PAVLOVIAN CONDITIONING AND TOLERANCE TO
CHOLECYSTOKININ-8 AND NALOXONE- INDUCED
MEAL SUPPRESSION

By
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ABSTRACT

Administration of the gut peptide, cholecystokinin (CCK), results in a suppression of meal size. The opiate-antagonist, naloxone (Nx), also suppresses feeding. With few exceptions, studies of the effect of either CCK or Nx have not examined the effects of repeated administrations, and thus there are little data concerning tolerance.

Experiment 1 was designed to investigate the effect of CCK following repeated daily injections. It was found that after several days of CCK, it no longer suppressed feeding; that is, tolerance to CCK had occurred. The demonstration of contingent tolerance in Experiment 2 confirms the results of Experiment 1 as well as the results obtained from Bednarz, Asin and Nadzan (1992), who showed that tolerance to CCK was dependent upon CCK and food being given at the same time. The results from Experiment 2 also demonstrate the importance of learning principles in mediating this tolerance; following a saline test, an over-consumption of sucrose was evident.

Experiments 3 and 4 extend these findings by demonstrating further, the importance of learning principles. Experiment 3 demonstrated that tolerance is only displayed when the drug is administered in the context of usual drug-predictive cues. Experiment 4, a latent inhibition experiment, assessed the prediction that pre-exposure to a conditioned stimulus (CS) should slow tolerance development. By demonstrating latent inhibition, this confirms the importance of learning principles.
Experiments 5 through 8 were designed to investigate tolerance to Nx. The importance of learning principles in mediating this tolerance was also assessed. Experiment 5 demonstrated that a dose of 1 mg/kg of Nx significantly decreased sucrose consumption. This suppression of intake diminishes, when animals were injected daily, as shown in Experiment 6. Experiment 7 showed that, like CCK, a contingency between food and Nx is necessary for tolerance to be demonstrated. The importance of learning principles was clearly shown in Experiment 8, where it was demonstrated that tolerance is only displayed when the drug is administered in the context of usual drug-predictive cues.

Much evidence suggests that CCK acts as an opiate-antagonist in the modulation of pain, and that Nx and CCK affect feeding in a similar manner. Experiments 1 through 8 show that tolerance to the meal-suppressive effect occurs when either CCK or Nx is given repeatedly. In a final experiment (Experiment 9), cross-tolerance to CCK- and Nx-induced meal suppression was assessed. Experiment 9 demonstrated that the tolerance that develops to CCK is symmetrical with respect to Nx. This result adds further support to the claim that CCK and Nx affect feeding behaviour in a similar manner. The mechanism(s) of action responsible for tolerance remains to be elucidated.
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CHAPTER 1

INTRODUCTION

In 1973, Gibbs, Young and Smith presented evidence that the gut hormone, cholecystokinin (CCK), may act as a satiety peptide. This paper was the first demonstration that a peptide could produce specific reductions in intake (via a reduction in meal-size), and it initiated research into the area of peptides and feeding. The suppression of intake by CCK-8 (the octapeptide form of CCK) has shown to be specific to food and dose-related in a variety of species (Gibbs, Young & Smith, 1972; 1973; Smith, Gibbs & Young, 1974; see Baile, McLaughlin & Della-Fera, 1986; Morely & Levine, 1985).

Another drug which suppresses feeding is the opiate-antagonist, naloxone (Nx). Holtzman (1974, 1975) was the first to demonstrate Nx’s ability to suppress feeding. Similar to CCK, the effects of Nx are generally dose-dependent, and are not limited to one species; mice, cats, and sheep demonstrate satiety when being administered Nx. With few exceptions, studies of the effect of either CCK or Nx in the regulation of food intake have not examined the effects of repeated injections, thus there are little data concerning tolerance (see Morely & Levine, 1985). Results of those few studies that have evaluated tolerance are conflicting.

Mineka and Snowdon (1978) reported that tolerance developed to the meal-suppressive effects of CCK over the course of repeated daily administrations of the
drug. Similar results were obtained by Bednarz, Asin, and Nadzan (1992), who demonstrated tolerance to CCK-8 after only 3 days of treatment. However, in a more recent study in which CCK-8 was infused via an indwelling intraperitoneal (IP) catheter at the start of every spontaneous meal, tolerance to the meal-suppressive effect was not reported (West, Fey & Woods, 1984). Various procedural differences exist in these protocols which may account for the various findings concerning tolerance to the meal-suppressive effects of CCK-8.

There are also various findings concerning tolerance to the meal-suppressive-effect of Nx. Brands, Thornhill, Hirst and Gowdy (1979) reported that tolerance developed to the meal-suppressive effect of Nx; following 10 days of treatment, Nx no longer suppressed feeding. A recent report by Kirkham (1990) however, has challenged this assertion of tolerance development, and tolerance to Nx’s meal-suppressive effects was not demonstrated when Nx was given bi-daily (Kirkham, 1990).

The present experiments were designed to assess further, tolerance to the meal-suppressive effects of CCK-8 and Nx. Results of recent research suggest that a complete understanding of tolerance requires an appreciation for the contribution of pharmacological conditioning. As suggested by Pavlov (1927), the usual drug administration situation corresponded to the conditioning paradigm: environmental cues uniquely present at the time of drug administration (e.g. location of injection, or drug administration rituals) constitute the CS (conditioned stimulus), with the actual systemic effect of the drug constituting the UCS (unconditioned stimulus). Subsequent
to Pavlov's original demonstrations, there have been many studies concerned with the conditioning of drug effects (see Siegel, 1989).

The development of an association between the environmental CS and the pharmacological UCS may be seen by administering an inert substance in the presence of the usual drug-signalling cues. The pharmacological CR (conditioned response) revealed by this procedure depends on the nature and mechanism of the pharmacological effect (see Eikelboom & Stewart, 1986, Siegel, 1987, 1989). For many effects of many drugs, the CR is an anticipatory compensation: drug-associated environmental cues elicit responses that are opposite to the drug effect. Drug compensatory CRs have been reported with respect to a variety of effects of many drugs (e.g. morphine, nicotine, ethanol; see Siegel, 1989).

The present research was conducted in an attempt to understand the role of Pavlovian conditioning in the development of tolerance to CCK-8- and Nx-induced meal-suppression. Both CCK-8 and Nx have been shown to suppress feeding in the short-term, and yet the results of long-term treatment of the drugs are less clear. Finally, a possible mechanism underlying tolerance development is addressed.
CHAPTER 2

CCK-8, TOLERANCE, AND PAVLOVIAN CONDITIONING

CCK-8 and Feeding

CCK is a polypeptide hormone which was isolated in 1971 as a 33 amino acid hormone from the porcine gastrointestinal tract (Mutt & Jorpes 1971). The sulfated N-terminal octapeptide form of CCK (CCK-8) has been shown to contain the biological activity necessary for CCK's full range of effects. The effects of CCK-8 on feeding behaviour have been known for several years, and rats have been the species most frequently studied. Overall, the results obtained from the studies on rats prompted the proposal that CCK released from the gut during meals acted peripherally to cause satiety. There is, in fact, good evidence that satiety elicited by peripherally administered CCK-8 is mediated by the vagus nerve (Smith, Jerome, Cushin, Eterno and Simansky, 1981). Bilateral vagotomy abolished the decreased food intake after CCK-8 injections in rats. Furthermore, CCK-induced satiety was abolished by severing the gastric but not celiac or hepatic branches of the vagus (Smith et al., 1981).

In the past 15 years, a large body of evidence has accumulated demonstrating a link between CCK peptides and satiety. In 1973, Gibbs et al. published a series of experiments which suggested that CCK may act as a satiety peptide. This paper was the first demonstration that a peptide could produce chemically and behaviourally
specific reductions in intake, and initiated research into the area of peptides and feeding. The administration of partly purified 33 amino-acid CCK peptide (CCK-33) decreased food intake in a dose-dependent manner, in 6-hour food-deprived rats. In addition, synthetically prepared CCK-8 also decreased food intake in a dose-dependent manner, as did cerulein (Gibbs et al., 1972, 1973; Smith et al., 1974).

To demonstrate that CCK's effect was not due to decreased motor ability required to consume pellets, Gibbs et al. (1973) offered liquid diet and again found that consumption was decreased in a dose-dependent fashion. The satiety effect was specific for food, as water intake was not influenced. The effect was also dependent upon dose. It has since been shown that the meal-suppressive effects of CCK-8 are short lived and result in meal termination sooner than when given saline (Koulisher, Moroder & Deschodt-Lanckman, 1982; Weingarten, 1983). CCK-8 administration also prolongs the intermeal interval (Hsaio, Wang & Schallart, 1979) and at low doses (less than or equal to 6 ug/kg), mimics the effects of nutrient perfusion in the duodenum (Linden, Hansen, Bednar, Forsberg, Sodersten & Uvnas-Moberg, 1987; Linden, Uvnas-Moberg, Forsberf, Bednar & Sodersten, 1989). Furthermore, rats injected with CCK-8, although eating less, still exhibit the normal behaviour sequence of satiety (Antin, Gibbs, Holt, Young & Smith, 1975). Consistent with this result and the inability of CCK-8 to produce a taste aversion (Gibbs et al. 1972, 1973; Mueller & Hsaio, 1977; Smith et al., 1974), others have shown that an injection of CCK-8 is not an aversive stimulus (see Baile et al., 1986; Linden et al., 1987; Smith et al., 1974, West et al., 1984; West, Greenwood, Marshall & Woods, 1987). However, much controversy
exists over whether the inhibition of food intake by CCK-8 represents a true satiating effect or whether its effects are secondary to toxicity or aversion. A discussion of this controversy can be found in Morley and Levine (1985) or Morley (1987). Overall, it would appear that at least at lower doses (i.e., less than or equal to 6 μg/kg), CCK-8 acts as a true satiety factor (Gibbs & Smith, 1984; Gibbs et al., 1973; Smith, 1984; Smith & Gibbs, 1975; 1979).

Further research on CCK indicates that CCK has a variety of properties, including the fact that the biological activity of CCK depends on the presence of a sulfate group on the seventh amino acid (see Baile et al., 1986). Furthermore, CCK-8 reduces intake in numerous species' including rats, rabbits, pigs, monkeys, mice, chickens, hamsters and humans. More CCK-8 is required to decrease food intake the longer the fast (see Baile et al., 1986; Morley, 1987; Morely, Barness, Gosnell & Levine, 1985), and in 24-h fasted rats, CCK is more potent in inhibiting feeding when injected in the light cycle than in the midportion of the dark cycle (Kraly, 1981). CCK-8 has also been shown to decrease sucrose consumption (Conover, Collins & Weingarten, 1988; 1989; Waldbillig & Barness, 1982; Weingarten, 1983), and to affect meal-termination, and not meal initiation (Gibbs et al., 1972, 1973; Weingarten, 1983).

Although the satiety effects of CCK-8 have amply been demonstrated, the precise mechanism of this effect remains unclear. A full discussion of CCK's possible mechanisms of action is beyond the scope of this thesis, and thus, only a brief discussion of the role of gastric emptying (the mechanism of action given the most
attention) will be addressed. It has been suggested that CCK-8 elicits satiety indirectly by enhancing contraction of the pyloric sphincter, thereby slowing the rate of gastric emptying and increasing gastric distension (Moran & McHugh, 1982). Since then, more evidence has accumulated which supports the assertion that CCK-induced satiety is mediated through a slowing of gastric emptying (Moran & McHugh, 1988).

