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# The Effects of Circadian Entrainment on Operant Conditioning

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The Effects of Circadian Entrainment on Operant Conditioning

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#### Abstract

The matching law has been a prevalent theory in behavior analysis for the past thirty years. This theory states that responding changes as a monotonic function of reinforcement. However, several studies have found bitonic functions. One reason for this discrepancy may be due to circadian entrainment. There is evidence that rats are sensitive to circadian rhythms and that rats are capable of entraining to two feeding times per day. Also, it may be that the biological makeup of rats consists of two separate rhythm oscillators. One involves food and the other involves light. The present experiments attempted to discover what role circadian rhythms have in shaping the VI response function. Rats were exposed to a series of conditions involving different session times as well as different reinforcement schedules. Although significant differences were found between VI schedule and response rate, there were no significant effects of circadian entrainment on the VI response function. This may be due to the sensitivity of circadian rhythms in animals. Future research is needed to determine what role entrainment does play in behavior analysis.

# The Effects of Circadian Entrainment on Operant Conditioning

The matching law (Herrnstein, 1961), has been a prevalent theory in behavior analysis during the last 30 years. Simply, this law states that the relative rate of responding on concurrent variable interval (VI) schedules is directly related to the relative rate of reinforcement (a VI schedule is one in which, on the average, a response produces a reinforcer every N seconds). Herrnstein (1970) subsequently expanded the matching law to simple VI schedules. According to his equation for simple schedules, the absolute rate of responding is a monotonic and hyperbolic function of reinforcement rate. In other words, as reinforcement rates increase, response rates increase also (see Figure 1). Several studies have confirmed the relationship predicted by matching. For example, Catania and Reynolds (1968) found that pigeons' rate of responding increases more rapidly at low rates of reinforcement than at higher rates, approaching an asymptote, but never decreasing.

Recently, the matching law has been attacked both on theoretical and empirical grounds (Timberlake, 1982; Warren-Boulton, Silberberg, Gray, and Ollom, 1985). Although matching has a high success rate in predicting Entrainment on Operant Conditioning 5 responding, it is largely a correlational measure (Timberlake, 1982). Further, the theoretical assumptions become unrealistic when applied to more complex behavioral situations. For instance, the additional parameters of background and intrinsic reinforcement (Herrnstein 1970, 1974) imply that whatever the animal is doing is reinforcing (Timberlake, 1982). However, the animal has to always be doing something because even just sitting in the corner of the chamber is itself an activity. It is difficult to discover what, if anything, is reinforcing about sitting in that particular corner (Timberlake, 1982).

Warren-Boulton, et al. (1985) suggested that the matching law's predictive value would greatly improve if the asymptote in Herrnstein's (1970) equation is allowed to vary monotonically (either increasing or decreasing) with reinforcement rate. In such a case, the equation can yield a bitonic function rather than the traditional monotonic one obtained from a fixed asymptote. Additionally, theories in the sub-field of behavioral economics have also challenged the matching law (Dougan, 1992). Such theories also predict bitonic functions. In this case, response rates increase and then decrease as reinforcement rate increases (see Figure 2).

Entrainment on Operant Conditioning 6 Dougan, Kuh, and Vink (1993) attempted to discover why some studies have yielded monotonic functions (Herrnstein, 1961, 1970; Catania and Reynolds, 1968) while others have yielded bitonic ones (Dougan, 1992; Warren-Boulton et al., 1985). Rats were exposed to four different VI schedules in either 10-minute or 30minute sessions. In the 10-minute sessions and in the first ten minutes of the 30-minute sessions, monotonic functions described the animals' response rate. However, bitonic functions were prevalent throughout the 30-minute sessions in general. Further, the later in the 30-minute time block, the more bitonic the function. However, Dougan et al., (1993) were unable to determine the cause of the within-session changes.

Campbell and Dougan (in press) assessed two variables, food density and elapsed time, as causes for the within-session effects seen in the Dougan et al., (1993) study. Rats were exposed to either 10-minute or 30-minute sessions. However, during half of the 10minute sessions, rats were pre-fed an amount of food equal to the average amount earned in the first 20 minutes of a 30-minute baseline session. To examine elapsed time, the response bar was only available during the first or third 10-minute blocks of the 30minute session. Results indicated bitonic functions under all conditions tested. Entrainment on Operant Conditioning 7

One explanation for the difference in response functions between Dougan et al., (1993) and Campbell and Dougan (in press) may be due to methodological differences in these two studies. For example, in the Dougan et al., (1993) study, the time of day that sessions were conducted was not consistent throughout the experiment and sessions were not always conducted every day. In contrast, the Campbell and Dougan (in press) study was conducted consistently at the same time of day, every day, for the duration of the experiment. It may be that circadian entrainment played a role in the animals' response rates because rats that are strictly entrained (sessions conducted in a consistent manner) may respond differently than those who are not strictly entrained (sessions conducted in an inconsistent manner).

