C). A computer in the adjacent room controlled the motors and recorded the goal tracking time (amount of time spent in contact with the sipper tube) in increments of 0.05 s. The total goal tracking time was recorded for the entire trial, and also stored into 5-s bins.

Sucrose solutions were prepared by weight, with 32 g sugar for every 68 g of water for 32% sucrose, 6 g sugar for every 94 g of water for 6% sucrose, 4 g sugar for

every 96 g of water for 4% sucrose, and 2 g sugar for every 98 g of water for 2% sucrose solutions. Distilled water and commercial sugar were used to prepare the solutions.

For Study A, rats received one trial/day for 17 trials. Animals were given 2 trials of context exposure, during which they were placed in the testing boxes for 5 min without introducing the sipper tube. Then, 10 preshift trials followed, in which animals were placed in the boxes, and after an average pretrial interval of 30 s (range: 15-45 s) the sipper tube was introduced. Downshifted animals received 32% sucrose solution during these trials, whereas unshifted animals received 4%. After 5 min, counting from the first lick, the sipper tube was retracted on the first break in contact with the sipper tube. The animals were removed after a mean posttrial interval of 30 s (range: 15-45 s). On trial 11 (and on the final four subsequent trials), all subjects received 4% sucrose. Control groups received access to the 4% solution in all except habituation trials. All groups were matched on the basis of sex. DPDPE (24 μg/kg) was given 15 min before trial 11 in one downshifted and one unshifted group. The other two groups received equal-volume saline injections.

For the two other studies (Studies B and C), rats received 20 preshift trials with access to 32% sucrose. Then, they received 10 postshift trials with access to either 4% sucrose (Study B) or either 2% or 6% sucrose (Study C). Control groups received 30 trials of 2%, 4%, or 6%. Aside from these differences, the procedures for all four experiments were the same.

Some pilot analyses suggested that there is a wave-like pattern of consummatory responding, which could show a microstructural oscillation underpinning approach-avoidance conflict. Figure 3 shows the average levels of goal tracking time (s) across a trial in 5-s bins for eight rats from Study A on trials 10, 11, 12, and 15. In the last preshift

trial, trial 10, the time spent in contact with the sipper tube remained steady during the first half of the trial and then dropped considerably toward the end of the trial. In trial 11, the first postshift trial, the pattern began to waver. The behavior became very variable by trial 12, but by trial 15 there was a recovery to a steadier pattern of responding as seen in the preshift period. A method of analysis had to be developed that could accommodate the pattern based on the data already collected.

The measure of consummatory behavior must be organized into bins for a pattern to emerge. Bin length affects the resolution of the consummatory pattern and, therefore, can have a great impact on the type of analysis proposed in this study. Bins that are too short are likely to be too variable to clearly reflect the presence of approach-avoidance conflict, whereas bins that are too long are likely to be insensitive. Since all previous data were collected in 5-s bins, this was the starting point for the analyses reported in this study.

Study A was the first to be analyzed because the number of trials in this study is typical of most cSNC experiments (see Flaherty, 1996). The experiment was designed to test the effects of DPDPE when injected on either the first or second postshift trial (Wood et al., 2005; Experiment 1). When the data were collected, the goal tracking time (in 0.05-s units) of each 300-s trial was stored into bins. Each datum represents 5 s of goal tracking. Although the measurements were done on a scale of 0-100 for each 5-s bin (5/0.05 = 100), the results will be described and presented on a 0-5 s scale for clarity. Bin scores of 2.5 s or greater reflect a 5-s period where the animal spent at least half of that time in contact with the sipper tube. Each trial was divided into waves by counting a series of bins with values above 2.5 as the rising phase of a wave, and the subsequent series of bins with values below 2.5 as the falling phase of the wave. Incomplete waves

(waves that did not have a falling phase, or a wave that continued past the end of the trial) were not counted. For example, a complete trial with no bin values below 2.5 was scored as a zero. Data from one of the animals in the unshifted group could not be located in the computer records for trials 13 and 14.

The data were analyzed on an individual subject basis. The following seven features were measured:

(1) *Frequency.* Frequency was scored as the total number of waves per trial. This measure reflects the overall variability in drinking behavior.

(2) *Period.* Period was defined as the average number of bins per wave. Frequency is inversely proportional to period, such that as period length increases, frequency decreases.

(3) *Amplitude.* Amplitude referred to the average difference between the highest bin value and the lowest bin value. Amplitude and period were also scored for the rising phase and falling phase of each wave. Amplitude reflects the strength of the approach or avoidance response. Stronger responses should yield scores near the maximum (5) or minimum (0), respectively.

(4) *Rising phase period.* Since the data are stored in 5-s bins and reflect goal tracking time instead of individual licks, burst duration as defined in previous studies could not be measured (e.g., Grigson, Spector, & Norgren, 1992). Therefore, a new measure was devised that reflected the relative time spent drinking. The rising phase, the series of bins in which the animal drinks more than half of the time (goal tracking scores at or above 50), should reflect the building of an approach response. The rising phase period was the number of bins contained therein.

(5) *Rising phase amplitude.* The rising phase amplitude was the highest bin value within the rising phase.

(6) *Falling phase period.* The falling phase was the portion of the wave in which the rat drank less than half the time (goal tracking scores below 2.5). The properties of the falling phase should reflect an avoidance response, similar to an interburst interval as defined by Grigson et al. (1992). The falling phase period was measured as the number of bins therein.

(7) *Falling phase amplitude.* The falling phase amplitude was the lowest bin value within the falling phase.

These seven measures, frequency, period, amplitude, rising period, rising amplitude, falling period, and falling amplitude, were examined to determine any differences between the shifted rats and unshifted controls. Figure 4 provides an example of each of these measures as plotted in an experimental and control animal on trial 11. For all statistical tests, the α value was set to 0.05. For brevity, individual *p* values will not be reported.

Study A, cSNC. Seven separate analyses of variance (ANOVAs) were used to detect differences between shifted and unshifted groups for each postshift trial, one for each measure. The postshift phase of the original contrast effect for Study A (Wood et al., 2005, Figure 1) is reproduced in Figure 5a. In the original report, there was a significant decrease in goal tracking time in the shifted group relative to the unshifted on trials 11-13. For the subsequent trials, the shifted rats recovered to the level of the unshifted controls.

The frequency measure (Figure 5b) also yielded significant differences on trials 11-13. On trial 11, the shifted animals showed a significantly higher number of waves

than unshifted controls, $F(1, 14) = 22.39$. This difference was also present on trial 12, $F(1, 14) = 11.38$ and trial 13, $F(1, 13) = 6.26$. On trials 14 and 15, the differences between groups disappeared, Fs < 1.05.

A series of ANOVAs indicated significant differences for the period measure (Figure 5c) on trial 11, $F(1, 10) = 14.53$, but these differences were nonsignificant on subsequent trials. The same was true for the rising period measure (Figure 5d), $F(1, 10) = 16.62$. The falling period (Figure 5e) showed no differences between groups on any trials.

Analysis of the amplitude (Figure 5f) and falling amplitude (Figure 5g) measures yielded no significant differences between groups. The rising amplitude (Figure 5h) indicated differences on trial 11, $F(1, 10) = 8.30$, and trial 13, $F(1, 9) = 5.24$, only.

Notice that there were no differences between groups on trial 10 for any of the measures, indicating that the differences arose as a consequence of the reward downshift and dissipated in conjunction with the recovery from cSNC. For subsequent studies, only the frequency measure will be analyzed, due to the inconsistent nature of the other measures. This decision is elaborated in detail in the Discussion section below.

Study A, DPDPE. Wood et al. (2005, Figure 1) reported a significant attenuation of cSNC on trial 11 after administration of DPDPE, as is reproduced in Figure 6a. Pairwise comparisons indicated a significant cSNC effect in the vehicle groups but not in the DPDPE-treated groups. There was a significant group effect on Trial 11. The difference between the two downshifted groups was also nonsignificant.

The DPDPE groups were next analyzed to determine the effects of DPDPE administered before Trial 11 on the frequency measure (Figure 6b). Shifted animals showed higher wave frequencies than unshifted animals in both drug and saline conditions. Both shifted groups eventually recovered to the level of unshifted controls.

DPDPE had no apparent effects on the frequency measure and, if anything, it was accompanied by an increase in frequency.

To support these findings, a drug by contrast by five postshift trials ANOVA showed a significant effect of contrast condition, $F(1, 14) = 21.63$, an effect of trial, $F(4, 11) = 10.87$, and a significant contrast by trial interaction, $F(4, 12) = 8.69$. The drug had no effect, $F < 1$. Separate drug by contrast ANOVAs for each trial revealed no effects of drug on the frequency measure for any trials, Fs < 1.

Study B, CRF vs. PRF. Frequency data from Study B were analyzed next. This particular experiment had a preshift phase twice as long as the preshift of Study A. The study was designed to examine the effects of partial reinforcement (PRF) on cSNC (Pellegrini et al., 2004, Experiment 1). Figure 7a shows the goal tracking time for the postshift phase of this study (reproduced from Pellegrini et al., 2004, Figure 1). Significant differences were found on postshift trials 21-27, 29, and 30 for the continuously reinforced (CRF) animals. PRF rats showed significant contrast on postshift trials 21-23 and 26, indicating faster recovery than their CRF counterparts. Shifted PRF group performance was significantly higher than shifted CRF group performance for postshift trials 21-26 (i.e., cSNC was significantly reduced for partially reinforced groups). Unshifted groups did not differ.

Figure 7b shows the frequency measure for the same experiment. A Contrast X Schedule X Trial ANOVA revealed significant effects of contrast, $F(1, 28) = 29.66$, schedule, $F(1, 28) = 6.30$, and trial, $F(9, 28) = 6.78$, with significant trial by contrast, trial by schedule, and trial by contrast by schedule interactions, Fs $(9, 28) > 3.06$.

Differences arise between the shifted and unshifted CRF groups in the postshift period, and appear to persist until the end of the experiment. Separate one-way ANOVAs

for each trial, with LSD posthoc comparisons, confirmed that there were no significant differences between the shifted and unshifted CRF groups in the last preshift trial, but significant differences emerged in the first postshift trial and persisted until the end of the experiment (except for trial 27), without recovery, Fs(1, 28) > 1.04.