However, some evidence suggests that gastric distension is not necessary for CCK-elicited satiety to occur (Conover et al., 1989; Gibbs et al., 1973). This conflict in the literature has recently been addressed by Schwartz, Netterville, McHugh and Moran (1991), who, while using a CCK analogue, proposed that a gastric load, or normal feeding signals arising from gastric distension, potentiate the direct action of CCK-8 on food intake. That is, the satiety action of CCK-8 contains both gastric and non-gastric components (Schwartz, Netterville, McHugh & Moran, 1991).

CCK and Tolerance

A series of experiments by Mineka and Snowdon (1978) indicated that after repeated daily IP injections of either the synthetic C-terminal octapeptide (CCK-8), or to a lesser extent, the natural extract of CCK, tolerance to the drug's intake-suppressive effect developed. After 6-9 days of repeated CCK administration, CCK no longer significantly suppressed intake of either powdered food or liquid diet. When a larger dose was introduced (greater than 2 ug/kg used in the tolerance development phase), the intake suppressive effects of both forms of CCK were reinstated.
Following a saline injection, the animals overconsumed the food given (a compensatory response). Although not mentioned by Mineka & Snowdon (1978), this overconsumption suggests a role for conditioning principles. As discussed previously, compensatory CRs may be observed when the usual drug associated cues are not followed by the drug, but rather a placebo is administered.

Subsequent experiments have indicated that the constant infusion (via osmotic minipump) of CCK-8 for 2 weeks (.1 or 1 ug/kg/hr) results in tolerance to the intake-suppressive effects of CCK-8 (Crawley & Beinfeld, 1983). In addition, Crawley and Beinfeld (1983) found no changes in body weight at any point during the 14 days of treatment. More recently, Bednarz, Asin and Nadzan (1992) demonstrated tolerance to CCK's meal-suppressive effect. Deprived animals given daily intraperitoneal injections of CCK-8 (10 nmol/kg) ten minutes prior to the delivery of a liquid diet demonstrated tolerance to CCK's meal-suppressive effect after three days of treatment. Tolerance, however, was not demonstrated when animals were given CCK-8 two hours following presentation of the liquid diet during the tolerance development phase, suggesting the importance of learning mechanisms in the development of tolerance.

In contrast to reports of CCK tolerance, West and colleagues (1984, 1987) concluded that tolerance does not develop to the meal-suppressive effect of CCK-8. In 1984, West and colleagues chronically administered CCK-8 (1.1ug/kg/meal) via an indwelling IP catheter at the start of every spontaneous meal. A spontaneous meal was defined as the consumption of 2 pellets within 15 seconds. It was reported that after 6 days of treatment, daily food intake remained constant, and following an initial
decrease in meal-size and duration (when CCK-8 was introduced), these variables remained unchanged. The frequency of meals, however, increased during CCK-8 treatment.

In sum, there is some evidence that tolerance develops to CCK’s meal-suppressive effects, and yet, the results are unclear. Furthermore, prior experiments concerning CCK-8 tolerance have not evaluated the contribution of conditioning to such tolerance.

Experiment 1: Tolerance to CCK-8

The present experiment was undertaken to investigate the effects of repeated administrations of CCK-8 and the role of learning principles in mediating these effects.

Method

Subjects

The subjects were 20 male Long-Evans hooded rats bred in the McMaster Psychology Department colony from stock originating from Blue Spruce Farms
(Altmont, NY). The rats were about 17 weeks old at the beginning of the experiment. The animals were housed in individual hanging cages in a colony room maintained at 21 degrees C on a 12:12 light-dark cycle. The lights came on at 7 am. Prior to the start of the experiment the animals were given continuous access to food (Purina Rat Chow) and water.

Procedure

Baseline. At 9:30 am daily (3.5 hours prior to the delivery of sucrose), metal food cups containing 100 grams of Purina Rat powdered chow were removed from the subjects’ cages and weighed, and the animals were weighed. At 10:00 am daily (3 hours prior to the delivery of sucrose), the animals were given 10 minute access to 5 ml of liquid diet (1:1 Carnation Evaporated Milk and water) in a 10 ml syringe fitted with a rubber stopper and drinking spout. The standard schedule of deprivation and preload feeding ensured the rats’ stomachs were empty of food at the beginning of the test period. At 1:00 pm daily, 30 ml of a 15% (wt/vol) sucrose solution was given to the animals. The solution was given in 100 ml graduated glass cylinders, equipped with metal drinking spouts inserted through rubber stoppers. Sucrose consumption was measured to the nearest 1 ml 30 min after the presentation. At 2:00 pm, the powdered food was presented, and remained in the cages until 9:30 am the following morning. This phase lasted 21 days. Prior to testing the effect of CCK-8 on sucrose consumption, baseline measures of body weight, powdered food intake and sucrose consumption were taken until stable levels of the measures were achieved.
Protocol. Rats were divided into 2 groups (n/group=10): the Saline group and the CCK group, and an attempt was made to match the groups for equivalent baseline sucrose intake and body weight. The procedure for this phase was identical to that of the baseline phase except that each rat received an injection, on average, 15 minutes before the presentation of the sucrose solution. Subjects in the CCK group received an IP injection of the synthetic C-terminal octapeptide of CCK (SQ 19,844, a gift of Squibb Institute for Medical Research, Princeton, NJ) in a dose of 6 ug/kg body weight. All injections were made up to a volume of 1 ml with 0.9 % saline, and prepared fresh daily. Subjects in the Saline group received 1 ml of 0.9 % saline. This phase lasted 9 days.

Results and Analysis

Mean scores of body weight, powdered food intake and sucrose intake are reported. Individual data points for the groups in Experiment 1 can be found in Appendix A. Figure 1 presents the mean body weight and powdered food intakes for each group. As can be seen, the two groups did not differ in mean body weight or powdered food intake throughout the experiment (Figure 1A and 1B, respectively). Separate mixed design repeated measures analysis of variance (ANOVA) of the body weight and powdered food intake data obtained from the Saline and CCK groups indicated no significant groups effect (Fs(1,18) < 1).
Figure 1: Mean Body Weight and Powdered Food Consumption across treatment days

Figure 1A: Mean Body Weight across treatment days

Figure 1B: Mean Powdered Food Consumption across treatment days
Figure 2: Mean Sucrose Consumption across treatment days
Figure 2 presents the effects of repeated CCK-8 administrations on sucrose intake. CCK-8 significantly suppressed meal size on the first day of drug administration compared to the saline-control group [t(18) = 3.6, p<.01]. From Day 1 to Day 7, however, there was a trend toward recovery of meal size during CCK-8 treatment. By Day 9, CCK-8 no longer suppressed sucrose intake as compared to saline group [F(1,18) < 1]. This result demonstrates that a dose as low as 6 ug/kg is sufficient to produce tolerance to repeated injections of CCK-8.

Discussion

The results of the present investigation demonstrate that both body weight and powdered chow intake are variables that are not greatly influenced by the repeated administration of CCK-8. This is probably due to the fact that CCK-8 has a very short (17 min in rats) plasma half-life (Koulisher et al., 1982). Results from the first administration of CCK-8 suggest that a dose of 6 ug/kg is sufficient to suppress intake when CCK-8 is administered 15 min prior to initiation of a test meal. This confirms previous reports of the satiety effect (Conover et al., 1988, 1989). Moreover, the effect of CCK-8 lessened over days. In other words, tolerance to the drug developed.
Experiment 2: Contingent Tolerance to CCK-8

Placing an explicit behavioural demand on a drug-affected system can profoundly affect the development of tolerance (see Poulos & Cappell, 1991). This type of phenomenon has often been referred to as contingent tolerance and it is usually demonstrated with a before-and after design. In this design, two groups of animals are given repeated behavioural tasks known to be affected by the drug (e.g., in the case of an anorectic drug, consumption serves as an assessment). During the tolerance development phase of the experiment, the "Before" Group is injected with the drug before each assessment, while the "After" Group is injected with the drug after each assessment. Thus, both the "Before" and "After" groups have the same pharmacological history; that is, they are injected with the same doses of the drug, equally often, and at the same intervals. However, the "Before" Group experiences a contingent relationship between the drug and the particular task, while the "After" group experiences the drug and the task in a non-contingent manner. Following the tolerance development phase, a tolerance test phase is given at which time both groups are injected with the drug before the particular task. With many effects of many drugs, tolerance is seen only in the "Before" (i.e., Contingent) Group (see Poulos & Cappell, 1991).

Recently, Bednarz et al., (1992) have demonstrated contingent tolerance to the meal-suppressive effect of CCK-8. Other meal-suppressive drugs have also shown to display contingent tolerance. Tolerance to the anorectic effect of amphetamine, for example, has shown to be entirely contingent (Carlton & Wolgin, 1971). Similar
results were found by Poulos, Wilkinson and Cappell (1981), who presented their results in the context of a "homeostatic theory" of tolerance. This homeostatic theory provides a much more comprehensive account for contingency phenomena than is provided by an alternative model; the loss-of-reinforcement hypothesis. The loss-of-reinforcement model suggests that tolerance will develop to drugs which disrupt an organism's ability to gain reinforcement (Schuster, Dockens & Woods, 1966; Woolverton, Kandel & Schuster, 1978). This loss-of-reinforcement model however, does not account for a variety of contingent tolerance phenomena including compensatory responses (see Poulos & Cappell, 1991). Thus, the homeostatic theory of tolerance was adopted to describe contingent tolerance.

The homeostatic theory of tolerance was more recently elaborated by Poulos and Cappell (1991), who proposed that a homeostatic disturbance is only detected if explicit behavioural demands are made on the system and that detection of such disturbances is necessary for processes of adaptation that restore homeostasis. These homeostatic corrections are unconditional responses, and it was also added that these homeostatic corrections result in tolerance. Thus, in the case of anorectic drugs, subjects getting the anorectic drug in the non-contingent relationship with food never experience a drug-induced homeostatic disturbance, and thus do not become tolerant to the drug.

Furthermore, under some circumstances, the homeostatic responses elicited by the drug-induced disturbances can be conditioned to drug-predictive cues. That is, homeostatic corrections can not only unconditionally be elicited by drug-induced
disturbances, but also by cues that signal these disturbances. In accordance with this assertion, in the demonstration of contingent tolerance to CCK-8. Bednarz et al. (1992) conclude:

"Alterations in drug metabolism or receptor mechanisms cannot fully account for the development of tolerance to CCK-8... Our results suggest that learning mechanisms and the animal’s motivational state may be involved in the development of tolerance to CCK-8" (Bednarz et al., 1992).

Experiment 1 used a contingent tolerance design, i.e., subjects received CCK before sucrose. Experiment 2 was conducted to evaluate whether the demonstration of tolerance to CCK-8 requires such a contingency, and to evaluate the contribution of "learning mechanisms" (i.e. homeostatic responses elicited by predrug cues) to contingent tolerance to CCK-8.

Method

Subjects

The subjects were 21 male Long-Evans hooded rats as described in Experiment 1. The rats were about 17 weeks old at the beginning of the experiment. The animals were housed and treated similarly to those described in Experiment 1, except that the lights came on at 12:30 pm.
Procedure

Baseline. The procedure for this phase of the experiment was similar to that of Experiment 1 except that the metal food cups were removed at 2:30 pm daily, and weighed. At 6:00 pm daily, 30 ml of a 10% (wt/vol) sucrose solution (in 50 ml glass cylinders) was given to the animals. This phase lasted 11 days.