Some recent evidence suggests that animals, in particular rats, are sensitive to circadian rhythms (Gallistel, 1990;). Bolles and Moot (1973) studied the effect of two meals a day on anticipatory behavior in the rat. Animals were fed twice a day (10:00 a.m. and 4:00 p.m.) while living in a chamber containing a running wheel with a food dispenser to its side. Additionally, half of the rats were exposed to a reversed light/dark cycle. Thus, half of the rats were fed twice daily in the dark while the other half were fed in the light.

All rats increased their wheel running activity just prior to each feeding time and this anticipatory behavior was greater in the rats that were fed in the dark. Anticipatory behavior seems to be dependent on an approximately 24 hour light dark cycle (Bolles and Moot, 1973; Bolles and Stokes, 1965). When the day (light/dark cycle) was shortened to 19 hours or lengthened to 27 hours, anticipatory behavior did not occur (Bolles and Stokes, 1965).

Furthermore, these types of food anticipatory behaviors tend to continue for at least one week after the removal of the feeding schedule (Rosenwasser, Pelchant, and Adler, 1984). It has been suggested that the suprachaiasmatic nucleus (SCN) in the hypothalamus of the brain is a sort of "Master Control" center for circadian activities in animals (Plata-Salaman and Oomura, 1987; Rossenwasser, Pelchant, and Adler, 1984). However, recent studies have provided evidence that overall circadian functioning is dependent on a multioscillator circadian system. In other words, the SCN may control a light-entrainable oscillator, but different oscillators control other rhythms, such as feeding behavior (Boulos and Logothetis, 1990; Rossenwasser et al., 1984).

Boulos and Logothetis (1990) have provided the

Entrainment on Operant Conditioning 9 strongest evidence for separate oscillators. Both rats with lesions in the SCN and without lesions were conditioned to obtain food by pushing either of two bars under light/dark (LD) cycles and light/light (LL) cycles. Rats were able to anticipate feedings on two different bars at two daily feeding times even when each bar produced reinforcement at one of the feeding times. Further, intact rats were able to discriminate between the two bars in the LD cycle better than lesioned and intact rats in the LL cycle. The SCN may mediate the light-entrainable oscillator so that rats are capable of anticipating meals in the absence of a LD cycle, but when the food-entrainable oscillator is controlled by the light-entrainable oscillator, discrimination ability and anticipatory behavior increase (Boulos and Logothetis, 1990).

Food anticipatory behavior seems to be at least partly independent of the light-entrainable oscillator (Boulos and Logothetis, 1990; Rossenwasser et al., 1984). Rossenwasser et al. (1984) showed that rats were able to anticipate feedings on a previous daily feeding schedule and that the light- and foodentrainable oscillators tend to run in parallel to each other under ad lib conditions. All rats in this study were fed at the same time each day. Possibly, the coupling of these two separate oscillators is dependent Entrainment on Operant Conditioning 10 on environmental conditions such as feeding schedules. During ad lib conditions, the food-entrainable oscillator operates separately from the lightentrainable oscillator. However, anticipatory behavior occurs during states of food deprivation when the food oscillator is controlled by the light oscillator (Rossenwasser et al., 1984). Such a mechanism would allow the animal to organize foraging behavior within a predictable as well as a non-predictable environment.

Circadian entrainment may effect the VI response function. If an animal is exposed to a predictable environment, it is possible that the animal will choose not to respond at one time because food will again be available at a predictable time in the future (Stephens and Krebs, 1986). If so, the differences between Dougan et al., (1993) and Campbell and Dougan (in press) could be explained as follows. The rats in Campbell and Dougan (in press) may have been able to anticipate the session times because both the food- and light-entrainable oscillators would have been strictly entrained to the laboratory conditions. Alternatively, the rats in the Dougan et al. (1993) were not able to anticipate the sessions because the oscillators were not strictly entrained to the environmental conditions.