PRF groups did not differ in the preshift, but the shifted group frequency was significantly above the unshifted group on the first postshift trial. Unlike the CRF groups, this difference disappeared on trial 25 and never reappeared. Once again, separate one-way ANOVAs for each trial, with LSD posthoc comparisons, supported these observations, Fs(1, 28) > 1.04.

The shifted PRF group recovered more quickly than the CRF groups, but how did they compare to each other? Again, they did not differ in the preshift period, but the PRF-trained rats showed higher frequencies on the first postshift trial. The differences disappeared for the next two trials, but by trial 24, the PRF trained rats were showing significantly lower frequencies than their CRF counterparts. This trend continued until the end of the experiment, with the exception of trial 27 when the differences were nonsignificant. Unshifted PRF and CRF groups differed only on trial 24, when all animals in the PRF group scored zero on the frequency measure. Separate one-way ANOVAs for each trial, with LSD posthoc comparisons, supported these assessments, Fs(1, 28) > 1.04.

Study C, 32-2 vs. 32-6. Finally, Study C (Pellegrini et al., 2004, Experiment 3) was analyzed using the frequency measure. This study was designed to test the effects of downshift magnitude on partial reinforcement in cSNC. The original contrast effects (Figure 8, postshift data reproduced from Pellegrini et al., 2004, Figure 4) showed that the contrast magnitude was a direct function of the discrepancy between preshift and

postshift solutions. Groups shifted from 32% to 6% showed less contrast and faster recovery than groups shifted to 2%. CRF groups shifted to 2% showed significant contrast on postshift trials 21-26, 29, and 30, while CRF groups shifted to 6% showed significant contrast only on postshift trials 21 and 22. As in Study B, PRF significantly reduced contrast effects and induced faster recovery. PRF groups shifted to 2% showed contrast on postshift trials 21-24, and PRF groups shifted to 6% differed significantly from controls only on the first postshift trial.

Figure 9 depicts the frequency measures for Study C. Rats shifted to 2% showed several differences between groups (Figure 9a). The most marked difference is in the unshifted control groups. The trend for the PRF trained control animals to show numerically higher frequencies than CRF trained controls continued from trial 20 to 30, but these differences were statistically significant only on trials 20-23 and 25. Shifted groups, 32-2P and 32-2C, differed only on trial 25, with the PRF group frequencies above the CRF group. Since the shifted groups were very similar, the differences in the control groups account for most differences between PRF and CRF groups that received 2% sucrose in the postshift phase. Group 32-2C had higher average frequencies than Group 2-2C on trials 21-24, 26, and 28, with recovery by trials 29 and 30. Group 32-2P had significantly lower frequencies than Group 2-2P on trial 20, but after the shift rose significantly above the controls on trials 24, and 25. This was the first instance in which differences occurred on the last preshift trial, with both 32-2 groups exhibiting lower frequencies their respective control groups on trial 20.

The 6% groups showed a different pattern of results. Independent one-way ANOVAs, with LSD posthoc comparisons, for all eight groups revealed that rats shifted to 6% sucrose exhibited higher frequencies than unshifted controls on trial 21,

independent of prior training with CRF or PRF schedules (Figure 9b). Beginning with trial 22 and continuing to the termination of the experiment, however, there were no significant differences between any groups receiving 6% sucrose in the postshift phase.

Discussion

Study A showed that the frequency measure is the most clear and reliable method of quantifying the wave-like patterns of consummatory behavior in downshifted rats, and showed consistent results across Studies A, B, and C. The other measures are less informative for a variety of reasons.

First and foremost, the other measures are yoked to the frequency measure. The frequency measure determines the number of waves available to calculate the other measures. If a particular trial contains no full waves (a frequency of zero), no other measure can be computed for that trial. Additionally, frequency affects the other measures dependently. For example, the number of waves (frequency) is inversely proportional to the period. Therefore, the periods become much longer for very low frequencies, or nonexistent for trials that do not include a complete wave. In addition, amplitude is dependent on the period, since longer periods are more likely to have a larger distribution of bin values. Correlations between these measures for each trial can be seen in Tables 3-8. In general, the correlations hold true for trials where the rats were undergoing a downshift, but break down in the preshift or after recovery from cSNC. The reduction in size of these correlations probably reflects the dependence on frequency, since unshifted animals show very low frequency scores, which results in less data in the other measures for comparison. The falling period and falling amplitude were not well correlated with the other measures, but they did not reflect differences between the

groups to begin with. These two measures scored near the floor for both groups across all trials, which doubtlessly limited their usefulness.

Overall, period, amplitude, rising period, falling period, rising amplitude, and falling amplitude, tend to either be redundant, expressing nothing that the frequency measure does not express, or fail to reflect the differences between groups. Due to their dependence on frequency, their utility for describing the data diminishes drastically with preshift data and trials after recovery.

While partial reinforcement had attenuating effects on the goal tracking measure of cSNC, frequency did not change (Study A) or increased (Study C) after the shift, and recovered across the postshift phase. In the cases where differences were found between PRF and CRF shifted groups, the PRF groups were inclined to recover faster than the CRF groups, as is found in the goal tracking measure. If frequency is a measure of conflict, then this means that partial reinforcement induces more oscillations early on, but allows conflict to subside more quickly than in a continuous reinforcement situation.

The average frequencies across the entire postshift phase were plotted according to the discrepancy between solutions for shifted groups in Studies B and C (Figure 10). The trend that emerges from these data is that larger discrepancies between solutions (i.e., shifts from 32-2 rather than 32-6) tend to generate higher frequencies, rising to a ceiling. When under partial reinforcement, the ceiling is reached at a higher discrepancy than when under continuous reinforcement. This can be understood in terms of using partial reinforcement to "inoculate" against conflict, via counterconditioning, as described by Pellegrini et al. (2004). With counterconditioning (of the avoidance response) from partial reinforcement working against conflict, a larger shift is required to reach the peak

frequency (i.e., induce peak conflict behavior as indicated by the frequency measure). A single experiment that reinforces this finding would be prudent.

Another interesting finding is that DPDPE had no significant effects on the frequency measure, even though it significantly attenuated the contrast effect in the overall goal tracking time. Since DPDPE affects the first postshift trial, but not the second, it is involved in the modulation of the initial reaction to reward downshift. It does not affect the later trials on which, according to Amsel's (1992) theory, conflict arises. While the drug significantly attenuated the contrast effect as assessed by the goal tracking measure, the frequency measure remained similar to animals who received saline. This partially validates the frequency measure as an assessment of conflict, rather than a redundant measure of cSNC as indicated by the goal tracking time, and demonstrates the dissociability of the two measures.

A potentially problematic result from Studies A, B, and C is the significant difference in the frequency measure between shifted and unshifted groups on the first postshift trial, when the rat has not had sufficient conditioning to induce conflict. It is possible that the conflict begins to arise at the end of the first postshift trial, and traditional measures used in cSNC are not sensitive to changes within the trial. This could also mean that frequency does not reflect conflict, but describes another aspect of cSNC. Exploration of changes within the first postshift trial is a practical direction for future analysis.

Effects of CDP on Frequency

In order to validate the frequency measure as a measure of conflict, a second experiment involving CDP was executed to complement the results of the first experiment. As described above, CDP has been shown to attenuate contrast selectively on

the second postshift trial (Flaherty et al., 1980), the trial in which conflict becomes involved, according to Amsel's (1992) theory. In Study A, DPDPE had no effect on frequency while it reduced goal tracking on the first postshift trial, where conflict is presumably not present. Within-trial data from prior experiments involving CDP and cSNC was unavailable, so an experiment was conducted to obtain the evidence. If CDP significantly attenuates the frequency measure while DPDPE has no effect (completing the double dissociation), the frequency measure can be considered a measure of conflict with greater confidence.

Method

Subjects. Subjects were 32 naïve Long Evans rats bred at the TCU vivarium, half of which were male and half female. The animals were 90 days of age at the start of testing, and housed under a 12:12 h light:dark cycle (lights on at 07:00 h). Subjects were deprived to 81-84% of their free-feeding body weight via a daily feeding at least 15 min after the daily trial. Water was freely available in the home cages.

Apparatus. The apparatus used in this experiment were described in Studies A, B, and C, except that the sipper tube was inserted such that it protruded 2 mm into the box instead of the 1.5 cm described above. Sipper tube length was adjusted in an attempt to more closely replicate the conditions used by Flaherty et al. (1980), and also to achieve a finer resolution of the drinking behavior. The 32% and 4% sucrose solutions were prepared as described in Studies A, B, and C.

Procedure. Subjects were divided into two groups for the preshift period, shifted and unshifted, and balanced according to sex and litter of origin.

The training program consisted of a mean 30 s pretrial interval (range: 20-40 s) in which the house light was turned on. At the end of this interval, the sipper tube was

inserted, and the rats were allowed to drink for 5 min following the first contact with the tube. At the end of the 5 min, the mean 30-s posttrial interval was repeated in which the house light was on but the sipper tube was retracted. Once the final interval ended, the house light turned off, and animals were removed from the testing box and placed in their home cages.

Each rat was always trained in the same testing box; two rats from each group were trained in each of the four boxes. Rats were trained in eight squads of four, each balanced by group. Squad membership remained constant, but the order of testing was varied daily. Downshifted rats received access to a 32% sucrose solution and unshifted rats received 4% sucrose solution. After 10 daily sessions of preshift training, the downshifted and unshifted groups were again divided into two groups each, matched according to responding on trial 10, thus forming four groups: 32-4V, 4-4V, 32-4CDP, and 4-4CDP. The balance for sex, litter, and testing box was maintained in the final group assignments. On all subsequent trials, all animals received 4% sucrose solution. Trials continued daily until the rats fully recovered from the effects of the downshift, for a total of 8 postshift trials.

Drugs. Chlordiazepoxide hydrochloride (Sigma, U.S.A.) was dissolved in biological saline to make a solution of 5.0 mg/ml. CDP (5.0 mg/kg) was administered to the CDP groups and equal volume saline injections to the vehicle groups 15 min before the start of trials 11 and 12.

Results

First, the goal tracking scores obtained during the preshift trials were analyzed. A 2 X 2 X 10 (Contrast X Drug X Trial) ANOVA revealed a significant effect of Trial, $F(9, 28) = 98.60$, and a significant Trial X Contrast interaction, $F(9, 28) = 2.38$. This reflected

the acquisition curve for goal tracking and the tendency for animals drinking 32% sucrose to exhibit higher goal tracking times than animals drinking 4% sucrose.