Protocol. Rats were divided into 3 groups \( n/group=7 \): the Contingent, the Non-Contingent and the Saline group, and an attempt was made to match the groups for equivalent baseline sucrose intake and body weight. Following the baseline period, the Contingent group was administered 9 IP injections of CCK-8 on alternate days, followed in 15 minutes by a 30-minute access to sucrose solution. On intervening days, the animals remained undisturbed in their home cages. Non-contingent group rats received identical treatment with the sole exception that these animals were never exposed to the sucrose solution (or water) while under the effects of CCK-8. Instead, their 30-minute access to the sucrose solution occurred on the intervening days. The CCK was obtained, prepared and delivered in a dose identical to that described in Experiment 1. Saline-group rats were injected with saline and allowed to drink the sucrose solution 15 minutes following each injection. These animals were also left undisturbed in their home cages on intervening days. Control injections were equivolumes (1 ml) of 0.9 % saline. This tolerance development phase was followed by a test session (Test Day 1) in which all animals were administered CCK-8, and after a 15 minute delay were allowed to drink the sucrose solution. For two days following this test, animals were given injections identical to those described during
the tolerance development phase. A second test day was conducted in which all
subjects received a saline injection prior to the presentation of the sucrose solution.

Results and Discussion

Mean scores of body weight, powdered food intake and sucrose intake are
reported. Individual data points for the groups in Experiment 2 can be found in
Appendix B. Figure 3 shows the mean body weights and powdered food intake for all
animals during the treatment days. As can be seen the 3 groups did not differ in body
weight or powdered food consumption across days (Figure 3A and 3B, respectively).
Separate mixed design repeated measures analysis of variance (ANOVA) of the body
weight and powdered food intake data obtained from the Contingent, Non-contingent
and Saline groups indicated no significant groups effect $[F(2,18) < 1]$.

Figure 4 presents the effects of repeated CCK-8 administrations on sucrose
consumption for the treatment days for all groups. An examination of Figure 4 reveals
that CCK-8 suppressed meal size on the first day of drug administration (Day 1) for
the Contingent group compared to both the Non-Contingent (which also received
CCK-8, but on an alternate day) and the Saline group (which received saline). The
Non-Contingent group and Saline group did not differ from one another, $p > .05$. As is
clear from Figure 4, however, from Session 1 to Session 9, there was a trend toward
recovery of meal size during CCK-8 treatment. By Session 9, CCK-8 no longer
Figure 3: Mean Body Weight and Powdered Food

Consumption across treatment days

Figure 3A: Mean Body Weight across treatment days

Figure 3B: Mean Powdered Food Consumption across treatment days
Figure 4: Mean Sucrose Consumption across treatment days

Consumption (ml)

Day

Contingent  Non-Contingent  Saline

CCK Contingent Tolerance
Figure 5: Mean Sucrose Consumption during Test Day 1
Figure 6: Mean Sucrose Consumption during Test Day 2

Saline to all
suppressed sucrose intake in the Contingent group as compared to both the Non-Contingent and Saline groups \( F(1,18) = .34, p>.05 \). This result confirms the results obtained in Experiment 1, as well as previous reports of tolerance development following repeated CCK-8 administration (Mineka & Snowdon, 1978).

Figure 5 shows the sucrose consumption during Test Day 1, in which CCK-8 was administered to all subjects. As depicted in Figure 5, rats in the Contingent group display substantial tolerance. That is, rats in the Contingent group drank more sucrose than rats in the other 2 groups. In contrast, there is no evidence of any tolerance at all in the Non-Contingent group. In fact, the level of sucrose consumption of the Non-Contingent group on the test day was not different from that of the Saline group that had received saline rather than CCK-8 during the previous tolerance-induction phase. This result confirms the importance of a contingent relationship between CCK and food for the development of tolerance. A one-way ANOVA indicated a significant difference among the groups during Test Day 1, \( F(2,18) = 19.57, p<.001 \). Pairwise comparisons were conducted by a Newman-Keuls test. The Contingent group differed from each of the other groups, \( p<.05 \). There was no significant difference between the Non-contingent and Saline groups.

The results of Test Day 2 (the saline test session) are shown in Figure 6. Figure 6 demonstrates the predicted compensatory response by the Contingent group rats; they ingested more sucrose than did rats in the other groups. The data summarized in Figure 6 were subjected to a one-way analysis of variance. The statistical analysis revealed a significant difference \( F(2,18) = 9.18, p<.001 \). Pairwise
comparisons were conducted by a Newman-Keuls test. The Contingent group differed from each of the other groups, $p < .05$. The Non-contingent and Saline groups did not differ from one another. The compensatory homeostatic response is evidence that an association has indeed been learned between the environmental CS and CCK’s meal-suppressive effect, and provides further evidence that learning principles are involved (Hinson & Siegel, 1983; see Siegel, 1987, 1989, 1991). Other predictions of an associative account of CCK-8 tolerance are evaluated in the following experiments.

Experiment 3: Environmental-specificity of tolerance to CCK-8

On the basis of the conditioning analysis, tolerance should not invariably result from repeated drug administrations. Rather, tolerance should be displayed only when the drug is administered in the context of the usual drug-predictive cues, because it is these cues that elicit the drug-compensatory CRs that mediate tolerance. In fact, results of many studies have demonstrated environmental specificity of tolerance (see Siegel, 1987, 1989, 1991). The present experiment evaluated environmental specificity of CCK-8 tolerance.
Method

Subjects

The subjects were 36 male Long-Evans hooded rats obtained from Charles River (Quebec, Canada). The rats were about 17 weeks old at the beginning of the experiment. The animals were housed and treated similarly to those described in Experiment 1.

Procedure

Baseline. Animals were randomly placed on one of two racks of cages. One of these racks was designated "Room" and the other, "Colony." Nine CCK and Nine Saline (Sal) animals were housed on each rack. The baseline procedure was identical to that described in Experiment 2, except that food cups were removed, starting at 8:15 am. One half an hour prior to the presentation of the sucrose solution, the rack of animals designated "Room" was wheeled into a distinctively different room. This room was an experimental room separate from the colony. The solution was prepared, measured and delivered in the manner described in Experiment 2, except that it was presented in 50 ml plastic graduated cylinders. At 1:10 pm (about an hour after sucrose presentation), the rack designated "Room" was wheeled back into the colony room after being in the distinctive room for about an hour and 40 min. At 1:15 pm, the powdered food was presented, and remained in the cages until the following morning. This phase lasted 16 days.
Protocol. Rats were divided into 4 groups: the Saline and CCK group in the colony (designated Sal-Col and CCK-Col, respectively) and the Saline and CCK group in the room (designated Sal-Room and CCK-Room, respectively), and an attempt was made to match the groups for equivalent baseline sucrose intake and body weight. The procedure for this phase was identical to that of the baseline phase except that each rat received an injection, on average, 15 minutes before the presentation of the sucrose solution. Both the CCK-Room and CCK-Col groups received an IP injection of CCK-8, which was obtained, prepared and delivered as outlined in Experiment 1. Control injections to groups Sal-Room and Sal-Col were equivolumes (1 ml) of 0.9 % saline. This tolerance development phase lasted 8 days and was followed by a tolerance test session (Test Day 1), in which all animals were administered CCK-8 in the distinctive room. For two days following this test, animals were treated as they were during the tolerance development phase. A second tolerance test session followed (Test Day 2) in which all animals were administered CCK-8 in the colony room. Again, 2 days intervened between this test day and Test Day 3 in which animals were again treated as they were during the tolerance development phase. During Test Day 3 saline injections were given to all animals in the environment in which the tolerance development phase had been conducted (i.e. in the distinctive room for groups CCK-Room and Sal-Room, and the colony room for groups CCK-Col and Sal-Col).
Results and Analysis

Mean scores of body weight, powdered food intake and sucrose intake are reported. Individual data points for the groups in Experiment 3 can be found in Appendix C. Figure 7 shows the mean body weights and powdered food intake for all animals during the treatment days. As can be seen in Figure 7A, the 4 groups did not differ in body weight throughout during the experiment. Figure 7B depicts the powdered food consumption across days for each group. Again, the 4 groups did not differ in powdered food intake throughout the experiment. Separate mixed design repeated measures analysis of variance (ANOVA) of the body weight and powdered food intake data obtained from the 4 groups indicated no significant groups effect \[F(3,32) = .68, \ p>.05, \text{ and } F(3,32) = 2.3, \ p>.05, \text{ respectively}.\]

Figure 8 presents the effects of repeated CCK-8 or saline administrations on sucrose intake during the tolerance development phase. An examination of Figure 8 reveals that CCK-8 suppressed meal size on the first day of drug administration for groups CCK-Room and CCK-Col compared to the saline-control groups, Sal-Room and Sal-Col. A 2 (drug; CCK or Saline) X 2 (environment; Colony or Room) ANOVA indicated a significant drug effect \[F(1,32) = 17.87, \ p<.01\]. The effect of environment and the interaction between the drug and environment were not significant \[F_{s}(1,32) < 1\]. As is clear from Figure 8, however, from Day 1 to Day 8, there was a trend toward recovery of meal size. By Day 8, CCK-8 no longer suppressed sucrose intake in groups CCK-Room and CCK-Col, as compared to the saline controls. The development of tolerance was tested statistically, and a 2 (drug;
Figure 7: Mean Body Weight and Powdered Food Consumption across treatment days

Figure 7A: Mean Body Weight across treatment days

Figure 7B: Mean Powdered Food Consumption across treatment days
Figure 8: Mean Sucrose Consumption across treatment days.
Figure 9: Mean Sucrose Consumption during Test Day 1
Figure 10: Mean Sucrose Consumption during Test Day 2

CCK in Colony
Figure 11: Mean Sucrose Consumption during Test Day 3

Consumption (ml)

CCK-Col  Sal-Col  CCK-Room  Sal-Room

Saline in Room or Colony
CCK or Saline) X 2 (environment; Colony or Room) ANOVA of the data obtained on Day 8 indicated no significant effects of drug, environment or an interaction of the two \([F(1,32) < 1]\).

Figure 9 depicts the mean sucrose intake during the first tolerance test session, conducted in the distinctive room. As indicated in Figure 9, rats in the two pretest drug-naive groups (Sal-Room and Sal-Col) exhibited a suppression of intake (compared to their intake seen on Day 8 of Figure 8 as well as the intake of the group E-Room) during the first tolerance test session, which was their first exposure to CCK-8. Rats with pretest experience with CCK-8 in the distinctive room where the first test session was conducted (i.e. rats in Group CCK-Room) displayed substantial tolerance during the first test session. Rats with pretest experience with CCK-8, but in a context other than the one in which Test 1 occurred (Group CCK-Col), were not as tolerant as rats in Group CCK-Room during the first test session. A one-way ANOVA indicated a significant difference among the groups during Test Day 1, \([F(3,32) = 4.34, p<.05]\). Pairwise comparisons were conducted by a Newman-Keuls test. Group CCK-Room differed from all other groups, \(p<.05\). Groups CCK-Col, Sal-Col and Sal-Room did not differ from one another.

Test Day 2 involved administering CCK-8 to all animals in the colony. The results of this Test Day 2 are shown in Figure 10. Rats in groups Sal-Room and Sal-Col again exhibited a suppression of intake during the second tolerance test session, compared to their baseline levels and to group CCK-Col. Rats with pretest experience with CCK-8 in the colony room where this second test session was conducted (i.e. rats
in Group CCK-Col), displayed tolerance during the second test session. Rats with pretest experience with CCK-8, but in a context other than the one in which Test 1 occurred (Group CCK-Room), were not as tolerant as rats in Group CCK-Col during the second test session. A one-way ANOVA indicated a significant difference among the groups during Test Day 2, \(F(3,32) = 3.89, p<.05\). Pairwise comparisons were conducted by a Newman-Keuls test. Group CCK-Col differed from all other groups, \(p<.05\). Groups Sal-Col, CCK-Room and Sal-Room did not differ from one another.