Herrnstein's (1970) equation predicts a monotonic function in all situations. However, Campbell and

Entrainment on Operant Conditioning 11 Dougan (in press) and Dougan et al., (1993) have demonstrated that within-session effects produce a bitonic function. The role of these effects still remains unclear. The following experiments will test the effects of a predictable vs. a non-predictable environment on the VI response function. Moreover, Experiments 1 and 2 will extend the findings of Rossenwasser et al. (1984) by examining food anticipatory behavior (bar pressing) during variable times as well as constant times. Further, based on studies that have shown higher response rates at night (Bolles and Moot, 1973; Johnson and Johnson, 1990), Experiment 3 will assess the difference between daytime and night-time sessions. It is expected that rats on a predictable food-entrainment cycle (constant session time, 12 hours light/12 hours dark) will produce different response functions than those on an unpredictable food entrainment cycle and that night sessions will yield higher response rates than day sessions.

# Experiment 1

## <u>Method</u>

Animals. The animals were 6 naive female Long-Evans hooded rats and were obtained from the animal colony at Illinois Wesleyan University. The rats were approximately 120 days old at the beginning Entrainment on Operant Conditioning 12 of the study. Animals were housed in six individual, opaque plastic tubs with water available at all times.

Apparatus. The conditioning apparatus consisted of two standard operant conditioning units for rats (BRS/LVE model RTC-028). Each chamber was 30 cm in length, 24 cm in width, and 26.5 cm in height. The side walls and the ceiling of the chamber were composed of plexi-glas, while the front and back walls were made of stainless steel. The floor consisted of metal bars separated in equal intervals. Two retractable bars were positioned on the right and left sides of the front wall 5 cm above the floor and 3 cm from the nearest side wall. Only the bar on the left side was used in this experiment. When extended, the bars projected 2.5 cm into the chamber and had a width of 3 cm; when retracted, the bars were flush with the wall.

Three cue lights of different colors were positioned 5 cm above each bar. Only the red light was used. A food cup projected into the chamber on the front wall between the two bars, 11 cm from the right wall. A water magazine was also located between the bars (11 cm from the left wall), but was not used in this study. The chamber was illuminated by a 5W light in the center of the front wall, 1 cm from the ceiling. Entrainment on Operant Conditioning 13

An IBM PC compatible computer, connected to a MED associations interface and running MED-PC software, was used for the programming of VI schedules and the collection of data. The PC was located in a separate room from the conditioning apparatus.

<u>Procedure.</u> All 6 rats were deprived to 80% of their ad libitum (free feeding) weight. Rats were then shaped by hand to press the left bar of the operant chamber for a 45 mg pellet of food (Noyes Improved Formula A). Once all animals were reliably pressing the bar, experimental conditions were implemented.

All animals were exposed to a total of twelve conditions. Each condition was defined by a combination of session times and VI reinforcement schedules. Session times occurred either at a constant time (11:00 a.m.) or at a variable time randomly determined from three alternatives (8:00 a.m., 11:00 a.m., and 4:00 p.m.). All rats were exposed to one 10 minute session once a day, seven days a week for the duration of the study. All conditions were counterbalanced across animals to create a withinsubjects design study.

Three variable interval schedules were utilized (VI 7.5, VI 30, and VI 480) in the study. These were the same series of schedules that were used in the Dougan et al., (1993) study except that the VI 15

Entrainment on Operant Conditioning 14 schedule was omitted due to time constraints. The order of the schedule presentations was counterbalanced across animals to avoid systematic order effects. Further, all three VI schedules were presented under one time condition (either same-time or variable-time) before the animal was switched to the other time condition. For example, if the animal began testing under same-time, VI 7.5, it would complete VI 30 and VI 480 in the same-time condition before testing on any schedule under the variable-time condition occurred. Also, no rat was conditioned in the same box for three consecutive days to avoid effects of unseen differences in the conditioning boxes.

Each animal was exposed to each VI schedule for 15 consecutive sessions before being switched to a new schedule. In the variable-session time condition, each rat was exposed to each possible session time four to six times under each schedule. Supplementary feedings to maintain 80% of ad libitum weight were implemented approximately one hour after the session was completed. Results

Response rates for each individual animal were calculated by dividing the total number of responses made by the number of minutes in the session (see Figure 3). Mean response rates were calculated using the data obtained from the last five days of each VI Entrainment on Operant Conditioning 15 schedule condition. Mean response rates for each time condition (variable-time and same-time) were also calculated (see Figure 4).

Within the variable-time condition, between session intervals were broken down into three blocks: short interval (less than or equal to 19 hours), medium interval (20 to 28 hours), and long interval (greater than or equal to 29 hours). Response rates for each between-session interval were calculated (see Figure 5). Mean response rates for the between session intervals can be found in Figure 6.