Postshift performance is shown in Figure 11a. A 2 X 2 X 8 (Contrast X Drug X Trial) ANOVA on the postshift period indicated significant effects of Trial, $F(7, 28) = 15.60$, Contrast, $F(1, 28) = 20.52$, and a Trial X Contrast interaction, $F(7, 28) = 8.39$. These effects reflected the contrast effect and subsequent recovery of downshifted animals to the level of unshifted controls (Figure 11a). Drug effects were not significant, although a Trial X Drug interaction approached, but never reached significance, $F(7, 28) = 2.05$, $p = 0.051$.

One way ANOVAs with LSD comparisons for each postshift trial revealed significant contrast effects on trials 11-15 for vehicle groups, and significant contrast effects on trials 11-16 for CDP groups.

For the Frequency measure, shown in Figure 11b, a 2 X 2 X 8 (Contrast X Drug X Trial) ANOVA on the postshift period demonstrated no significant within- or between-subject effects, Fs < 1.4. Similarly, one-way ANOVAs with LSD comparisons for each postshift trial exposed no significant differences between any of the groups throughout the postshift phase.

Discussion

In light of these results, the goal tracking times were plotted according to gender, as shown in Figure 12. The result was that the female subjects appeared to be insensitive to the effects of CDP. Flaherty et al. (1980) used male rats exclusively in all of their experiments with CDP. The male rats from the present experiment appeared to be sensitive to the effects of the drug, but not in the manner found by previous research. In both the control group and the shifted group, CDP administration tended to enhance

consummatory behavior, such that the goal tracking times were above that of their vehicle counterparts. On trial 13, when CDP was no longer given, the contrast effect again looked normal, with both CDP groups responding similarly to the vehicle groups. It is possible that control group animals in previous experiments were responding near the ceiling for licking behavior, minimizing the influence of CDP in unshifted subjects while allowing a significant increase in shifted animals. It should be noted, however, that this experiment was novel in that injections occurred on trials 11 and 12, rather than only on one of these trials, and this procedural difference may have also influenced the results. Another reason this experiment may have failed to replicate previous CDP studies is the injection time. In the present study, CDP was administered 15 min before testing, whereas Flaherty et al. (1980) and Flaherty et al. (1986) administered CDP 30 mins prior to testing.

The failure of the rats to recover from contrast within the first five postshift trials was also unusual. For example, compare these results with those of Study A, in which the saline groups recovered by trial 14. This suggests an additional factor may have influenced the experiment. For example, the shortened sipper tube introduced in The present experiment may have increased the effort required to perform the drinking behavior, which additively affected consummatory suppression.

The lack of differences in the frequency measure may be a reflection of the unusual results of this experiment, or it may also indicate the presence of an uncontrolled factor. When compared to Study A, the pattern of results in the shifted vehicle group is as expected, starting with low frequencies which increase after the shift and eventually recover. The unshifted control groups begin with higher frequencies at the end of the preshift, which continue across the postshift period, instead of staying near the floor as in

Study A. Changes in sipper tube length could have induced a degree of conflict in the control groups or otherwise affected the frequency measures. One could speculate that increased effort to perform a behavior might affect the relative value of the reward, such that rats receiving 4% sucrose would drink less than rats drinking 32% not only because of less benefit from 4%, but also because the cost of the behavior more heavily influences the cost/benefit ratio for drinking the smaller solution than the larger solution. In turn, this could create a conflict between approach to the solution and avoidance of the energy expenditure required for drinking, thus influencing frequency.

General Discussion

The present experiments provide some evidence consistent with the concept of conflict developed by Miller (1944), using consummatory behavior in the cSNC paradigm. The present study was encouraged by the application of the classic ideas of conflict theory (Miller, 1944) and frustration theory (Amsel, 1992) to the case of cSNC. The basic theoretical claim underlying these studies is that anticipatory frustration conditioned during reward downshift provides the avoidance component of the approach-avoidance conflict that ensues in cSNC (Papini, 2003; Wood et al., 2005). Within-trial variations in consummatory behavior could be related to conflict, and the frequency measure was devised to detect such variability. To determine the importance of the frequency measure, several questions may be asked.

First, does frequency tell us anything at all about consummatory behavior, or is it an arbitrary factor? Evidence from Studies A, B, and C show that there are usually no differences in frequency in the preshift phase, but they arise in the postshift phase. Thus frequency seems to be related to the reward downshift. Additionally, the frequency of shifted rats recovers to the level of unshifted controls, similar to goal tracking time. The

relevance of the frequency measure lies, therefore, in its emergence during the postshift phase, and in the transient nature of these changes.

Second, does frequency tell us something new, or is it a redundant measure of cSNC shown by more traditional measures? Particularly interesting are the situations in which goal tracking differs from frequency. For example, partial reinforcement attenuates goal tracking times but can increase frequency, even if recovery occurs on the same trial for both measures, as was the case in Study B. Also, DPDPE attenuates goal tracking on trial 11, while the frequency remains unaffected. These differences dissociate the two measures and establish frequency as an index of something new, not a redundant reflection of goal tracking times.

Next, does frequency capture conflict in cSNC, or is it an index of some other factor involved? Evidence that frequency is a reflection of conflict comes from the orientation of the data. After the downshift, when conflict is predicted to increase according to Amsel's (1992) theory, the frequency measure increases in shifted animals. Goal tracking, which is more closely associated to the drinking behavior itself, decreases after the shift. The increase in frequency during the theoretical peak of conflict is consistent with the view that frequency is a reflection of conflict.

Another behavioral clue that is consistent with this view comes from the effects of partial reinforcement on cSNC. PRF reduced goal tracking times, but increased frequency early in the postshift trials. According to Amsel's (1992) theory, PRF should countercondition frustration by pairing the memory of reward loss in a previous trial to the reward in subsequent trials. This reduces the disruption in drinking after the downshift, but the aversive properties of the frustration are likely to remain intact. This is measured by goal tracking as more drinking (relative to CRF shifted rats), which

increases the amount of experience with the shifted solution. More experience with the solution will arouse the aversive association more often, causing greater conflict which registers as higher frequencies. In addition, PRF speeds the recovery of contrast in goal tracking. Recovery is presumably due to counterconditioning. In PRF rats, counterconditioning is already active on the first shifted trial, which results in faster recovery for goal tracking. Conflict diminishes as the expectation of the large reward weakens and the expectation for the small reward grows. Frequency recovers more quickly in PRF rats because the expectation of the large reward has already been weakened by counterconditioning during preshift trials.

Further behavioral evidence for frequency as a measure of conflict is derived from differential shift magnitudes. Larger shifts should result in more conflict than smaller shifts, since larger losses of reward should create stronger avoidance drives. Indeed, frequencies increase more after the shift when the disparity between solutions is greater.

The interpretation that frequency measures conflict is also consistent with pharmacological evidence from the opioid agonist DPDPE. According to Wood et al. (2005), DPDPE selectively reduces goal tracking scores when administered on trial 11 when primary frustration occurs. Conflict is engaged on trial 12, when the expectation of frustration is aroused. Because of this dissociation, DPDPE should not affect conflict. Indeed, DPDPE had no effect on the frequency measure in Study A.

There is also evidence that is not consistent with the view that frequency is a measure of conflict. For example, the dissociation between primary and secondary frustration on trials 11 and 12 implies that conflict is not involved on the first postshift trial since the competing expectations have not yet developed. However, a significant increase in frequency was present on the first postshift trial in every instance reported

here in which there were differences in frequency found between downshifted and unshifted rats in the postshift phase. Because of this, it could be argued that frequency captures some other aspect of the cSNC situation besides conflict. The other implication is that the distinction between primary and secondary frustration and when each becomes established is not as clear as most interpretations of Amsel's (1992) theory predict.

The other finding that questions frequency as a measure of conflict is the failure to reduce conflict when under the influence of CDP. If CDP selectively attenuated frequency in the present experiment, then it would be very difficult to argue that the frequency measure is not related to conflict. However, no differences were found between any of the groups, a result inconsistent with the results from Studies A, B, and C, and also with the literature on the effects of CDP on cSNC (Flaherty, 1996). The problems with The present experiment discussed previously render the overall verdict of the effects of CDP on frequency inconclusive.

It is unknown how other behaviors change when frequency changes. For example, after the downshift, other behaviors have been shown to increase in occurrence, such as activity levels (Papini & Dudley, 1997). It is unclear whether frequency captures avoidance of the sipper tube, or approach to other stimuli, such as search for the missing reward. Flaherty proposed a multi-stage model of cSNC, which describes detection, rejection, search and recovery (Flaherty, 1996; Mitchell & Flaherty, 1998). Frequency may be related to both the rejection and search stages described by this model, which would explain differences on frequency in the first postshift trial.

This research has potential implications for the study of conflict, anxiety, and stress. At present, little research in these fields has focused on microanalyses of behavior. The method of analysis in these experiments is innovative in that it emphasizes the

importance of examining microstructural changes in behavior. Potential applications of this method to the cSNC paradigm include assessment of the onset of anxiety and manipulations that modulate the anxiety. Since agents that affect only the first postshift trial (i.e., DPDPE) have no effect on the frequency measure, the pattern of behavior represented by frequency suggests that conflict may arise in the first postshift trial. This means that interpretations of Amsel's (1992) theory may need to be revised to incorporate the onset of conflict in the first postshift trial. There may be differences related to the nature of the behaviors measured in cSNC and iSNC. Traversing a runway for food involves a different type of response and different types of stimuli compared to drinking a sucrose solution. In iSNC, measurements of behavior are purely anticipatory, while in cSNC the reward is constantly sampled throughout testing. In cSNC, the conflict may potentially begin to develop during the measurement of the behavior. The connection between cSNC and iSNC is clear, but the behavioral effects cannot be clearly translated from one situation to the other. Translation from theory to behavior is not always a perfect fit, either. The oscillation described in theory by Miller (1944) was observed by Jones (1970) as hesitation in the runway, not as clean oscillations around an equilibrium point. It is difficult to predict how "oscillations" translate into patterns of consummatory behavior, how those will relate to the oscillations seen in the iSNC situation, and which, if any, more purely relates to conflict.

This kind of analysis can be applied to other situations in which a more conventional measure of anxiety is unavailable. Furthermore, a new method for measuring conflict could allow more accuracy in determining the effectiveness of various agents on behavior, notably, anxiolytic drugs. Future studies should target anxiolytic drugs for further validation of the frequency measure as a measure of anxiety.