The results of a placebo test session (Test Day 3) are presented in Figure 11. During Test Day 3 all animals received a saline injection in the environment in which the tolerance phase was given (i.e. in the room for rats in groups CCK-Room and Sal-Room, and in the colony for rats in groups CCK-Col and Sal-Col). Figure 11 demonstrates the predicted compensatory response, i.e., over-consumption by the CCK groups. The data summarized in Figure 11 were subjected to separate one-way analyses of variance for each environment. The statistical analysis revealed that the group CCK-Room differed from Sal-Room and that the group CCK-Col differed from Sal-Col \(F(1,16) = 6.06, p<.05\) and \(F(1,16) = 4.65, p<.05\), respectively.

Discussion

The results of the present experiment confirm and extend the results obtained in Experiments 1 and 2. As in the previous experiments, tolerance developed to the intake-suppressive effect of CCK-8. The results obtained in the present experiment
extend previous findings by demonstrating that the display of tolerance to the intake-suppressive effects of CCK-8 is more pronounced when the drug is administered in the conjunction with environmental stimuli previously associated with the drug (compared with administration in an alternative environment). These results obtained confirm the results of many studies which have demonstrated environmental specificity of tolerance to a variety of drugs (see Siegel, 1987, 1989, 1991).

According to the conditioning model, this attenuated suppression of intake results from a partial cancellation of the drug’s intake-suppressive effect by the drug compensatory CR elicited by the particular environment in which the drug was presented. Furthermore, presentation of the drug in an environment not previously associated with the drug lacks a CR to attenuate the drug effect, and thus, tolerance is not observed (see Siegel & MacRae, 1984). The results from Test 3 indicate that a compensatory CR is observed when the usual pre-drug cues are not followed by the usual pharmacological consequences. Such drug-compensatory CRs, evidenced in anticipation of a drug, would be expected to attenuate the drug effect as the association between the CS and the UCS is strengthened by repeated pairings (see Siegel, 1986, 1989). This is consistent with previous reports, in which compensatory CRs have been observed with several other drugs for which environmental specificity has been demonstrated (see Siegel & MacRae, 1984). The presence of such compensatory responses further supports the hypothesis that Pavlovian conditioning contributes to the tolerance found to CCK’s intake-suppressive effects, as it is these responses that are suggested to mediate tolerance.
Experiment 4: CS Pre-exposure and tolerance to CCK-8

The results of Experiments 2 and 3 have provided evidence that conditioning contributes to CCK-8 tolerance. If such tolerance is indeed a manifestation of a conditioning process, it would further be expected that manipulations of the putative CS (i.e., environmental cues present at the time of drug administration) known to be effective in retarding CR acquisition, would similarly retard the acquisition of CCK tolerance.

One technique that is effective in retarding the acquisition of CRs is to repeatedly present the CS alone prior to its pairing with the UCS. It has been reported that in many conditioning preparations, involving a variety of species, presentations of the CS prior to the start of acquisition serve to decrease the effectiveness of that CS when it is subsequently paired with the UCS during conditioning. This phenomenon has been termed "latent inhibition" or the "CS pre-exposure effect." Reviews of the latent inhibition literature can be found elsewhere (see Siegel, 1969, 1977, 1986, 1989).

According to the conditioning interpretation, inasmuch as tolerance reflects an association between the predrug environmental CS and the pharmacological UCS, the course of tolerance acquisition should be affected by the relative novelty of
environmental cues present at the time of drug administration. Thus, animals with much experience with the administration procedure prior to its pairing with a drug should be relatively slower in the development of tolerance, compared with animals with minimal prior experience with these environmental cues, despite the fact that both groups suffer the systemic effects of the same dose of CCK-8, given the same number of times and at the same interval (see Siegel, 1969, 1977, 1986, 1989, Siegel, Krank & Hinson, 1987). A demonstration of latent inhibition in the present experiment would support another prediction of the conditioning model of tolerance.

Method

Subjects

The subjects were 32 male Long-Evans hooded rats like those described in Experiment 1. The rats were about 19 weeks old at the beginning of the experiment. The animals were housed and treated similarly to those described in Experiment 1.

Procedure

Baseline. The baseline procedure was similar to that described in Experiment 2, except that food cups were removed, starting at 9:00 am. Unlike the previous experiments, the food cups were not weighed (i.e. powdered food intake was not measured) in this experiment. One half an hour prior to the presentation of the
sucrose solution, half of the animals were randomly selected, and were placed, in their home-cages, on a rack and wheeled into a distinctively different room. The solution was prepared, measured and delivered similarly to that described in Experiment 2. At 1:50 pm, the rack was wheeled back into the colony room, and the animals placed back on to their respective spaces on the racks in the colony room. At 2:00 pm, the powdered food was presented, and remained in the cages until the following morning. This phase lasted 10 days.

Protocol. Rats were divided into 4 groups (n/group=8) and an attempt was made to match for equivalent baseline sucrose intake and body weight. Two groups of rats, designated Sal-Col/ CCK-Col and Sal-Col/ CCK-Room, received sucrose in the colony during the baseline and pre-exposure phases. The two remaining groups of rats, designated Sal-Room/ CCK-Room and Sal-Room/ CCK-Col, received sucrose in the room during the baseline and pre-exposure phases. The procedure for the pre-exposure phase of the experiment was identical to that of the baseline phase except that each rat received an injection of saline, on average, 15 minutes before presentation of the sucrose solution. All animals received an IP injection of 1 ml of 0.9 % saline. This CS-preexposure phase lasted 14 days and was followed by 11 days of CCK-8 treatment. During the CCK-8 treatment phase, animals in groups Sal-Col/ CCK-Col and Sal-Room/ CCK-Col received CCK-8 in the colony room. In contrast, animals in groups Sal-Col/ CCK-Room and Sal-Room/ CCK-Room received CCK-8 in the distinctive room. On CCK-8 treatment days (days 15-25), animals received an injection of CCK-8, on average, 15 minutes prior to the presentation of the
sucrose solution. The CCK-8 was obtained, prepared and delivered in a dose identical to that described in Experiment 1.

Results and Analysis

Mean scores of body weight and sucrose intake are reported. Individual data points for the groups in Experiment 4 can be found in Appendix D. Figure 12 shows the mean body weights during the treatment days. As can be seen in Figure 12, all 3 groups did not differ in body weight throughout the experiment. A mixed design repeated measures analysis of variance (ANOVA) of the body weights obtained from the 4 groups indicated no significant groups effect \[F(3,28) < 1\]. Figure 13 presents the mean sucrose consumption for the CCK-8 treatment days for all subjects. Although not shown, the sucrose consumption during the CS-preexposure phase of the study was stable. It should be noted that the conditioning theory of tolerance suggests that the group with the greater experience with cues that will signal CCK-8, prior to the pairing of these cues with the drug, should be slower in the acquisition of tolerance. That is, groups Sal-Room/CCK-Room and Sal-Col/CCK-Col should be more retarded than groups Sal-Room/CCK-Col and Sal-Col/CCK-Room in the development tolerance to CCK's meal-suppressive effects.

Figure 13 shows the effects of repeated CCK-8 administrations on sucrose consumption for each group. An examination of Day 1 in Figure 13 reveals that all groups evidenced similar suppressions in meal size following the first administration
Figure 12: Mean Body Weight across treatment days

CCK CS Pre-exposure
Figure 13: Mean Sucrose Consumption for all groups.
of CCK-8. There were no significant differences in the amount of sucrose consumed on Day 1 of CCK-8 treatment. A 2 (pre-exposure room; Room or Colony) X 2 (tolerance development room; Room or Colony) ANOVA indicated no significant main effects or interactions \( F_s(1,28) < 1.3, p > .05 \). Sucrose consumption increased on subsequent drug sessions, with the increase being greater for groups Sal-Room/CCK-Col and Sal-Col/CCK-Room than for groups Sal-Room/CCK-Room and Sal-Col/CCK-Col.

As is clear in Figure 13, by Day 6, CCK-8 no longer suppressed sucrose intake in groups Sal-Room/CCK-Col and Sal-Col/CCK-Room, as compared to groups Sal-Room/CCK-Room and Sal-Col/CCK-Col. The Day 6 data were subjected to a 2 (pre-exposure room; Room or Colony) X 2 (tolerance development room; Room or Colony) ANOVA. The analysis revealed a significant interaction \( F(1,28) = 17.39, p < .001 \). The source of the interaction is clear in Figure 13. Groups injected with CCK-8 in the pre-exposure environment (Sal-Room/CCK-Room and Sal-Col/CCK-Col) were consuming less sucrose (i.e. they were less tolerant to CCK) than groups injected with CCK-8 in the alternative environment (Sal-Room/CCK-Col and Sal-Col/CCK-Room).

Discussion

The results of the present experiment confirm and extend the results obtained in Experiments 1-3. As in previous experiments, following repeated administration of CCK-8, tolerance develops to the intake-suppressive effect of CCK-8. This also
confirms an earlier report of tolerance to CCK-8 (Mineka & Snowdon, 1978). The results obtained in the present experiment extend previous findings by demonstrating that the display of tolerance to the intake-suppressive effect of CCK-8 is less pronounced when the drug is administered in the conjunction with environmental stimuli previously associated with saline.

On the basis of any systemic theories of tolerance, it might be expected that all groups should become equally tolerant to the intake-suppressive effects of CCK-8. All groups displayed equivalent levels of consumption the first time they received the drug, and both groups had equivalent experience with the systemic effects of the drug. Nevertheless, tolerance was more marked in groups Sal-Room/CCK-Col and Sal-Col/CCK-Room. The results obtained confirm the results of many studies which have demonstrated the CS-preexposure effect of tolerance to a variety of drugs (see Siegel, 1977, 1983, 1986, 1989). That is, tolerance is less pronounced when the drug is administered in the context of the saline predrug cues than when it is administered in the context of alternative cues (see Siegel, 1977, 1983, 1986, 1989).

Summary and Conclusions

These CCK experiments demonstrated not only that tolerance could develop to CCK’s meal-suppressive effect, but also that this tolerance was affected by Pavlovian conditioning manipulations. The demonstration of tolerance to CCK-8 confirms the
results obtained by Mineka and Snowdon (1978), but calls into question the
conclusions stated by West et al. (1984). West et al. (1984) concluded that tolerance
did not develop to CCK-8 as meal size was still significantly less than saline treated
animals following repeated CCK-8 administration. However, a closer examination of
the data revealed a significant trend of increasing meal size over the CCK-8 treatment
days; that is, the development of tolerance. Experiments 2-4 demonstrate the
importance of learning principles in the development of tolerance to CCK-8.