A two-way within subjects Analysis of Variance (ANOVA) was used to test the probability that the outcome was due to chance. The independent variables in this study were session time and VI schedule while the dependent variable was the response rate in the operant chamber. There was a significant main effect of VI schedule on the rate of responding (F [2,10] = 18.609, p < 0.0001). However, there was no significant main effect of circadian entrainment (F [1,5] = 0.0054) nor was there any significant interaction (F [2,10] = 3.34).

Furthermore, there was no significant main effect of between session intervals on the response function (F [1,5] = 0.069) nor was there a significant interaction (F [4,20] = 2.947).

# <u>Discussion</u>

This experiment confirmed the bitonic nature of responding that was found in recent studies (Campbell and Dougan, in press; Dougan, et al., 1993; Warren-Boulten, et al., 1985). The lack of significance with regard to circadian entrainment does not mean that circadian rhythms do not influence responding in an operant chamber. This study did not take into account the normal nocturnal activity of rats. Rats typically engage in a great deal of activity at night and sleep during the day. Circadian entrainment may occur more effectively during the night hours since this is the time that rats are typically more active. Experiment 2 assessed the effects of variable- and same-time conditions that take place during the night.

Experiment 2

#### <u>Method</u>

Animals. The animals were the same 6 female Long-Evans hooded rats that were used in Experiment 1. Animals were approximately 350 days old at the start of the experiment.

Apparatus. The conditioning apparatus consisted of the same two operant chambers used in Experiment 1. Also, the same MED-PC software was used for programming the VI schedules and collecting the data.

Procedure. All 6 rats were deprived to 80% of

Entrainment on Operant Conditioning 17 their ad libitum weight and randomly exposed to the same session time conditions and VI schedule conditions as in Experiment 1. The procedure for conducting sessions was the same as in Experiment 1, except that the light/dark cycle in the housing room was reversed. The lights turned off at 7:00 a.m. and turned on at 7:00 p.m. so that during the day, it was dark in the animal colony. The animals were given two weeks to adjust to the new light/dark cycle before experimental procedures began.

#### <u>Results</u>

Response rates for each individual animal were calculated by dividing the total number of responses made by the number of minutes in the session. All data points were taken from the last five days of each VI schedule condition (see Figure 7). Mean response rates for each time condition (same- and variable-time) were also calculated (see Figure 8). As in Experiment 1, the short, medium, and long between-session intervals were examined and can be found in Figure 9. Mean response rates for the between session intervals were also calculated (see Figure 10).

A two-way within subjects ANOVA was used for data analysis. There was a significant main effect of VI schedule (F [2,10] = 25.707, p < 0.0001). However, there was no significant main effect of circadian Entrainment on Operant Conditioning 18 entrainment (F [1,5] = 0.816) nor was there a significant interaction (F [2,10] = 1.278). As in Experiment 1, there was no significant main effect of between session interval (F [2,10] = 2.55) nor was there a significant interaction between VI schedule and between session intervals (F [4,20] = 0.359). Discussion

The collective results of Experiments 1 and 2 indicate circadian rhythms do not have an effect on the VI response function in a situation where both the food-entrainable oscillator and the light-entrainable oscillator are coupled to each other. However, this still does not determine the effect of day-time vs. night-time sessions because the light/dark cycle was reversed in a separate experiment from the original. Experiment 3 assessed any differences in day-time vs. night-time responding.

## Experiment 3

#### <u>Method</u>

<u>Animals.</u> The animals were 6 experimentally experienced female Long-Evans hooded rats obtained from the animal colony at Illinois Wesleyan University. The animals were approximately 300 days old at the beginning of the study.

Animals were housed in six separate stainless steel home cages in a room with 12 hours light (6:00 Entrainment on Operant Conditioning 19 a.m. to 6:00 p.m.) and 12 hours dark. The front wall and floor of each cage was wire mesh. Water was freely available in the home cage for the duration of the experiment.

<u>Apparatus.</u> The conditioning apparatus consisted of the same two operant chambers used in Experiments 1 and 2.

<u>Procedure.</u> Although the 6 animals had previous experimental experience, they needed to be shaped by hand to press the bar in these specific operant chambers. Once all the subjects were reliably pressing the bar, the experimental procedures began.

All animals experienced two session-time conditions and four VI schedule conditions. This experiment was also a within-subject design study. Sessions were conducted 12 hours apart (11:00 a.m. and 11:00 p.m.). In each time condition, each animal was exposed to four VI schedules (VI 7.5, VI 15, VI 30, and VI 480) for ten consecutive days. For both time conditions, all four VI schedules were completed before the animal was exposed to the other time condition. Each 25 minute session was conducted once a day, seven days a week.