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Table 1
A Sampling of Animal Models of Anxiety

	"Innate" tendencies	Presentation of aversive reinforcers	Omission of appetitive reinforcers
No conflict	• Hole-board exploration • Defensive burying	• One-way avoidance • Conditioned taste aversion • Potentiated startle • Fear conditioning • Escape	• Partial reinforcement acquisition effect • Frustration effect
Conflict	• Elevated Plus maze • Food neophobia • Light/dark test	• Partial punishment extinction effect • Operant conflict • Two-way avoidance • Passive avoidance	• Extinction • Successive negative contrast • Partial reinforcement extinction effect

Table 2

Summary of experiments available for reanalysis of data

Experiment	Strain	Groups	*n*=	Preshift trials	Postshift trials
A	Long-Evans	32-4 V	8	10	5
		4-4 V	8		
		32-4 DPDPE	8		
		4-4 DPDPE	8		
B	Wistar	32-4C	8	20	10
		4-4C	8		
		32-4P	8		
		4-4P	8		
C	Wistar	32-2C	8	20	10
		2-2C	8		
		32-6C	8		
		6-6C	8		
		32-2P	8		
		2-2P	8		
		32-6P	8		
		6-6P	8		

Note. In all cases, consummatory behavior was recorded in 5-s bins.

Table 3
Pearson's coefficients of correlation between measures on trial 10, Study A

	Period	Amplitude	Rising Period	Rising Amplitude	Falling Period	Falling Amplitude
Frequency	-.442	-.169	-.432	.347	-.338	.697
Period		.865(**)	.998(**)	.413	.521	-.646
Amplitude			.872(**)	.730(*)	.346	-.408
Rising Period				.439	.461	-.620
Rising Amplitude					-.121	.326
Falling Period						-.642

* $p < 0.05$ (2-tailed).
** $p < 0.01$ (2-tailed).

Table 4
Pearson's coefficients of correlation between measures on trial 11, Study A

	Period	Amplitude	Rising Period	Rising Amplitude	Falling Period	Falling Amplitude
Frequency	-.785(**)	-.768(**)	-.778(**)	-.775(**)	.165	.353
Period		.736(**)	.995(**)	.608(*)	-.254	-.460
Amplitude			.710(**)	.686(*)	.045	-.751(**)
Rising Period				.634(*)	-.345	-.400
Rising Amplitude					-.444	-.036
Falling Period						-.465

* $p < 0.05$ (2-tailed).
** $p < 0.01$ (2-tailed).

Table 5
Pearson's coefficients of correlation between measures on trial 12, Study A

	Period	Amplitude	Rising Period	Rising Amplitude	Falling Period	Falling Amplitude
Frequency	-.881(**)	-.470	-.907(**)	-.718(**)	.668(*)	.074
Period		.684(*)	.997(**)	.581(*)	-.363	-.458
Amplitude			.653(*)	.652(*)	.113	-.819(**)
Rising Period				.601(*)	-.433	-.402
Rising Amplitude					-.473	-.099
Falling Period						-.506

* $p < 0.05$ (2-tailed).
** $p < 0.01$ (2-tailed).

Table 6
Pearson's coefficients of correlation between measures on trial 13, Study A

	Period	Amplitude	Rising Period	Rising Amplitude	Falling Period	Falling Amplitude
Frequency	-.726(*)	-.294	-.565	-.452	-.354	.041
Period		.518	.661(*)	-.006	.612(*)	-.506
Amplitude			.506	.219	.145	-.851(**)
Rising Period				.502	-.190	-.220
Rising Amplitude					-.537	.326
Falling Period						-.429

* $p < 0.05$ (2-tailed).
** $p < 0.01$ (2-tailed).

Table 7
Pearson's coefficients of correlation between measures on trial 14, Study A

	Period	Amplitude	Rising Period	Rising Amplitude	Falling Period	Falling Amplitude
Frequency	-.799(*)	.161	-.841(**)	-.222	.804(*)	-.333
Period		.164	.995(**)	.250	-.512	-.051
Amplitude			.119	.593	.295	-.873(**)
Rising Period				.240	-.597	-.001
Rising Amplitude					-.049	-.124
Falling Period						-.394

* $p < 0.05$ (2-tailed).
** $p < 0.01$ (2-tailed).

Table 8
Pearson's coefficients of correlation between measures on trial 15, Study A

	Period	Amplitude	Rising Period	Rising Amplitude	Falling Period	Falling Amplitude
Frequency	-.897(*)	-.388	-.892(*)	-.579	.025	.330
Period		.161	1.000(**)	.561	-.270	-.071
Amplitude			.148	.795	.534	-.992(**)
Rising Period				.551	-.290	-.059
Rising Amplitude					.316	-.713
Falling Period						-.552

* $p < 0.05$ (2-tailed).
** $p < 0.01$ (2-tailed).

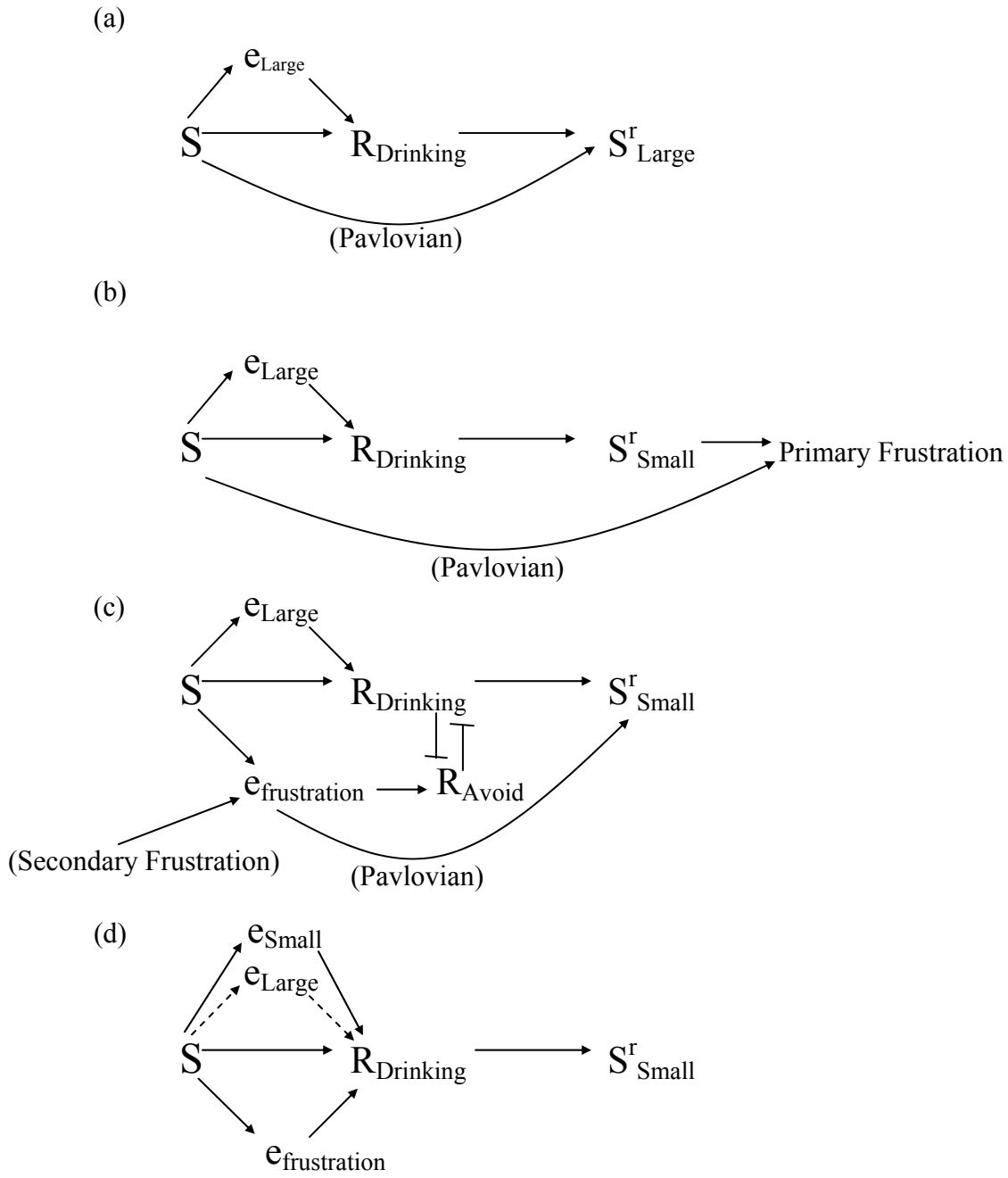


Figure 1. Amsel's (1992) theory applied to cSNC: (a) preshift trials, when an expectation for the large reward arises from pavlovian pairings between the test chamber and 32% sucrose; (b) trial 11, in which the expectation of 32% sucrose is violated by receiving the 4% sucrose which generates primary frustration, which in turn is paired with the contextual stimuli; (c) trial 12, in which the contextual cues now arouse competing expectations for reward and frustration, and in which an expectation of frustration is paired with reward; and (d) trial 15, in which the aversive aspect of the expectation of frustration has been counterconditioned, and the expectation for the small reward has become stronger and the expectation for the large reward has diminished.