The demonstration of contingent tolerance to CCK-8 in Experiment 2, confirms
the results of Bednarz et al. (1992), and extends these results by empirically testing the
importance of conditioning principles in mediating this tolerance. Bednarz et al.
(1992) suggested that learning mechanisms may be involved in tolerance to CCK-8,
and the results of Experiment 2 support this claim. When a saline test day was given,
an over-consumption of the sucrose meal was evident. This result suggests that an
association has indeed been learned between the environmental CS and CCK’s meal-
suppressive effect. Experiment 3 extends these findings by showing that tolerance is
only displayed when the drug is administered in the context of usual drug-predictive
cues. Finally, the demonstration of latent inhibition in Experiment 4 supports yet
another prediction of the conditioning model of tolerance, and confirms the importance
of Pavlovian principles.
CHAPTER 3

NX, TOLERANCE, AND PAVLOVIAN CONDITIONING

Opiates and Feeding

Endogenous opioid peptides have been shown to play an important role in the regulation of feeding (for reviews see Morley, 1987; Morely, Levine, Yim & Lowy, 1987; Reid, 1985). Those studying morphine addiction were the first to notice the importance of opioid peptides in feeding; after the administration of morphine, rats often started eating (Lowy & Yim, 1983; see Morley, 1987; Morely et al., 1985; Reid, 1985). Administration of morphine to either the paraventricular nucleus (PVN) (2-20 nmol) or ventro-medial hypothalamus (VMH) (2.7-10.3 nmol) of satiated rats increased food intake in a dose-dependent manner (McLean & Hoebel, 1983; Tepperman, Hirst, & Gowdy, 1981). In addition, Sanger and McCarthy (1980) have shown that ad lib-fed rats injected peripherally with morphine increase intake when intake is measured at 4 h, whereas the same dose in 24 h fasted rats, results in a decrease in food intake for 2 hours. In addition, the effects of small doses of morphine, have shown to increase nutrient as well as saccharin solution intake. However, some investigators have found that peripherally administered opioids inhibit feeding (King, Castellanos, Kastin, Berzas, Mawk, Olson & Olson, 1979).
Naloxone and Feeding

The importance of opioid peptides was further demonstrated by Holtzman (1974, 1975) who showed that Nx can reduce the intake of nutrients in rats. Dry food intake was suppressed, in a dose-dependent manner (1-10 mg/kg) by Nx (Brands et al., 1979; Carey, Ross & Enns, 1981; Holtzman, 1974). Nx, administered both peripherally and centrally, also reduces food intake in female genetically obese (Zucker) rats and their normal weight counterparts (McLaughlin & Baile, 1984; Thornhill, Taylor, Marshall & Parent, 1982). Nx suppresses food intake in many species (rats, mice, guinea pigs, cats, rabbits, sheep, wolves, squirrels, rabbits and human beings; see Baile et al., 1986; Morley, 1987; Reid, 1985).

The major effect of naloxone is to decrease the size of the meal (McLaughlin & Baile, 1984). Holtzman’s initial finding (1974) was that Nx reduced the intake of a fluid food. Since then, Nx has been shown to reduce intake of sweet (sucrose or saccharin), salt, sour, or bitter solutions when presented to either fluid-deprived, or non-deprived rats (Cooper & Holtzman, 1981; Lynch & Libby, 1983; Wu, Lind, Stapleton & Reid, 1981). In addition, the latency to initiate a meal following Nx treatment is not affected, suggesting that Nx affects responsiveness with respect to satiation functions, rather than functions associated with initiation of intake (Kirkham, 1990; Reid, 1985). Furthermore, the Nx effect on eating is apt to be at central neural receptors, inasmuch as a quaternary analogue ofNx, which presumably does not cross the blood-brain barrier, does not decrease intakes of saccharin or saline solutions (Cooper & Turkish, 1983).
Nx has been shown to reduce the intake of a sucrose solution in rats drinking with open gastric fistulas (Kirkham, 1990; Rockwood & Reid, 1982). These results suggest that Nx has effects that are not dependent on post-ingestional absorption of sucrose, as well as suggesting that Nx’s effect is related to palatability functions (Kirkham, 1990).

**Naloxone and Tolerance**

There are a small number of studies investigating the effects of repeated administration of Nx on intake. In one report, Nx (10 mg/kg) was administered in the dark portion of the light cycle for 10 days and resulted in an initial decrease in 4-hour pellet food intake. On the 10th day of administration however, Nx failed to suppress intake significantly (Brands et al., 1979). This result suggests that tolerance develops to the intake-suppressive effects of Nx. When Nx was discontinued, and saline was administered, consumption was significantly higher than that on the tenth day of Nx administration, suggesting the existence of a compensatory response. In addition, the present experiment produced no significant decreases in weight gain (Brands et al., 1979).

A recent report has failed to demonstrate tolerance to Nx’s meal-suppressive effects following repeated administration of Nx (5 mg/kg bi-daily) (Kirkham, 1990). However, this regimen did not present Nx and the food in a contingent manner. As discussed previously, tolerance to a wide variety of drugs has shown to demand a contingency for tolerance to be demonstrated. Furthermore, the demonstration of
contingent tolerance to CCK (another meal-suppressive drug) in Experiment 2 suggests the lack of tolerance is attributable to the lack of a contingency. The present experiments were undertaken to determine if tolerance could occur to the meal-suppressive effects of Nx, and whether this tolerance was mediated by Pavlovian conditioning.

Experiment 5: A Naloxone Dose-Response Study

The purpose of the present experiment was to obtain dose-response data on Nx's ability to suppress sucrose consumption.

Method

Subjects

The subjects were 40 male Long-Evans hooded rats like those described in Experiment 3. The rats were about 16 weeks old at the beginning of the experiment. The animals were housed and treated similarly to those described in Experiment 1.
Procedure

Baseline. The baseline procedure was identical to that described in Experiment 2, except that the food cups were removed starting at 9:00 am. This phase lasted 7 days.

Protocol. Rats were divided into 5 groups (n/group=8), and an attempt was made to match the groups for equivalent baseline sucrose intake and body weight. Each group was administered one of the following doses of Nx: 0 mg/kg; .25 mg/kg; .5 mg/kg; 1 mg/kg; 2 mg/kg. The procedure for this phase was identical to that of the baseline phase except that each rat received an injection, on average, 30 minutes before the presentation of the sucrose solution. All animals received an IP injection of 1 ml of 0.9 % saline on the Saline Day (the first injection day). This was followed by the Nx Day (the second injection day) in which animals received their appropriate dose of Nx. Naloxone hydrochloride (Sigma Chemical Co. St. Louis, MO), was dissolved in isotonic saline and injected IP in a volume of 1 ml/kg body weight. Stock solutions of .25, .5, 1 and 2 mg/ml of naloxone were prepared.

Results and Discussion

Mean scores of sucrose intake are reported. Individual data points for the groups in Experiment 5 can be found in Appendix E. Figure 14 depicts the mean sucrose intake for all groups during the Saline day and the Nx day. A one-way ANOVA on the Saline day indicated no difference among the groups \([F(4,35) < 1]\).
Figure 14: Mean Sucrose Intake during the Saline and Naloxone Days

Consumption (ml)

Dose (mg/kg)

Saline
Naloxone

Nx Dose-Response
Figure 14 shows that Nx greatly reduced sucrose intake at the .25, .5, 1 and 2 mg/kg dose levels compared to the intakes following the saline injection on the preceding day. A one-way ANOVA indicated a significant difference among the groups during the Nx Day, \[ F(4,35) = 3.24, p<.05 \]. Pairwise comparisons were conducted by a Newman-Keuls test. The Saline group differed from the .25, 1 and 2 mg groups, \( p<.05 \). The Saline group did not differ significantly from the .5 mg dose. Groups .25, .5, 1 and 2 mg Nx did not differ from one another. These data extend previous reports that naloxone attenuates sucrose and saccharin intake in acute or chronically-deprived rats, by showing that 10% sucrose intake can be reduced by the administration of naloxone (see Lynch & Libby, 1983). The reduction of food intake by naloxone has been demonstrated a number of times (Baile et al., 1986; Brands et al., 1979; Cooper, 1980; Holtzman, 1974; Lynch & Libby, 1983; McLaughlin & Baile, 1984; Morley & Levine, 1985; Sanger & McCarthy, 1980).

**Experiment 6: Tolerance to Naloxone**

Tolerance to Nx’s meal-suppressive effect has been shown to develop following 10 treatment days in which Nx and food are given in a contingent manner (Brands et al., 1979). However, more recently, it has been proposed that tolerance does not develop to Nx’s meal-suppressive effects (Kirkham, 1990). Tolerance to a
wide variety of drugs has shown to demand a contingency for tolerance to be demonstrated, and in Kirkham's (1990) failure to demonstrate tolerance to Nx's meal-suppressive effects, there was no contingency between the food and the injection. Thus, the lack of tolerance to Nx may be explained by this lack of contingency. The present experiment was undertaken in order to determine if tolerance could occur to the meal-suppressive effects of Nx if a contingency between the food and Nx was given, and whether this tolerance was mediated by Pavlovian conditioning.

Method

Subjects

The subjects were 20 male Long-Evans hooded rats like those described in Experiment 1. The rats were about 13 weeks old at the beginning of the experiment. The animals were housed and treated similarly to those described in Experiment 1.

Procedure

Baseline. The baseline procedure was identical to that described in Experiment 2, except that the food cups were removed starting at 9:00 am. This phase lasted 11 days.
Protocol. Rats were divided into 2 groups (n/group=10), and an attempt was made to match the groups for equivalent baseline sucrose intake and body weight. One group (Saline group) was administered saline (1 ml/kg), while the other (Nx group) was given Nx in a dose of 1 mg/kg. This dose of Nx was shown in Experiment 5 to suppress intake significantly, and as effectively as a 2 mg/kg dose. Naloxone hydrochloride (Sigma Chemical C. St. Louis, MO), was dissolved in isotonic saline and injected IP in a volume of 1 ml/kg body weight. The procedure for this phase was identical to that of the baseline phase except that each rat received an injection, on average, 30 minutes before the presentation of the sucrose solution. This phase lasted 9 days. This tolerance development phase was followed by a Test Day in which saline was administered to all animals.

Results and Analysis

Mean scores of body weight, powdered food intake and sucrose intake are reported. Individual data points for the groups in Experiment 6 can be found in Appendix F. Figure 15 shows the mean body weights and powdered food intake in both groups. As can be seen in Figure 15, body weight or powdered food intake were similar for the two groups throughout the experiment (Figure 15A, and Figure 15B, respectively). A mixed design repeated measures analysis of variance (ANOVA) of the body weights and powdered food intake obtained from the 2 groups indicated no significant groups effect [F(1,18) < 1].
Figure 15: Mean Body Weight and Powdered Food

Consumption across treatment days

Figure 15A: Mean Body Weight across treatment days

Figure 15B: Mean Powdered Food Consumption across treatment days
Figure 16: Mean Sucrose Consumption across treatment days

Consumption (ml)

Day

Saline    Nx
Figure 17: Mean Sucrose Consumption during the Saline Test Day

Consumption (ml)

Saline

Nx

Saline to all
Figure 16 displays the sucrose consumption during the treatment days. An examination of Day 1 of Nx treatment of Figure 16 reveals that the Nx group evidenced a suppression of intake following the first administration of Nx, compared to the Saline group, which received a saline injection. This suppression of intake was significant \([F(1,18) = 50.06, p<.001]\).

As is clear from Figure 16, however, from Nx Day 1 to Day 9, there was a trend toward recovery of meal size during Nx treatment for the Nx group. The increase in sucrose consumption of the Nx was confirmed by a one way ANOVA, which indicated that the Nx and Saline groups did not differ \([F(1,18) = .15, p>.05]\). Figure 17 depicts the mean sucrose intake during the Test Day. As indicated in Figure 17, and as would be expected, rats which received saline, when expecting Nx (i.e. the Nx group), exhibited a compensatory effect. This compensatory effect was in the opposite direction than that produced by Nx, and resulted in a significantly greater sucrose intake than that exhibited by subjects in the saline group \([F(1,8) = 14.41, p<.01]\).