The presentation of schedules was counterbalanced across subjects to control for systematic order effects. No rat was conditioned in the same box for Entrainment on Operant Conditioning 20 more than three days in order to control for unseen differences in the conditioning chambers. Supplementary feedings to maintain 80% of ad libitum weight were given approximately 12 hours after each session.

## <u>Results</u>

The response rates for each individual animal in each time condition were calculated by dividing the number of responses made by the number of minutes in the session. The data used was taken from the last five days of running under each VI schedule (see Figure 11). Mean response rates for both the day-time and the night-time condition were also calculated (see Figure 12).

A two-way within subjects ANOVA was used to test the statistical significance of the data. There was a significant main effect of VI schedule on the rate of responding (F [3,15] = 32.622, p < 0.0001). However, there was no significant main effect of session time (F [2,10] = 2.55) nor was there any significant interaction (F [3,15] = 0.5119).

# General Discussion

Experiments 1 and 2 were designed to test the effects of a predictable vs. a non-predictable session time on the VI response function, while Experiment 3 sought to determine the difference between day-time and Entrainment on Operant Conditioning 21 night-time sessions. In all instances, the foodentrainable oscillator was coupled to the lightentrainable oscillator. It was expected that exposure to a predictable environment would cause a different response rate than exposure to an non-predictable environment. Also, sessions conducted at night were expected to produce an elevated response rate.

However, the results of these experiments did not confirm these hypotheses and there are several implications of this. First, the findings of Campbell and Dougan (in press) are extended because bitonic functions were found in a situation in which matching typically predicts monotonic ones (Herrnstein, 1970, 1974). Further, these results support recent findings in the realm of behavioral economics (Dougan, 1992). The theories of matching and behavioral economics predict different rates of responding in an operant chamber, and these results help to unify the varying concepts of reinforcement on VI schedules.

These results also have methodological implications. There has existed for some time in behavior analysis a certain "laboratory lore" that suggests that experimental sessions should be conducted at a consistent time, every day. Since this was never empirically shown to be the case, researchers frequently skip a day or two during experimentation or

Entrainment on Operant Conditioning 22 run experiments at varying times from day to day. For example, many researchers do not conduct experiments on weekends. These present studies provide evidence that this "lore" may in fact not be true and occasionally skipping a day will not adversely affect the experiment. Of course, such variable methods of experimentation could add variability or cause other harmful effects that were not examined in the scope of these experiments. One aspect that has been largely ignored in the past is the role of biology in operant conditioning. The present studies attempted to provide evidence for biological influences on the animal's behavior in an operant setting. Previous studies have examined food anticipatory behaviors and found that under states of food deprivation, this type of anticipatory behavior tends to occur (Bolles and Moot, 1973; Boulos and Logothetis, 1990; Rossenwasser et al., 1984). One proposed reason for this phenomena is that there are two separate oscillators that operate in animals (Rossenwasser et al., 1984). The present study attempted to extend these results into the realm of behavior analysis.

However, biological functions are very difficult to control for in an operant setting and it may be that the experimental procedures that were utilized in these experiments were not sensitive enough to account for Entrainment on Operant Conditioning 23

circadian rhythms. Rats have been shown to be nocturnal feeders, but this feeding activity tends to take place during the hours just after dusk or right after dawn rather than during periods of complete darkness (Gallistel, 1990). In the laboratory, there is no gradual lighting or darkening of the cage. The lights turn on at full brightness and turn off into complete darkness. In the night-time conditions of both Experiments 2 and 3, the rats were taken from a dark room and placed directly into the light of the experimental chamber. Since this environment is unlike that of rats in the wild, the rats may have been unable to entrain to such artificial conditions. In other words, the food-entrainable oscillator may have operated as if it were still under ad lib conditions. Possibly, an environment that takes into account the environmental conditions of wild rats would yield better results. Moreover, the variable session times in Experiments 1 and 2 were randomly chosen from three times within an eight hour period (8:00 a.m., 11:00 a.m., and 4:00 p.m.). This is largely due to time constraints and availability of the operant boxes. However, to be truly random, the time conditions would need to vary within the entire 24 hour period rather than just 1/3 of the hours within the light/dark cycle. Because rats have been shown capable of entraining to

Entrainment on Operant Conditioning 24 two meal times a day (Bolles and Moot, 1973; Boulos and Logothetis, 1990), there is a possibility that the rats will be able to entrain to the random feeding times if sessions are consistently at one of three times. Therefore, a study in which the session times are allowed to vary anywhere within the 24 light/dark cycle should more fully reflect the role of circadian rhythms in operant conditioning.