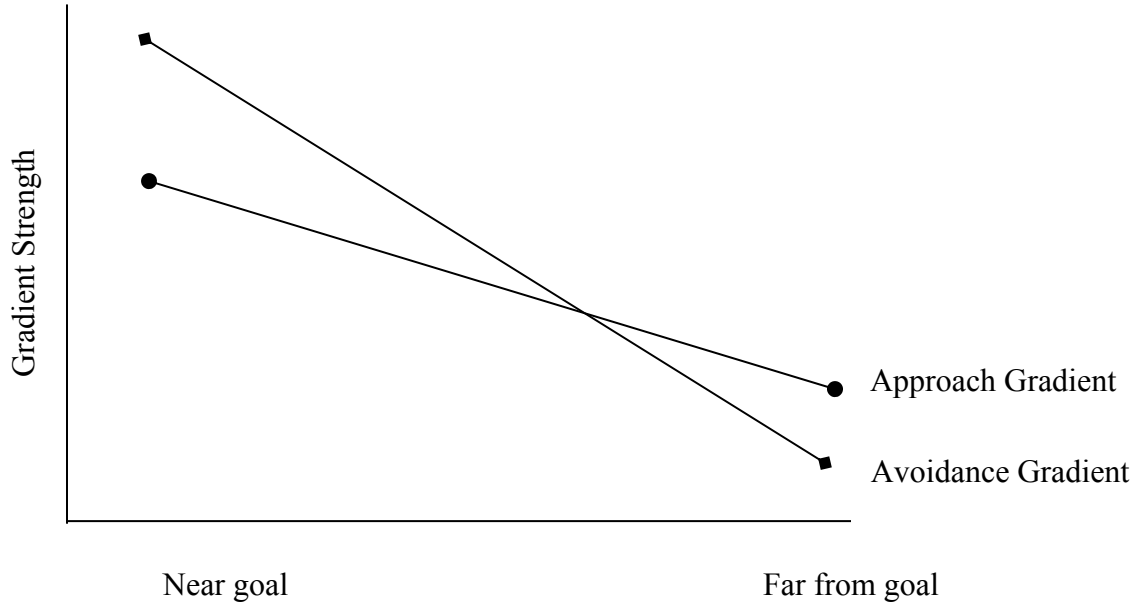


Figure 2. Approach and avoidance gradients as described by Miller (1944).

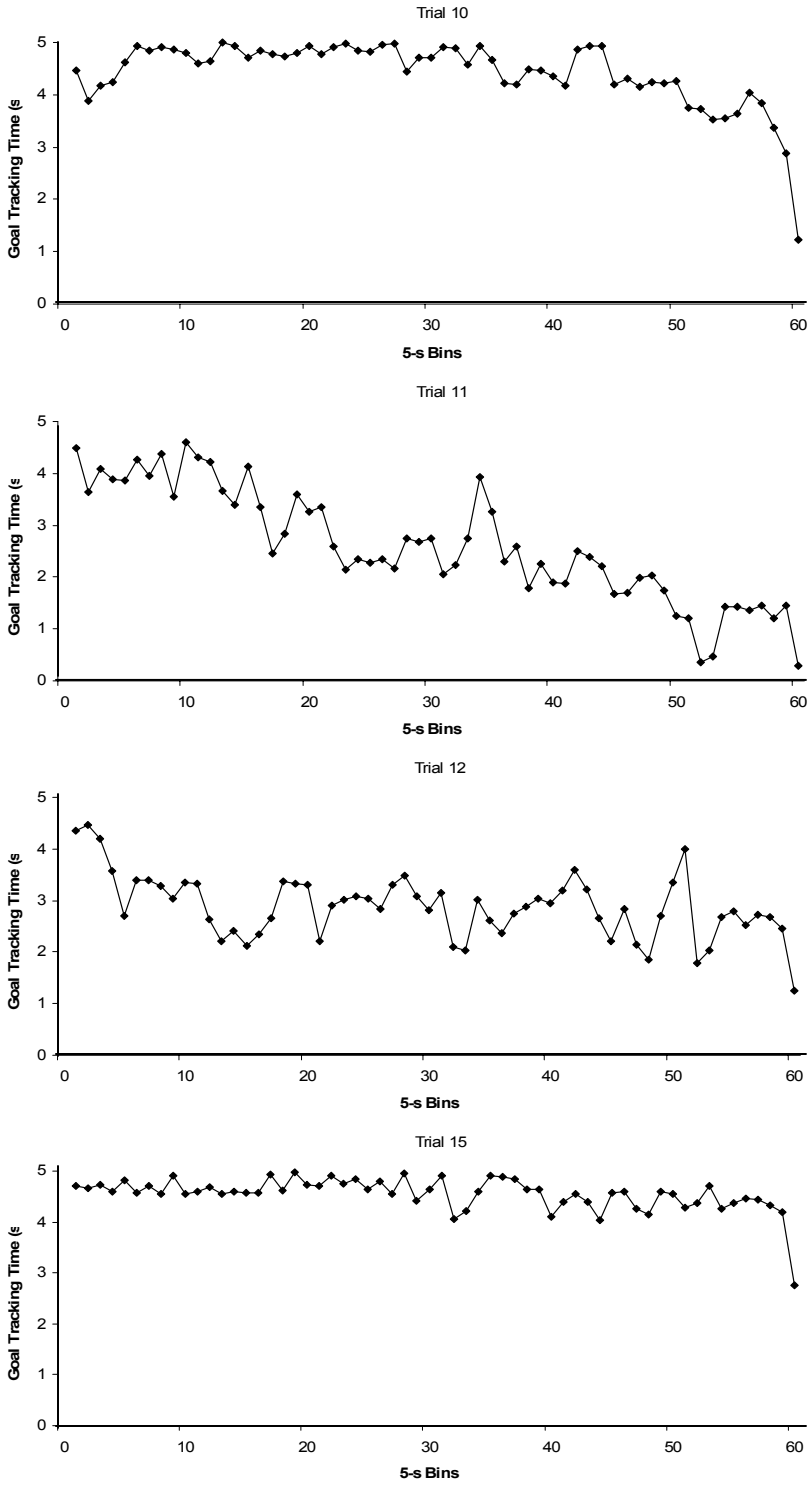
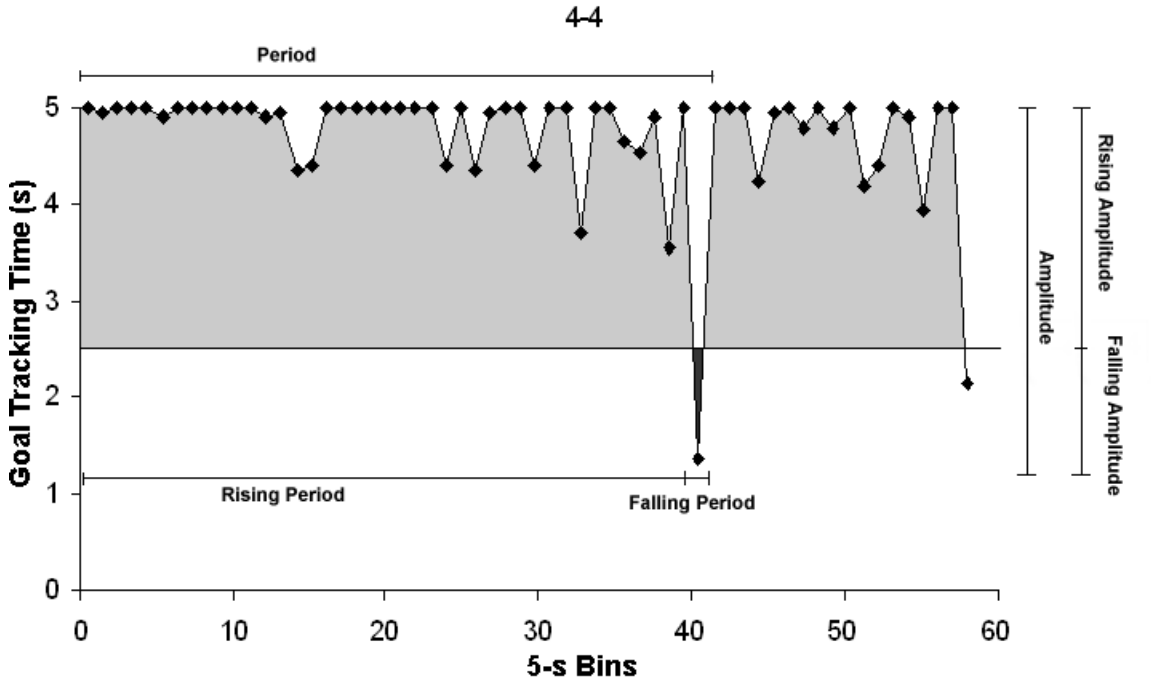


Figure 3. Average goal tracking scores for shifted rats in Study A in 5-s bins for (a) trial 10, (b) trial 11, (c) trial 12, and (d) trial 15.

(a)



(b)

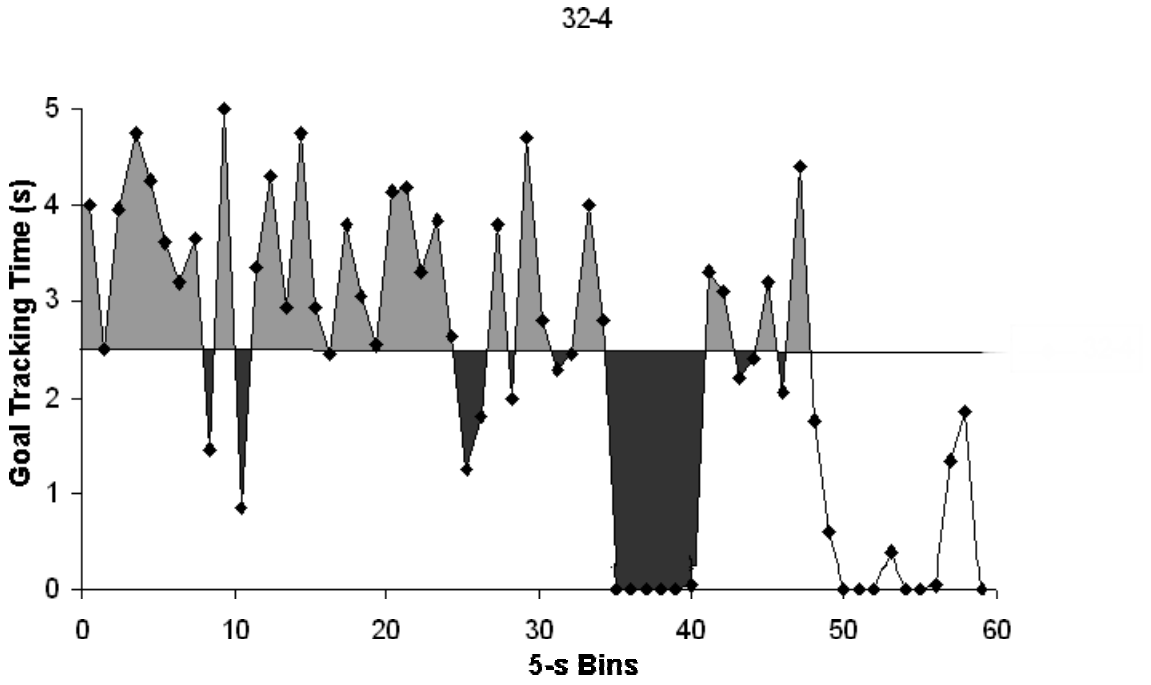


Figure 4. Sample binned data for (a) an unshifted rat, and (b) a shifted rat on trial 11.