Discussion

Nx produced no consistent effect on either body weight, nor powdered food intake. This result confirms previous reports, and suggests that although Nx is effective in reducing intake of a test meal, these reductions in feeding were subsequently restored, such that body weight was maintained, and powdered food
intake was not affected (see Brands et al., 1979; Cooper, 1980; Marks-Kaufman & Kanarek, 1990; Reid, 1985).

The intake-suppressive effects of Nx in the present experiment confirm previous reports of the satiety effect of Nx (Baile et al., 1986; Brands et al., 1979; Cooper, 1980; Holtzman, 1974; Lynch & Libby, 1983; McLaughlin & Baile, 1984; Morley & Levine, 1985; Sanger & McCarthy, 1980). This satiety effect lessened over days. This finding confirms an earlier report of tolerance to Nx’s intake-suppressive effect (Brands et al., 1979). Furthermore, similar to the demonstration by Brands et al. (1979), the demonstration of tolerance was shown to demand a contingency between Nx and the sucrose solution. Such a contingency was not implemented by Kirkham (1990), and tolerance was not demonstrated.

Experiment 7: Contingent Tolerance to Naloxone

As discussed previously in Experiment 2, placing an explicit behavioural demand on a drug-affected system can profoundly affect the development of tolerance (see Poulos & Cappell, 1991). Furthermore, many anorectic drugs have shown to display contingent tolerance. Subjects getting the anorectic drug in the non-contingent relationship with food never experience a drug-induced homeostatic disturbance. Thus, the subjects do not become tolerant to the drug (see Poulos & Cappell, 1991).
The demonstration of tolerance to Nx's meal-suppressive effects by Brands et al. (1979) and in Experiment 6 may be explained by the presence of a contingency. The failure of Kirkham (1990) to demonstrate tolerance may be explained by the lack of such a contingency.

The present experiment was conducted to evaluate whether the a contingency between Nx and food was indeed necessary for tolerance development, and to determine if "learning mechanisms" (i.e. homeostatic responses elicited by predrug cues) contribute to contingent tolerance to Nx.

Method

Subjects

The subjects were 21 male Long-Evans hooded rats like those described in Experiment 1. The rats were about 16 weeks old at the beginning of the experiment. The animals were housed and treated similarly to those described in Experiment 1.

Procedure

Baseline. The baseline procedure was identical to that described in Experiment 2, except that the food cups were removed starting at 9:00 am. This phase lasted 13 days.
Protocol. The procedure for this phase of the experiment was similar to that of Experiment 2 (Contingent tolerance to CCK), except that both the Non-Contingent (n=7) and Contingent (n=7) groups received an injection of Nx, which was obtained, prepared and delivered as outlined in Experiment 6. Rats in the Saline group (n=7) received 1 ml/kg of 0.9 % saline. The subjects in the Contingent were administered 7 IP injections on alternate days, followed in 30 minutes by a 30-minute access to sucrose solution. Non-contingent-group rats received identical treatment except their 30-minute access to the sucrose solution occurred on the intervening days. Saline was administered to the Saline group, and sucrose was given 30 minutes following the injection. This tolerance development phase lasted 7 days.

Following the tolerance development phase, 2 Test Days were given like those described in Experiment 2 (Contingent tolerance to CCK). Similar to Experiment 2, during Test Day 1, Nx was administered to all animals. For two days following this test, animals were given injections similar to those described during the tolerance development phase. During Test Day 2, saline was administered to all of the animals.

Results and Discussion

Mean scores of body weight, powdered food intake and sucrose intake are reported. Individual data points for the groups in Experiment 7 can be found in Appendix G. Figure 18 shows the mean body weights and powdered food intake
Figure 18: Mean Body Weight and Powdered Food

Consumption across treatment days

Figure 18A: Mean Body Weight across treatment days

Figure 18B: Mean Powdered Food Consumption across treatment days
Figure 19: Mean Sucrose Consumption across treatment days

Nx Contingent Tolerance
Figure 20: Mean Sucrose Consumption during Test Day 1
Figure 21: Mean Sucrose Consumption during Test Day 2
during treatment days. As can be seen in Figure 18, rats in the 3 groups displayed similar weights and intakes during the experiment (Figure 18A, and Figure 18B, respectively). A mixed design repeated measures analysis of variance (ANOVA) of the body weights and powdered food intake obtained from the 3 groups indicated no significant groups effect [$F(2,18) < 1$].

Figure 19 presents the effects of repeated Nx administrations on sucrose consumption for the treatment days for all groups. Examination of Figure 19 reveals that naloxone significantly suppressed meal size on the first day of drug administration (Day 1) for the Contingent group compared to both the Non-Contingent (which received sucrose on the following day) and the Saline group [$F(2,18) = 20.58$, $p<.0001$]. The Non-Contingent and Saline groups did not differ from one-another, $p>.05$. From Session 1 to Session 7, however, there was a trend toward recovery of meal size during Nx treatment. By Session 7, Nx no longer suppressed sucrose intake in the Contingent group as compared to both the Non-Contingent and Saline group [$F(2,18) = .01$, $p>.05$]. This result confirms the results found in Experiment 6, as well as previous reports that following repeated Nx administration, tolerance develops to Nx’s meal-suppressive effect (Brands et al., 1979).

Figure 20 shows the sucrose consumption during Test Day 1, in which Nx was administered to all subjects. As depicted in Figure 20, rats in the Contingent group display substantial tolerance. In contrast, there is no evidence of any tolerance at all in the Non-Contingent group. Sucrose consumption in the Non-Contingent group on the test day was not different from that of the Saline group that had received saline
rather than Nx during the previous tolerance-induction phase. This result confirms the importance of a contingent relationship between Nx and food for the development of tolerance, and explains Kirkham’s (1990) inability to demonstrate tolerance. A one-way ANOVA indicated a significant difference among the groups during Test Day 1, $F(2,18) = 18.82, p<.001$. Pairwise comparisons were conducted by a Newman-Keuls test. The Contingent group differed from each of the other groups, $ps<.05$. The Non-Contingent group and Saline group did not differ significantly from each other.

The results of a placebo (saline) test session (Test Day 2) are shown on Figure 21. Figure 21 shows the predicted over-consumption by the Contingent group. A one-way ANOVA of the data revealed a significant difference among the groups $F(2,18) = 4.38, p<.05$. Pairwise comparisons were conducted by a Newman-Keuls test. The Contingent group differed from each of the other groups, $ps<.05$. The Non-contingent group and saline group did not significantly differ. The compensatory response is evidence that an association has indeed been learned between the environmental CS and Nx’s meal-suppressive effect, and confirms previous reports of compensatory responses following saline administration to Nx-tolerant rats (Brands et al., 1979).
Experiment 8: Environmental Specificity of Tolerance

On the basis of the conditioning analysis, tolerance should only be displayed when a drug is administered in the context of the usual drug-predictive cues. The results from Experiment 3 indicate that tolerance to CCK is indeed, environmentally-specific. Tolerance develops to both CCK- and Nx’s suppression of intake, and the importance of learning principles has already been demonstrated by the compensatory increase in intake during a saline administration. The present experiment further assessed the contribution of learning principles to Nx tolerance by investigating environmental specificity of Nx tolerance.

Method

Subjects

The subjects were 36 male Long-Evans hooded rats like those described in Experiment 1. The rats were about 14 weeks old at the beginning of the experiment. The animals were housed and treated similarly to those described in Experiment 1.

Procedure

Baseline. The baseline phase of this experiment was identical to that in Experiment 3, except that at 9:00 am, the food cups were removed. Also, sucrose
although prepared and measured in a manner like that described in Experiment 3, was delivered in 50 ml glass cylinders. As described in Experiment 3, Nine Nx and nine Saline (Sal) rats were housed on one of 2 racks ("Room" or Colony"). At 1:40 pm (about an hour following the presentation of sucrose), the rack designated "Room" was wheeled back into the colony room (after remaining in the distinctive room for about an hour and 40 minutes) and at 2:00 pm, the powdered food was presented, and remained in the cages until the following morning. This phase lasted 11 days.

Protocol. The procedure for this phase of the experiment was similar to that of Experiment 3 (a CCK-environmental specificity experiment), except that both the Nx-Room and Nx-Col groups (n/group=9) received Nx. Nx was obtained, prepared and delivered as outlined in Experiment 6. Groups (n/group=9) Sal-Room and Sal-Col were injected with 1 ml/kg of 0.9 % saline. This tolerance development phase lasted 8 days and was followed by a tolerance test session (Test Day 1), in which all animals were administered Nx in the distinctive room. For two days following this test, animals were given injections identical to those described during the tolerance development phase. A second tolerance test session followed (Test Day 2) in which all animals were administered Nx in the colony room. Again, 2 days intervened between this test day and Test Day 3. During Test Day 3, saline injections were given to all animals in the distinctive environment. For two days following this test, animals were given injections identical to those described during the tolerance development phase. A final tolerance test session followed (Test Day 4) in which all animals were administered saline in the colony room.
Results and Analysis

Mean scores of body weight, powdered food intake and sucrose intake are reported. Individual data points for the groups in Experiment 8 can be found in Appendix H. Figure 22 shows the mean body weights and powdered food intake during treatment days. As can be seen in Figure 22, rats in all 4 groups displayed similar weights and intakes during the experiment (Figure 22A, and Figure 22B, respectively). A mixed design repeated measures analysis of variance (ANOVA) of the body weights and powdered food intake obtained from the 4 groups indicated no significant groups effect [$F(3,32) < 1$].

Figure 23 presents the mean sucrose intake during the treatment days. An examination of Figure 23 reveals that Nx significantly suppressed meal size for groups Nx-Room and Nx-Col compared to saline, which was administered to the saline-control groups, Sal-Room and Sal-Col. A 2 (drug; Nx or Saline) X 2 (environment; Colony or Room) ANOVA indicated a significant drug effect [$F(1,32) = 41.74$, \(p<.001\)]. The effect of environment and the interaction of the drug and environment were not significant [$F(1,32) < 1$]. As is clear from Figure 23, however, from Day 1 to Day 8, there was a trend toward recovery of meal size during naloxone treatment. Data obtained from Day 8 of treatment were subjected to a 2 (drug; Nx or Saline) X 2 (environment; Colony or Room) ANOVA. The analysis revealed no significant effects of drug, room or the interaction of the two [$F(3,32) < 1$].
Figure 22: Mean Body Weight and Powdered Food

Consumption across treatment days

Figure 22A: Mean Body Weight across treatment days

Figure 22B: Mean Powdered Food Consumption across treatment days
Figure 23: Mean Sucrose Consumption across treatment days

Consumption (ml)

Day

Nx-Col  Sal-Col  Nx-Room  Sal-Room

Nx Environmental Specificity
Figure 24: Mean Sucrose Consumption during Test Day 1

Consumption (ml)

Nx-Col  Sal-Col  Nx-Room  Sal-Room

Nx in Room
Figure 25: Mean Sucrose Consumption during Test Day 2
Figure 26: Mean Sucrose Consumption during Test Day 3

Saline in Room
Figure 27: Mean Sucrose Consumption during Test Day 4
Figure 24, depicts the mean sucrose intake during the first test session in which all animals were administered Nx in the "Room". As indicated in Figure 24, rats in the two pretest drug-naive groups (Sal-Room and Sal-Col) exhibited a suppression of intake (compared to their intake seen on Day 8 of Figure 23 as well as the intake of the group Nx-Room) during the first tolerance test session. Also, rats with pretest experience with Nx in the distinctive room where the first test session was conducted (i.e., rats in Group Nx-Room) displayed substantial tolerance during the first test session. Rats with pretest experience with Nx, but in a context other than the one in which Test 1 occurred (Group Nx-Col), were not as tolerant as rats in Group Nx-Room during the first test session. A one-way ANOVA indicated a significant difference among the groups during Test Day 1, \[ F(3,32) = 9.06, p<.001 \]. Pairwise comparisons were conducted by a Newman-Keuls test. Group Nx-Room differed from all other groups, \( p<.05 \). The groups Nx-Col, Sal-Col and Sal-Room did not significantly differ from each other.