The next logical step is to conduct a study in which the rats live in the operant chamber 24 hours a day for a period lasting two to three weeks. In previous experiments, the rats' anticipatory behaviors were measured in the environment in which the rat lived (Bolles and Moot, 1973; Bolles and Stokes, 1965; Boulos and Logothetis, 1990; Rossenwasser et al., 1984). For example, Bolles and Moot (1973) had the rats live in a chamber that contained a running wheel, food cup, and water dispenser. In the present experiments, the rats were moved from the home cage to the operant chamber for the experimental procedures. It may be that the act of being handled and moved to another cage confounded the data in some way. An experiment in which the animals live in the operant boxes would control for this.

Additional research might investigate circadian influences in other species as well as rats. There are

Entrainment on Operant Conditioning 25 several different species that entrain to different periods of light. For instance, animals that live closer to the poles will be exposed to different light cycles that those that originate midway between the poles and the equator. It would be interesting to see in what way these animals differ in responding to those that are entrained to an approximate 12 hour light/12 hour dark cycle that is the norm for laboratory animals. Future experiments are needed to explore the role of circadian rhythms in other species and to compare the behavior across species to see if any generalizations exist.

The present study attempted to discover what role circadian entrainment has in shaping the VI response function. Although the results of these experiments confirmed the bitonicity of the response function, they failed to support past findings of anticipatory behavior. Future research in which the animals live in the experimental chamber and that takes into account the animals' natural environment will be able to accurately assess the role of circadian rhythms in behavior analysis.

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# Author Note

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# Figure Captions

<u>Figure 1.</u> Example of Herrnstein's monotonic matching prediction. Mean rate of response per minute plotted as a function of reinforcement.

Figure 2. Bitonic function predicted by behavioral economics. Mean rate of response per minute plotted as a function of reinforcement.

<u>Figure 3.</u> Rate of response per individual animal plotted as a function of VI reinforcement schedule for variable- and same-time conditions.

Figure 4. Mean rate of response plotted as a function of VI reinforcement schedule for variable- and sametime conditions.

Figure 5. Rate of response per individual animal plotted as a function VI reinforcement schedule for between-session intervals.

<u>Figure 6.</u> Mean rate of response plotted as a function VI reinforcement schedule for between session intervals.

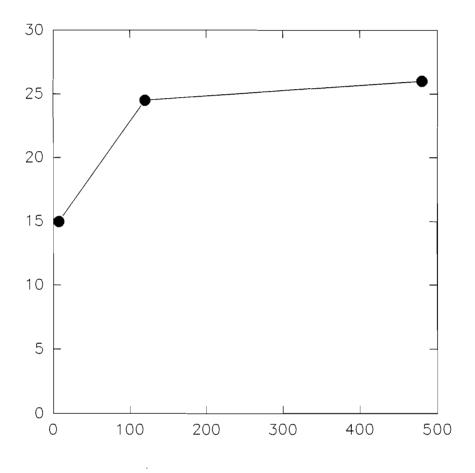
Figure 7. Rate of response per individual animal plotted as a function of VI reinforcement schedule for variable- and same-time conditions in a reversed light/dark cycle.

<u>Figure 8.</u> Mean rate of response plotted as a function of VI reinforcement schedule for variable- and sameEntrainment on Operant Conditioning 31 time conditions on a reversed light/dark cycle. <u>Figure 9.</u> Rate of response per individual animal plotted as a function of VI reinforcement schedule for between session intervals in a reversed light/dark cycle.

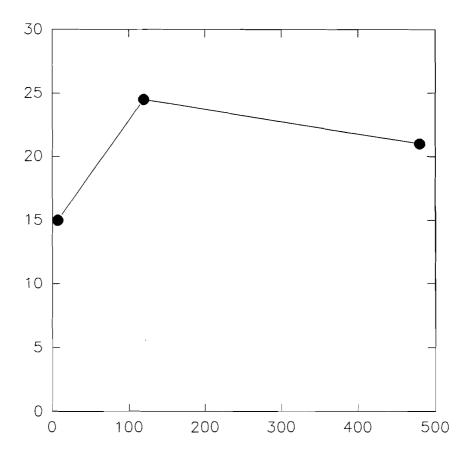
Figure 10. Mean rate of response plotted as a function of VI reinforcement schedule for between session intervals in a reversed light/dark cycle.

Figure 11. Rate of response per individual animals plotted as a function of VI reinforcement schedule for day-time and night-time conditions.

Figure 12. Mean rate of response plotted as a function of VI reinforcement schedule for day-time and nighttime conditions.