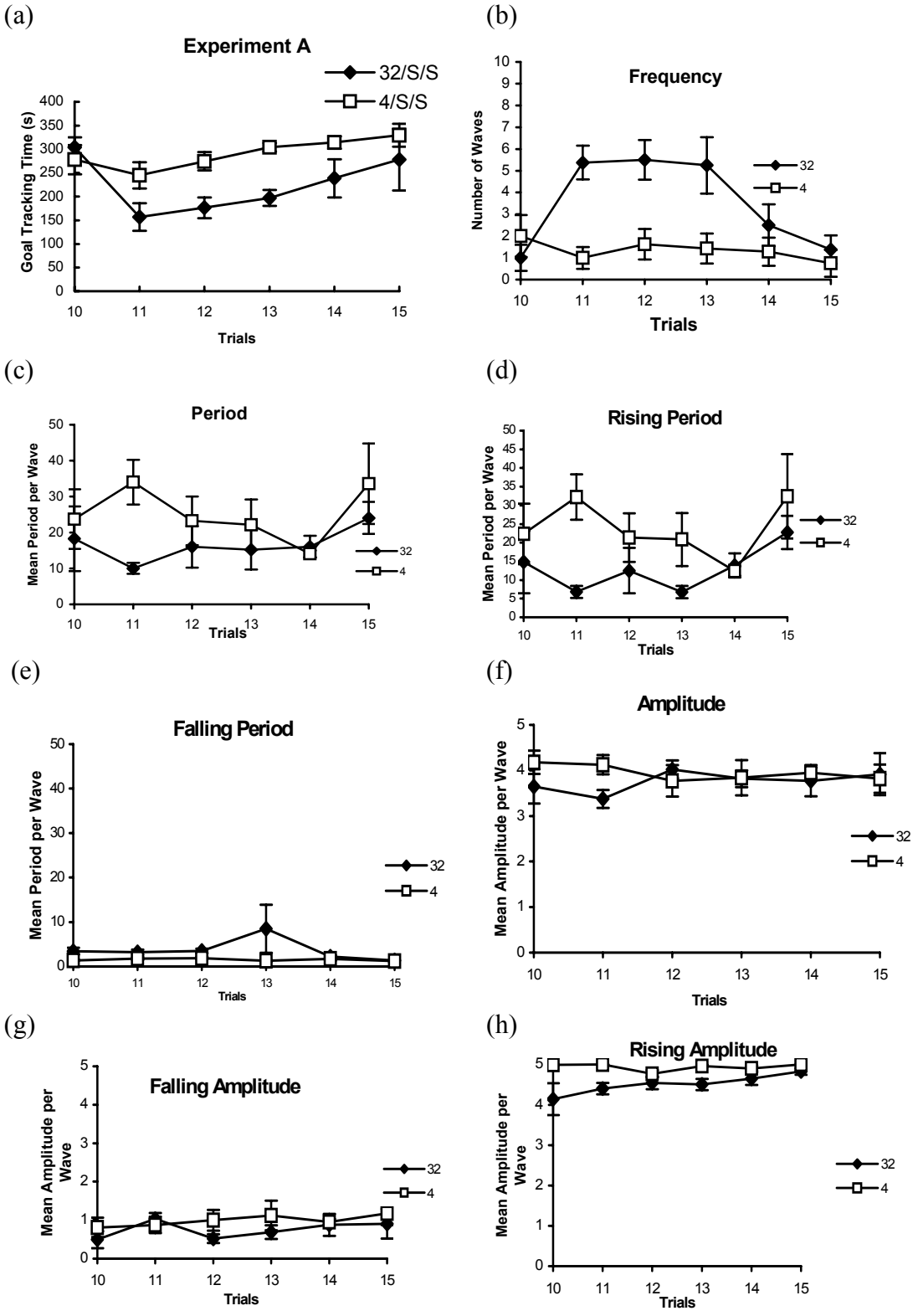
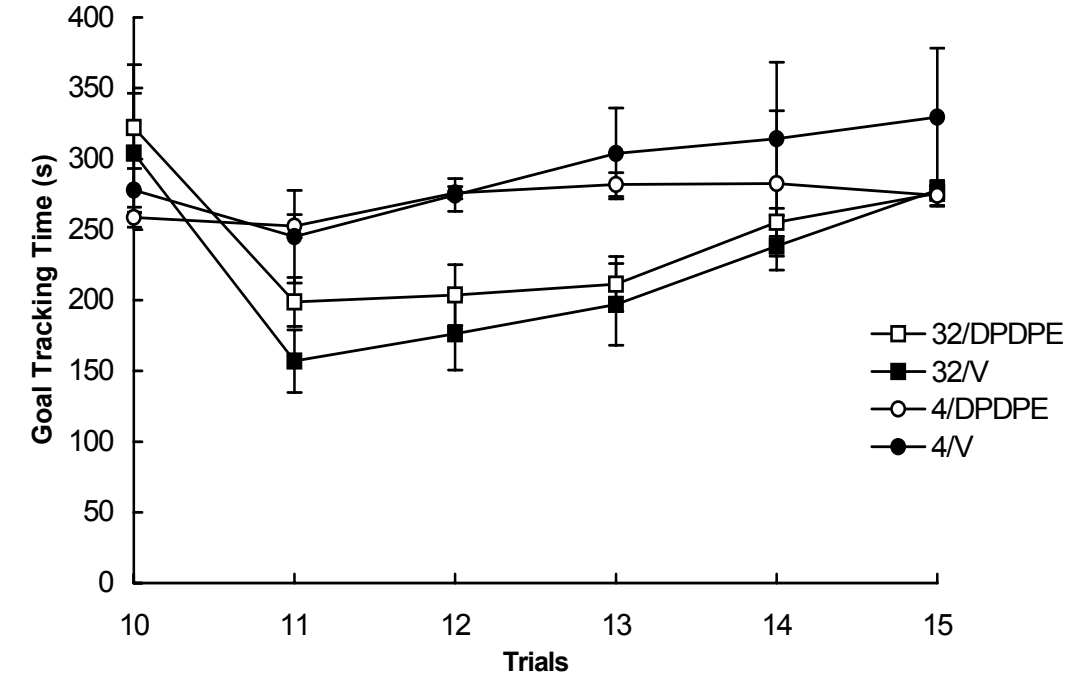


Figure 5. Postshift data for each trial from Study A saline groups: (a) goal tracking, (b) frequency, (c) period, (d) rising period, (e) falling period, (f) amplitude, (g) falling amplitude, and (h) rising amplitude scores.

(a)



(b)

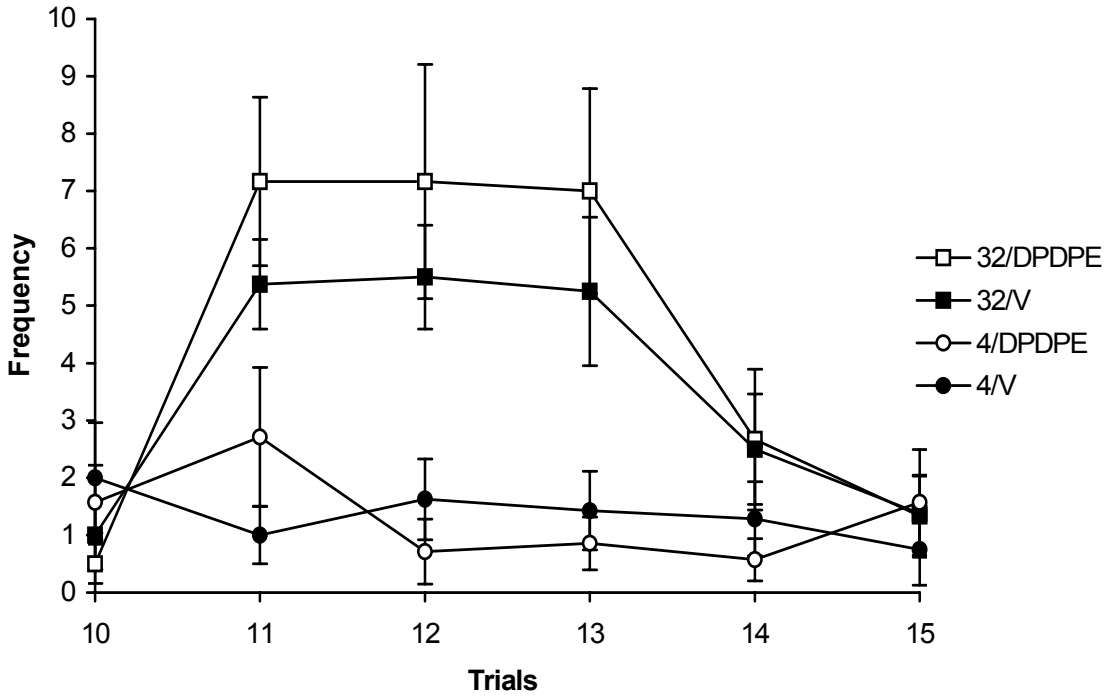
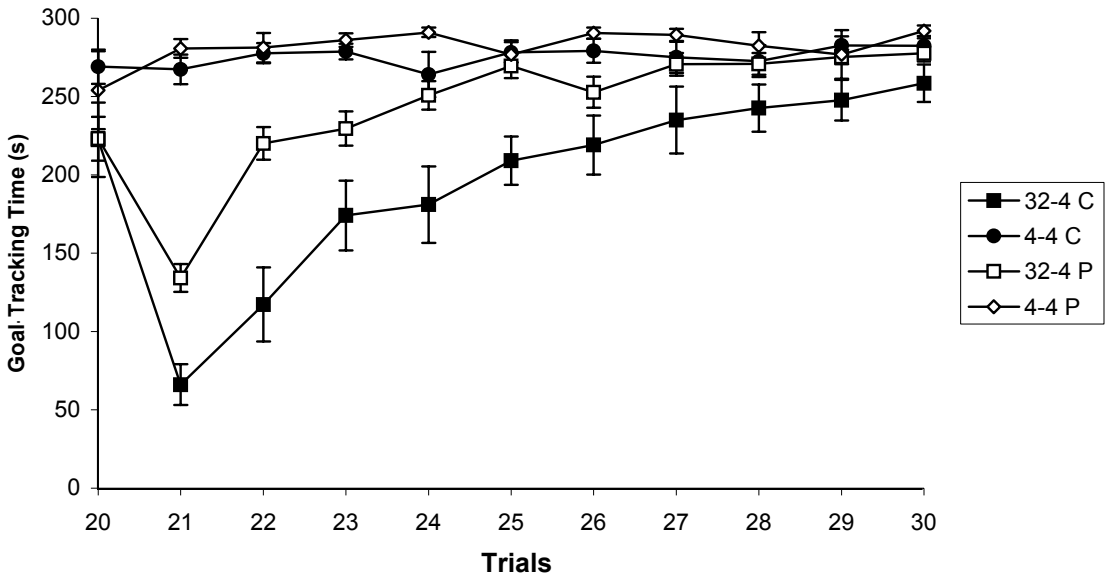


Figure 6. Postshift (a) goal tracking times and (b) frequency scores for Study A, saline and DPDPE groups.