As is apparent from Figure 25, the results from Test Day 2 yielded similar results to those obtained in Test 1. During Test 2, all rats were administered Nx in the Colony. Rats in groups Sal-Room and Sal-Col exhibited a suppression of intake again during the second tolerance test session, compared to their baseline levels and to group Nx-Col. As would be expected, rats with pretest experience with Nx in the colony room where the second test session was conducted (i.e., rats in Group Nx-Col) displayed tolerance during the second test session. Rats with pretest experience with Nx, but in a context other than the one in which Test 1 occurred (Group Nx-Room),
were not as tolerant as rats in Group Nx-Col during the second test session. A one-way ANOVA indicated a significant difference among the groups during Test Day 2, $F(3,32) = 10.70, p<.001$. Pairwise comparisons were conducted by a Newman-Keuls test. Group Nx-Col differed from all other groups, $p<.05$. Groups Nx-Room, Sal-Room and Sal-Col did not significantly differ from each other.

The results of a placebo test session conducted in the distinctive room (Test Day 3) are presented in Figure 26. Figure 26 demonstrates the predicted over-consumption by the group Nx-Room due to a compensatory response. The data summarized in Figure 26 were subjected to a one-way analysis of variance. The statistical analysis revealed that the group Nx-Room differed from all other groups $F(3,32) = 4.89, p<.001$. Groups Nx-Col, Sal-Col and Sal-Room did not significantly differ from each other. The results of a placebo test session conducted in the colony room (Test Day 4) are presented in Figure 27. Figure 27 demonstrates the predicted over-consumption by the group Nx-Col due to a compensatory response. The data summarized in Figure 27, were subjected to a one-way analysis of variance. The statistical analysis revealed that the group Nx-Col differed from all other groups $F(3,32) = 3.70, p<.05$. Groups Sal-Col, Sal-Room and Nx-Room did not significantly differ from each other.
Discussion

The results of the present experiment confirm and extend the results obtained in Experiments 6 and 7. As in Experiments 6 and 7, tolerance developed to the intake-suppressive effect of Nx. The results obtained in the present experiment extend previous findings by demonstrating that the display of tolerance to the intake-suppressive effects of Nx is more pronounced when the drug is administered in the conjunction with environmental stimuli previously associated with the drug, compared with administration in an alternative environment. These results confirm the results found with CCK (Experiment 3 of the present report), and with many other studies which have demonstrated environmental specificity of tolerance to a variety of drugs (see Siegel, 1987, 1989). That is, tolerance is more pronounced when the drug is administered in the context of the usual predrug cues than when it is administered in the context of alternative cues (see Siegel, 1987, 1989, 1991).

The results from Tests 3 and 4 indicate that a compensatory CR is observed when the usual pre-drug cues are not followed by the usual pharmacological consequences. This confirms the results of Experiments 6 and 7, and previous reports of an overconsumption of intake following the withdrawal of Nx (Brands et al., 1979). This is consistent with previous reports, in which compensatory CRs have been observed with several other drugs, for which environmental specificity has been demonstrated (see Siegel & MacRae, 1984).
Summary and Conclusions

These Nx experiments demonstrate not only that tolerance can develop to Nx’s meal-suppressive effect, but also that this tolerance is affected by Pavlovian principles. Experiment 5 demonstrated that a dose of 1 mg/kg could significantly decrease sucrose consumption. This decrease in consumption lessened however, when animals were injected daily, as shown in Experiment 6. This result confirms the results obtained by Brands et al. (1979). Experiment 7 shows that a contingency between Nx and food is necessary for tolerance to be demonstrated, and thus resolves the conflict in the literature concerning tolerance to Nx; Kirkham (1990) did not present Nx and the food in a contingent manner. The final experiment (Experiment 8) demonstrated the importance of learning principles in the development of tolerance to CCK, as animals were more tolerant to Nx in the environment in which they previously received Nx. The involvement of learning principles was further shown when a saline test day was given in Experiments 6, 7 and 8. An over-consumption of the sucrose meal was evident in each of these experiments, suggesting that an association had indeed been learned between the environmental CS and Nx’s meal-suppressive effect.
CHAPTER 4

CCK AND OPIATE INTERACTIONS

Generally, opiates and CCK have been shown to display opposite effects in various physiological systems (including feeding behaviour), and it has been suggested that these two peptide systems interact at some level to modify the effects of one another. Evidence in support of a relationship between opioids and CCK is the fact that these neuropeptides share a similar distribution of nerve terminals (see Wilson, Denson, Bedford & Hunsinger, 1983). In addition, some investigators have found that a K+ stimulated release of CCK from perfused cortical and hypothalamic tissue was suppressed by the addition of opiate agonists and that this suppression was blocked by naloxone (see Baile et al., 1986). Recently, it has been demonstrated that CCK-8 can suppress the binding of $^3$H-etorphine to opiate receptors in the rat brain (Wang, Fan, Ren & Han, 1989).

Various studies involving CCK-8, opiates and analgesia have indicated that at low doses, CCK-8 acts as an opiate antagonist. At higher doses of CCK-8 however, CCK-8 attains some analgesic properties of its own (see Baber, Dourish & Hill, 1989; Baile et al., 1986; Dourish, Hawley & Iversen, 1988; Dourish, O’Neill, Coughlan, Kitchener, Hawley & Iversen, 1990; Faris et al., 1983; O’Neill, Dourish & Iversen, 1989). Nx has also been shown to possess agonist activity in a variety of behavioural
and in vitro tests at high doses, while it acts as an opiate antagonist at low doses (see Fernandez-Torre, Gonzalez & Del Rio, 1988). Furthermore, the administration of CCK antagonists has shown to potentiate the effects of opiates, and even prevent morphine tolerance (see Baile et al., 1986; see Dourish et al., 1988, 1990; O’Neill et al., 1989; Parsons & Holtzman, 1991; Rattray, Jordan & De Belleruche, 1988; Wang, Wang & Han, 1990). Recently, Wiertelak, Maier and Watkins, 1992, demonstrated that CCK released from the rat spinal cord can inhibit analgesia which was conditioned to a particular environment. As CCK is proposed to act as an opioid antagonist in the modulation of pain, perhaps a similar CCK action is also occurring in the regulation of feeding. This claim is supported by reports that hunger and pain are indeed mediated by similar opioid receptor mechanisms (see Blass, Fitzgerald & Kehoe, 1987; Hamm & Knisely, 1986; McGivern, Berka, Berntson, Walker & Sandman, 1979).

Although a thorough investigation has been given to the interaction of CCK and opiates in pain research, such an investigation in feeding is lacking. Some work however, suggests that such an interaction exists (see Baile et al., 1986; Faris et al., 1983; Morley, 1980; Reid, 1985). Wilson et al. (1983) showed CCK’s (2 ug/kg) suppression of feeding could be antagonized by morphine (10 mg/kg). Furthermore, CCK’s suppression of feeding was potentiated by the opioid antagonist, Nx (4 mg/kg). The results obtained by Wilson et al. (1983) suggest that the CCK-8 effect on eating may be a result of alterations in the activity of endogenous opioid pathways (Baile et al., 1986; Morley, 1980; Wilson et al., 1983).
Although evidence from various studies support an interaction between opiates and CCK, neither the site(s) nor the mechanism(s) of the interaction is clear. There are many ways in which CCK and opiates may interact. For example, separate CCK and opiate receptors may be localized to a common cell/collection of cells which may directly mediate the effects of CCK and/or opiates. Alternatively, a common receptor may exist for CCK and opiates. CCK and opiate receptors may also be on separate cells which converge on a common effector, which may, in-turn, mediate the effects of CCK and opiates. Alternatively, separate CCK and opiate cells may project to separate cells, which, in-turn, converge on an effector. In sum, a number of different possibilities for the interaction of CCK and opiates exist, and a discussion of all of these possibilities is beyond the scope of this paper. Instead, the data are clear that CCK and opiates interact on a functional level; that is, in some way, CCK and opiates interact to affect feeding behaviour.

Experiment 9: Cross-Tolerance to CCK-8- and Naloxone-Induced Meal Suppression

The results of Experiments 1-8 demonstrated that tolerance to the meal-suppressive effect of both CCK-8 and Nx can be demonstrated when either drug is
given repeatedly. Furthermore, it is hypothesized that CCK acts as an opiate-antagonist in the modulation of pain, and may also act as an opiate-antagonist in the regulation of feeding (see Baber et al., 1989; Baile et al., 1986; Dourish et al., 1988, 1990; O’Neill et al., 1989). Indeed, CCK-8 and Nx share a variety of characteristics which include their ability to suppress feeding in a dose-dependent manner (presumably without malaise) as well as affect only meal termination, as opposed to meal initiation (see Baile et al., 1986; Gibbs et al., 1972; 1973; Kirkham, 1990; Weingarten, 1983). The present study was undertaken to demonstrate whether or not cross-tolerance to CCK- and Nx-induced meal suppression could be demonstrated.

Method

Subjects

The subjects were 42 male Long-Evans hooded rats like those described in Experiment 1. The rats were about 17 weeks old at the beginning of the experiment. The animals were treated and housed similarly to those described in Experiment 1.

Procedure

Baseline. The baseline period was similar to that described in Experiment 2, except that the food cups were removed, starting at 9:00 am. This phase lasted 11 days.
Protocol. Rats were divided into 6 groups (n/group=7), and an attempt was made to match for equivalent baseline sucrose intake and body weight: the CCK-CCK, CCK-Nx, Nx-Nx, Nx-CCK, Sal-CCK, and Sal-Nx groups. The labels provided for the groups were determined by what the group received during the tolerance development phase (drug listed before the hyphen) and during the tolerance test session (drug listed after the hyphen). The procedure for the tolerance development phase was identical to that of the baseline phase except that each rat received an injection, on average, 22 minutes before the presentation of the sucrose solution. The tolerance development phase involved administering rats in groups CCK-CCK and CCK-Nx, a total of 9 daily injections of CCK-8, which was obtained and delivered as outlined in Experiment 1, except that the injections were made up to a volume of .5 ml in the present experiment and not 1 ml. The injections were followed in 22 minutes by a 30-minute access to sucrose solution. Rats in groups Nx-Nx and Nx-CCK received identical treatment as the CCK-8 groups listed above, with the sole exception that these animals were injected with Nx. Nn was obtained, prepared and delivered as outlined in Experiment 6. Rats in groups Sal-CCK and Sal-Nx, were injected with .9% saline (1 ml/kg) and allowed to drink the sucrose solution 22 minutes following each injection.

This tolerance development phase was followed by a test session (Test Day 1) in which animals in groups CCK-CCK, Nx-CCK and Sal-CCK were administered CCK-8, and animals in groups Nx-Nx, CCK-Nx and Sal-Nx were administered Nx. After a 22 minute delay all animals were allowed to consume the sucrose solution. For two days following this test, animals were given injections identical to those
described during the tolerance development phase. A second test day was conducted in which all subjects received a saline injection prior to the presentation of the sucrose solution. All animals received an IP injection of 1 ml/kg of 0.9 % saline on Test Day 2.