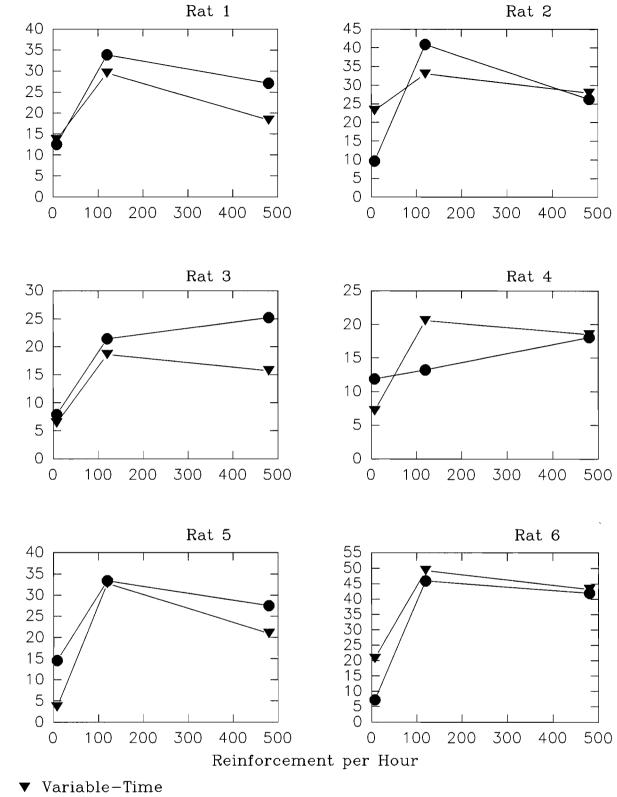


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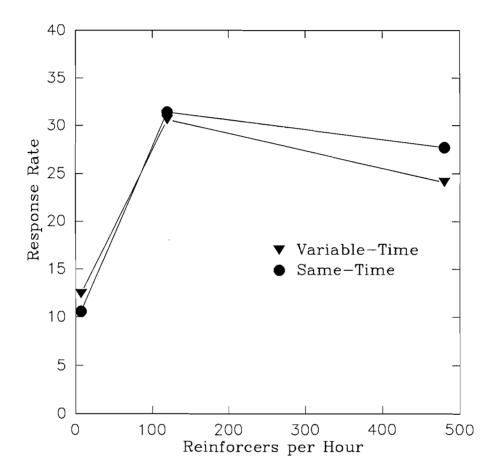
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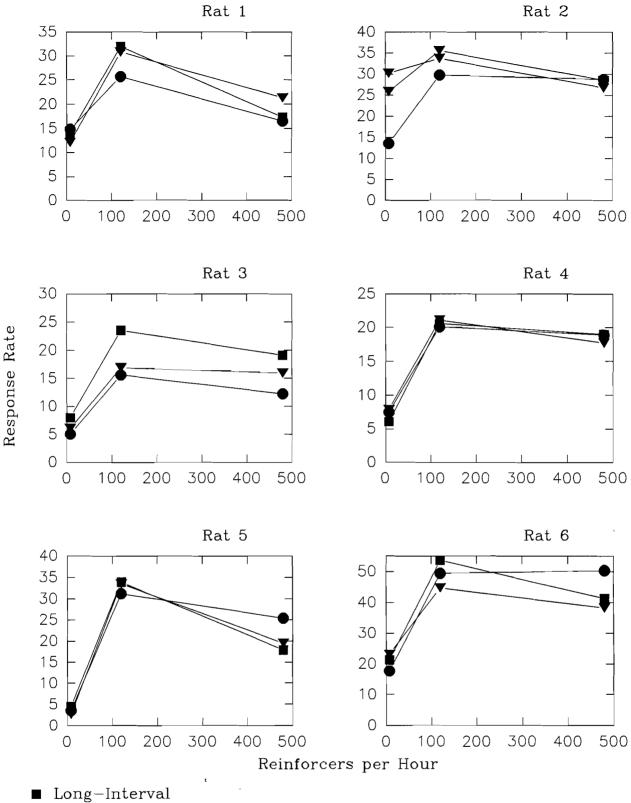
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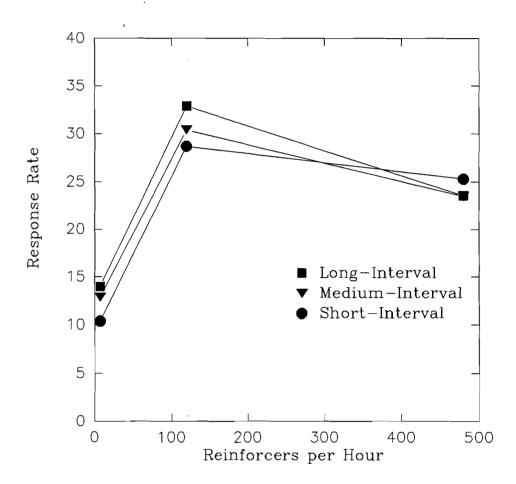
• Same-Time