(a)



(b)

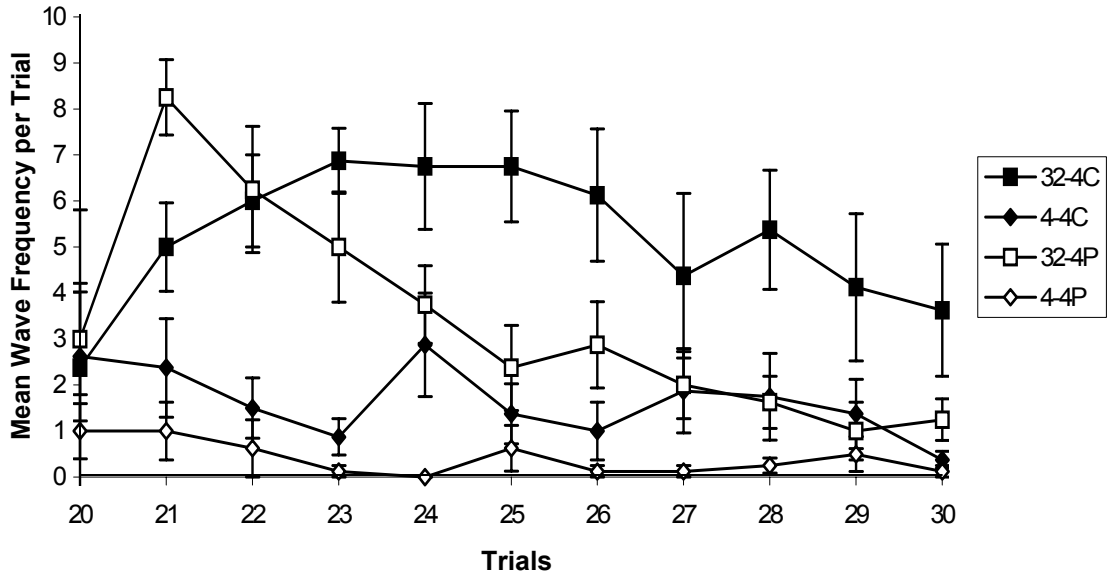
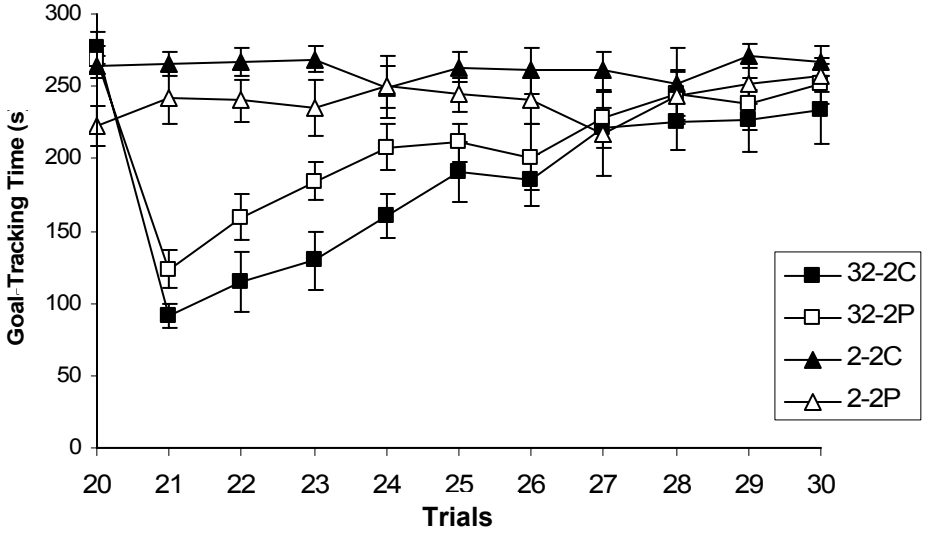


Figure 7. Postshift (a) goal tracking times and (b) frequency scores for Study B, CRF and PRF groups.

(a)



(b)

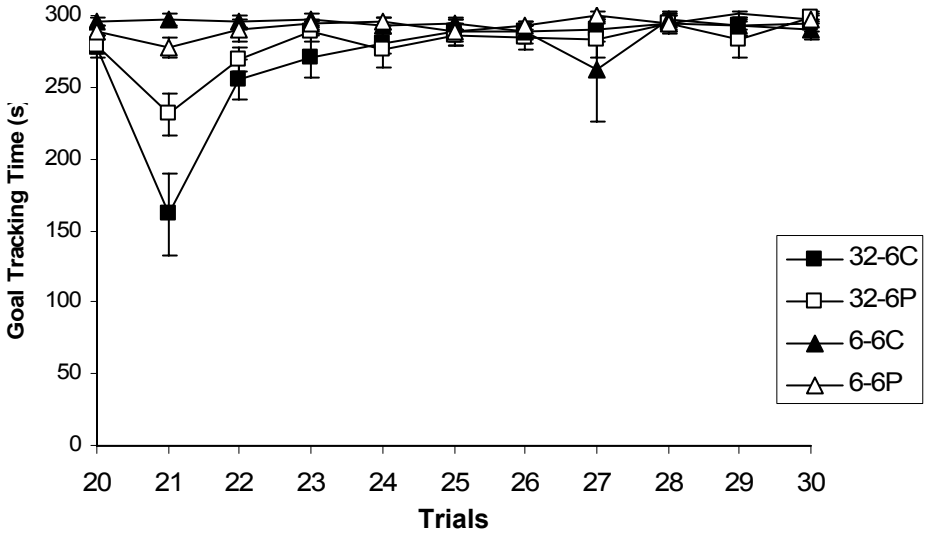
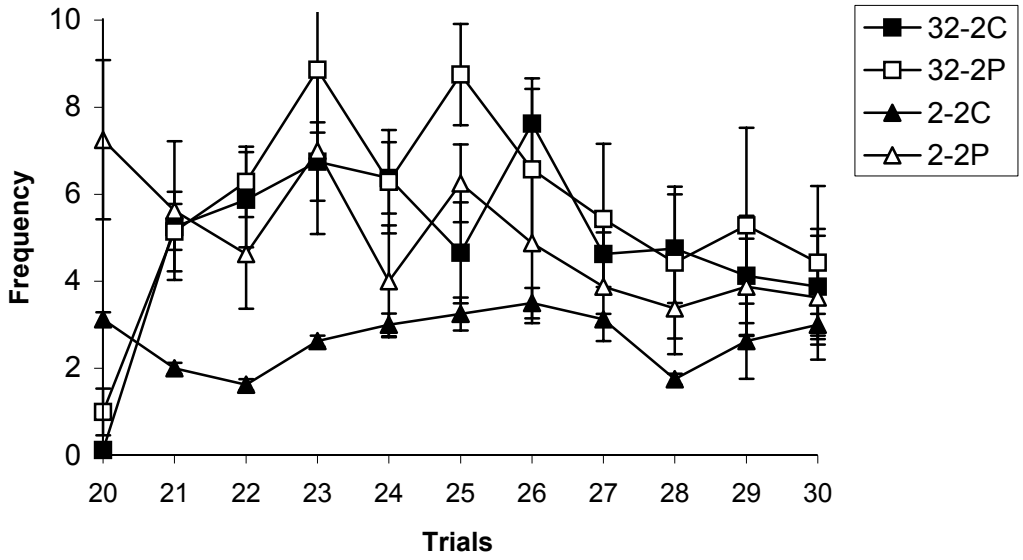


Figure 8. Postshift goal tracking times for (a) rats receiving 2% sucrose and (b) rats receiving 6% sucrose in the postshift phase of Study C, CRF and PRF groups.

(a)



(b)

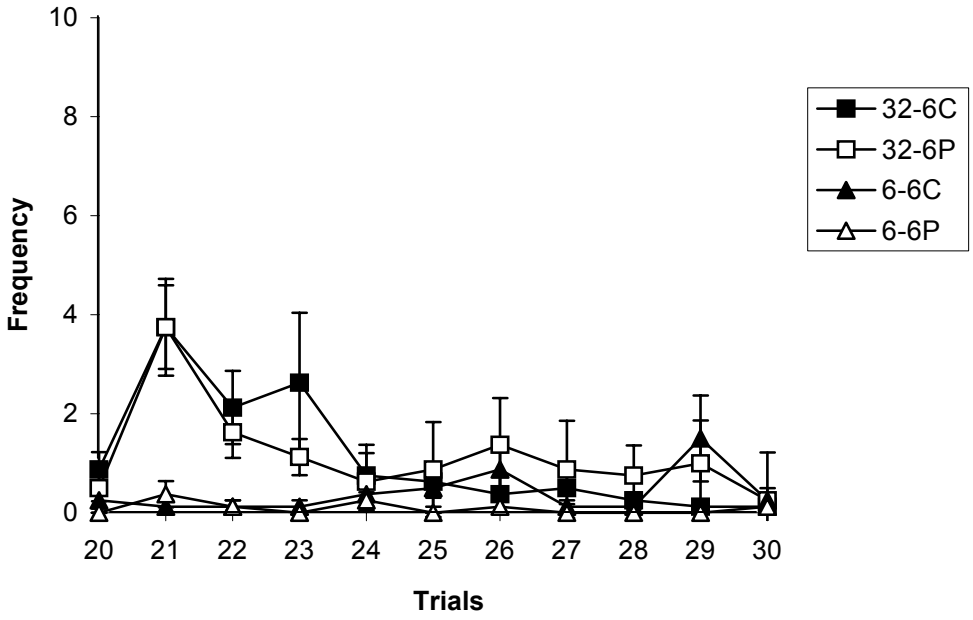


Figure 9. Postshift frequency scores for (a) rats receiving 2% sucrose and (b) rats receiving 6% sucrose in the postshift phase of Study C, CRF and PRF groups.