Results

Mean scores of body weight, powdered food intake and sucrose intake are reported. Individual data points for the groups in Experiment 9 can be found in Appendix I. Figure 28 shows the mean body weights and powdered food intake during treatment days. As can be seen in Figure 28, rats in all 6 groups displayed similar weights and intakes during the experiment (Figure 28A, and Figure 28B, respectively). A mixed design repeated measures analysis of variance (ANOVA) of the body weights and powdered food intake obtained from the 6 groups indicated no significant groups effect [Fs(5,36) < 1].

Figure 29 presents the effects of repeated CCK-8, Nx or saline administrations on sucrose consumption for the treatment days. An examination of Figure 29 reveals that CCK-8 suppressed meal size on the first day of drug administration (Day 1) for the CCK-CCK and CCK-Nx group, and that Nx suppressed intake in the groups Nx-Nx and Nx-CCK compared to both the Sal-CCK and Sal-Nx groups. The data summarized in Figure 29, Day 1 were collapsed into 3 groups, namely CCK (groups
Figure 28: Mean Body Weight and Powdered Food

Consumption across treatment days

Figure 28A: Mean Body Weight across treatment days

Figure 28B: Mean Powdered Food Consumption across treatment days
Figure 29: Mean Sucrose Consumption across treatment days

Cross-tolerance
Figure 30: Mean Sucrose Consumption during Test Day 1

Cross-tolerance test
Figure 31: Mean Sucrose Consumption during Test Day 2
CCK-CCK and CCK-Nx), Nx (groups Nx-Nx and Nx-CCK) and saline (groups Sal-CCK and Sal-Nx) and this was subjected to a one-way analysis of variance. The statistical analysis revealed a significant difference \( F(2,39) = 25.74, p<0.00001 \).

Pairwise comparisons were conducted by a Newman-Keuls test. The Saline group (Sal-CCK and Sal-Nx) differed from the CCK (CCK-CCK and CCK-Nx) and Nx (Nx-Nx and Nx-CCK) groups. The CCK and Nx groups did not differ from one another.

As is clear from Figure 29, however, from Session 1 to Session 9, there was a trend toward recovery of meal size during CCK-8 and Nx treatment. By Session 9, neither CCK-8 or Nx suppressed sucrose intake in the treatment groups as compared to both the saline controls (i.e Sal-CCK and Sal-Nal).

Figure 30 shows the sucrose consumption during Test Day 1; that is, the session in which CCK-8 was administered to subjects in groups CCK-CCK, Nx-CCK, and Sal-CCK, and Nx was administered to subjects in groups Nx-Nx, CCK-Nx and Sal-Nx. As depicted in Figure 30, rats administered CCK-8 in the tolerance development phase and administered Nx on the test day showed similar intakes to those animals administered CCK-8 during the tolerance development phase and given CCK-8 on the test day. Similarly, animals treated with Nx during the tolerance development phase were equally tolerant to Nx and CCK-8 administered during the test session. Animals in group Sal-CCK and Sal-Nx displayed the normal suppression of intake following administration of either CCK-8 or Nx, respectively. The data was subjected to a 3 (training drug; CCK, Nx or saline) X 2 (test drug; CCK or Nx) ANOVA which indicated a significant main effect of the training drug \( F(2,36) = \)
28.50, p<.00001]. Pairwise comparisons were conducted by a Newman-Keuls test on the main effect of training drug. Groups Sal-CCK and Sal-Nx differed from all the other groups, but did not differ from one another. Groups CCK-CCK, CCK-Nx, Nx-Nx and Nx-CCK did not differ from one another.

The results of Test Day 2 (the saline test session) are shown on Figure 31. Figure 31 demonstrates the predicted over-consumption by the groups CCK-CCK, CCK-Nx, Nx-Nx, and Nx-CCK, due to a compensatory response. The data was subjected to a 3 (training drug; CCK, Nx or saline) X 2 (test day 1 drug; CCK or Nx) ANOVA which indicated a significant main effect of the training drug [F(2,36) = 4.20, p<.05]. Pairwise comparisons were conducted by a Newman-Keuls test on the main effect of training drug. Groups Sal-CCK and Sal-Nx differed from all the other groups, but did not differ from one another. Groups CCK-CCK, CCK-Nx, Nx-Nx and Nx-CCK did not differ from one another.

Discussion

Consistent with previous reports as well as the results from Experiments 1-8, repeated administration of either CCK-8 or Nx produced no significant effect on either body weight or powdered food intake. Rats receiving CCK-8 on a daily basis were tolerant to the meal-suppressive effect of CCK-8 and were cross-tolerant to the meal-suppressive effect of Nx. Similarly, rats tolerant to the meal-suppressive effect of Nx
were cross-tolerant to the meal-suppressive effect of CCK-8; therefore, the cross-tolerance observed in rats maintained on either CCK-8 or Nx is symmetrical.

The results from Test 2 indicate that a compensatory CR is observed when the usual predrug cues are not followed by the usual pharmacological consequences. The over-consumption displayed, was equal in magnitude for both the CCK (data from group CCK-CCK and CCK-Nx) and Nx (data from groups Nx-Nx and Nx-CCK) groups.

Summary and Conclusions

Opiate and CCK peptides have shown to display opposite effects in various physiological systems (including feeding behaviour), and it has been suggested that these two peptide systems interact at some level to modify the effects of one another. Although the discussion of an interaction between CCK and opiates has been primarily in the area of pain regulation, such an interaction has also be seen in the regulation of feeding.

In a classic demonstration, Wilson et al. (1983) showed that morphine antagonized, while Nx potentiated, CCK's suppression of feeding. Thus, it may be that CCK acts as an opiate-antagonist in the regulation of feeding, as well as in the regulation of pain. Experiment 9 showed that the tolerance that develops to CCK-8 is symmetrical with respect to Nx. This result suggests that CCK-8 and Nx affect feeding behaviour in a similar manner.
CHAPTER 5

GENERAL DISCUSSION, IMPLICATIONS, AND CONCLUSIONS

This thesis investigated whether or not tolerance developed to CCK-8 and Nx, and whether learning principles played a role in this tolerance. Tolerance to CCK-8 has been shown to develop following repeated daily administration, and is affected by conditioning procedures. For example, the demonstration of a compensatory over consumption response during saline treatment, confirms the involvement of Pavlovian principles. In addition, tolerance to CCK-8 has been shown to be contingent, as well as environmentally specific. Finally, tolerance to CCK-8 is subject to latent inhibition.

Tolerance to Nx's meal-suppressive effect has been shown to be entirely contingent as well as environmentally specific. The contribution of learning is also evident by the demonstration of saline-elicited compensatory responses in the series of experiments conducted on Nx. Taken as a whole, evidence which suggests CCK to be an opiate-antagonist in the regulation of pain, suggests that CCK and Nx may affect feeding behaviour in a similar manner. In discussing a possible mechanism of tolerance development, perhaps a summary of the role of endogenous opioids and anticipation is necessary.
It has been reported that the ingestion of palatable, sweet solutions stimulates opioid release within the brain (see Kirkham, 1990). In addition, it has been argued that because rats do not drink large quantities of a palatable solution on their first exposure but instead, increase their intake gradually, endogenous opioids may be released in central taste pathways by the anticipation of repeated tests and thereafter, may mediate enhanced acceptance of sweets (Lynch & Libby, 1983). Indeed, classically conditioned stimuli are capable of eliciting endogenous opioid release, or causing opioid receptor sensitivity (see Kehoe & Blass, 1989; Matzel & Miller, 1987; Wiertelak et al., 1992).

Chronic opiate antagonist treatment appears to increase the number of mu, delta and kappa receptors, both in vivo and in vitro (see Kirkham, 1990; Lahti & Collins, 1978). Chronic treatment of Nx or CCK may also increase endogenous opiate activity, although this has not yet been tested. Tolerance to CCK-8 and/or Nx’s meal-suppressive effects may then be accounted for by such an up-regulation of receptors or by an increase in endogenous opiate activity. An increased level of opioid activity may be via an increase in endogenous opioid release, or by an increased sensitivity of opioid receptors. In addition, as discussed above, this increase in endogenous opiate activity may be learned (see Kehoe & Blass, 1989; Matzel & Miller, 1987; Wiertelak et al., 1992). Thus, the compensatory CR seen during the administration of saline in association with the Nx- or CCK-associated cues, may be explained by conditioned CCK- or Nx-associated endogenous opioid release. This would, in turn, result in a greater consumption of sucrose.
The ability of CCK-8 to act as an opiate antagonist in the modulation of pain provides some evidence to suggest that CCK-8 and Nx affect feeding behaviour in a similar manner. Furthermore, it has been proposed that repeated administration of CCK-8 would result in an increase in the endogenous opioid activity, which would account for the tolerance. This mechanism has yet to be tested empirically, and thus further studies should concentrate their efforts on the mechanism of tolerance development.

**Testing of the Hypothesized Mechanism of Tolerance Development**

The present findings suggest several areas of further investigation. One major area of inquiry concerns empirically testing the hypothesized mechanism of tolerance development. That is, a test for increased opiate activity during CCK-8 and/or Nx tolerance should be conducted. The first step here is to investigate directly, with measurement of opiate activity through assays, or through the analgesic responses, of tolerant and non-tolerant animals following a saline test. If animals are capable of stimulating endogenous opiate activity, and do so as a means of developing tolerance to an opiate-antagonist, then one can expect more analgesia in the tolerant animals. Another approach to this problem would be to test animals given CCK-8 or Nx and food in a contingent manner versus animals given CCK-8 or Nx and food in a non-contingent manner following both a drug treatment day, as well as a saline day. As the present experiments have indicated the importance of a contingency between food and the drug for tolerance development, it is expected that under such circumstances,
greater analgesia will be present in the contingent group. The contingent group after all, will have made compensatory responses in the form of increased opiate activity. These responses will not be seen in the non-contingent group as this group is not tolerant to the drug.

A second question concerns whether or not just the simple anticipation of sucrose can result in an increase of endogenous opiate activity. It has been hypothesized that anticipation of sucrose may elicit an increase in opiate activity, but to date, this has not been tested empirically (see Lynch & Libby, 1983). One approach to this problem would be to implement a discriminative design in which one room is paired with sucrose and the other room is not. If the anticipation of sucrose can increase endogenous opiate activity, then it is expected that there will be a greater analgesic response in an environment paired with sucrose. This demonstration of anticipatory endogenous opiate release would add further support to the hypothesis that tolerance to CCK or Nx is mediated by an anticipatory increase in opiate activity.

In summary, the present experiments demonstrate that tolerance to the meal-suppressive effects of CCK-8 and Nx does develop. Furthermore, learning mechanisms contribute to this tolerance. The demonstration of cross-tolerance between CCK-8 and Nx suggests that CCK-8 and Nx affect feeding behaviour in a similar manner. An increase in endogenous opiate activity has been proposed to be a possible mechanism responsible for tolerance development. Future experiments should test and assess the validity of the proposed mechanism of action.
REFERENCES


APPENDIX A:

Data compiled from Experiment 1
Body weights (g) during treatment days 1-9.

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### Powdered food intake (g) during treatment days 1-9.

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APPENDIX B:

Data compiled from Experiment 2
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Powdered food intake (g) during treatment days 1-9.

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APPENDIX F:

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APPENDIX G:

Data compiled from Experiment 7
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APPENDIX I:

Data compiled from Experiment 9
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# Sucrose intake (ml) during treatment days 1-9

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