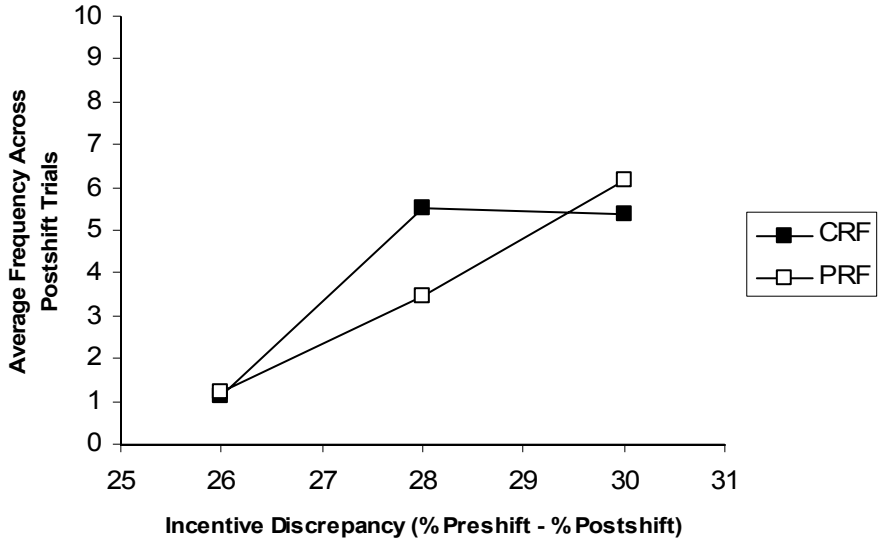
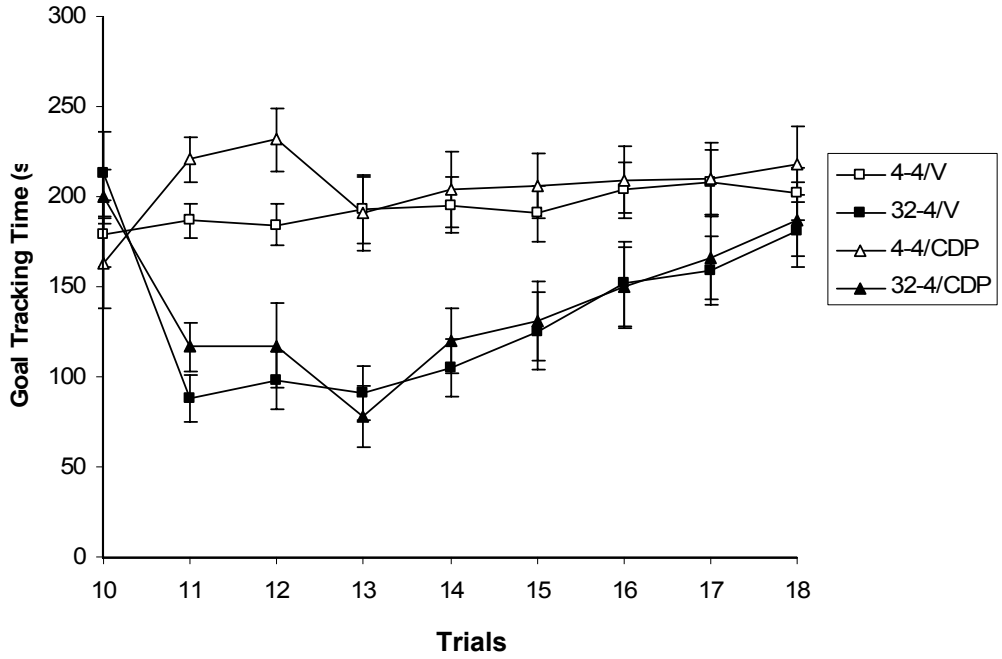


Figure 10. Average frequency across postshift trials as a function of incentive discrepancy for PRF and CRF groups from Studies A and B.

(a)



(b)

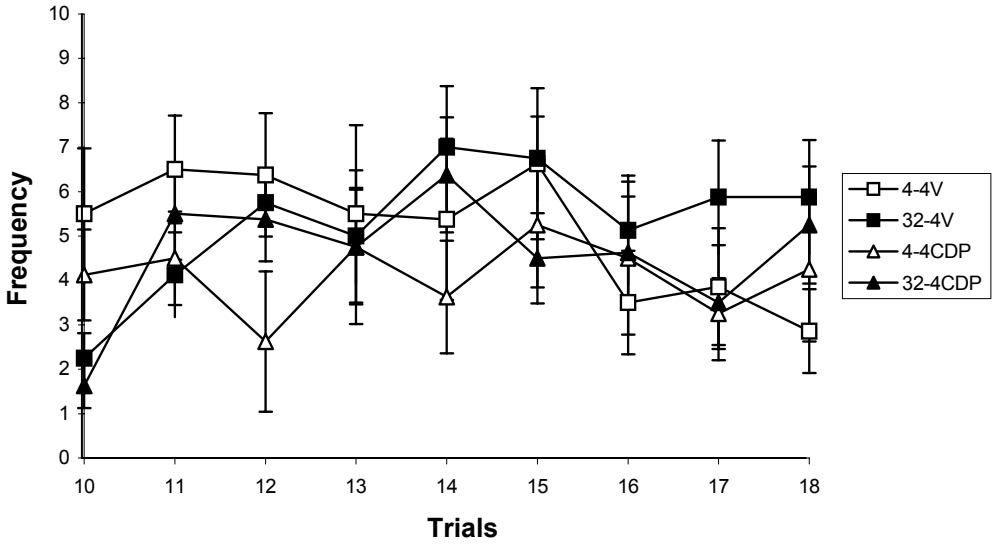
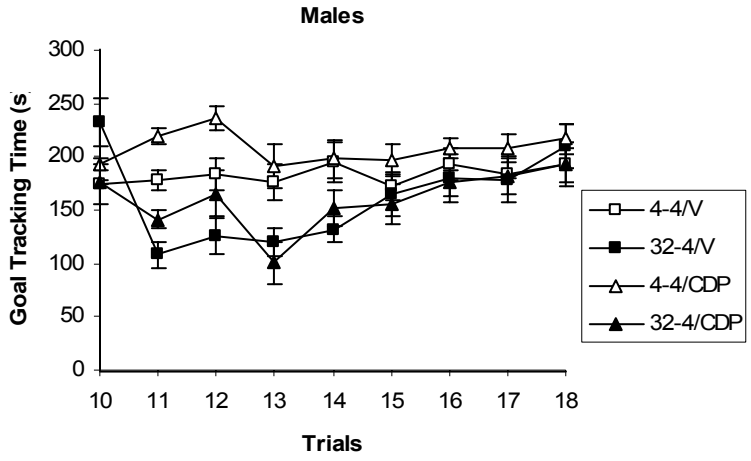


Figure 11. Postshift (a) goal tracking times and (b) frequency scores for saline and CDP groups.

(a)



(b)

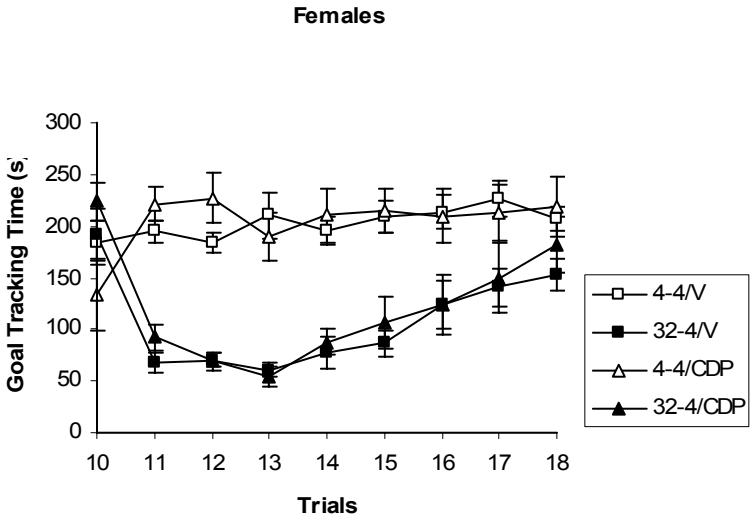


Figure 12. Goal tracking times for (a) males and (b) females in the postshift phase for CDP and Saline groups.

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Presentations	Wood, M., Daniel, A. M., & Papini, M. R. Role of the opioid system in consummatory successive negative contrast. Paper presented at the Psychonomic Society, 45th Annual Meeting, Minneapolis, Minnesota, November 18-21, 2004. Daniel, A. M., Wood, M. D., Pellegrini, S. P., Norris, J. N., & Papini, M. R. (2005). Contextual control of consummatory successive negative contrast. Poster presented at the Psychonomic Society, 46th Annual Meeting, Toronto, Ontario, November 10-13, 2005. Pellegrini, S.P., Wood, M. D., Daniel, A. M., & Papini, M. R., (2005). Opioid receptors modulate recovery from consummatory successive negative contrast. Paper presented at the Psychonomic Society, 46th Annual Meeting, Toronto, Ontario, November 10-13, 2005.
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ABSTRACT

MICROSTRUCTURE OF APPROACH-AVOIDANCE
CONFLICT IN THE SUCCESSIVE NEGATIVE
CONTRAST PARADIGM

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Rats drink less of a 4% sucrose solution when they have had prior experience with a 32% sucrose solution than rats that receive only 4% sucrose. This phenomenon is known as consummatory successive negative contrast. Little attention has been paid to the importance of microstructural changes within trials during cSNC. In the first experiment, with the idea of conflict in mind, new measures were devised to measure within-trial variability in cSNC from previously collected data. Frequency best captured such changes, and a second experiment was conducted to determine its validity as a measure of conflict, using the anxiolytic chlordiazepoxide (CDP). CDP did not reliably reduce contrast in rats, rendering the experiment inconclusive. Behavioral and pharmacological evidence were weighed, with the determination that frequency should be explored further as a new measure for within-trial variability, and that the source of this variability should be investigated.