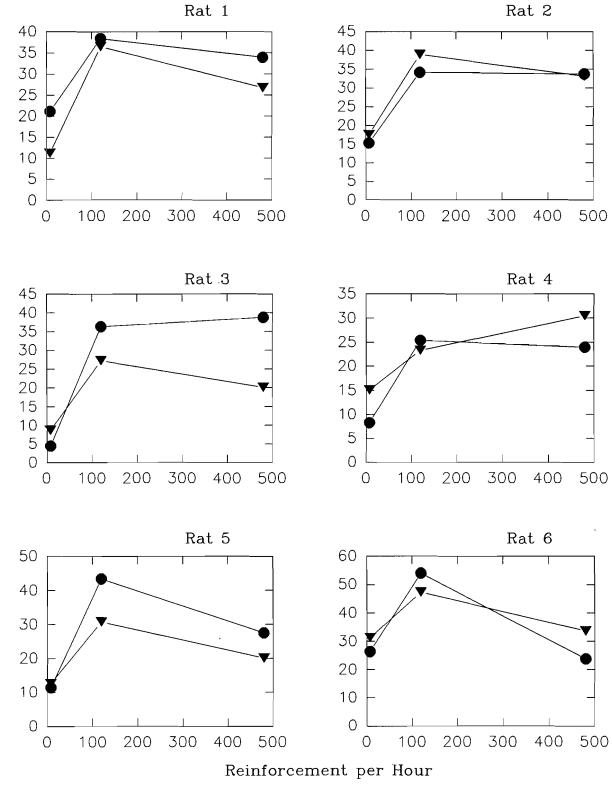
**Response Rate** 





- ▼ Medium-Interval
- Short-Interval

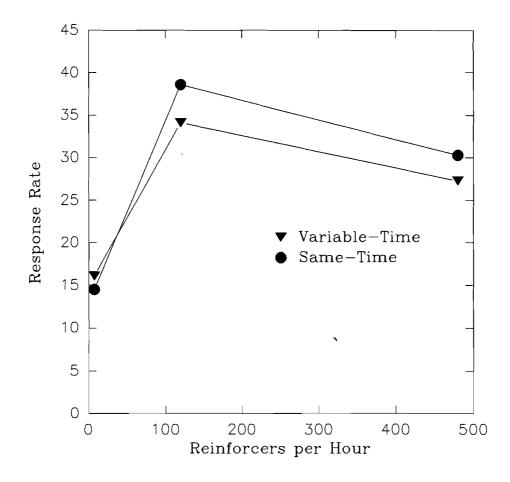




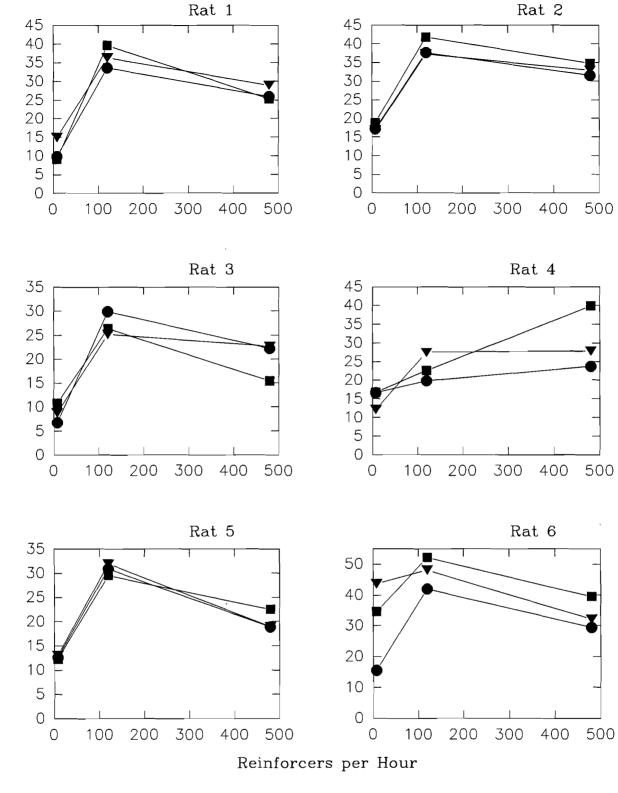
▼ Variable-Time

**Response** Rate

● Same-Time



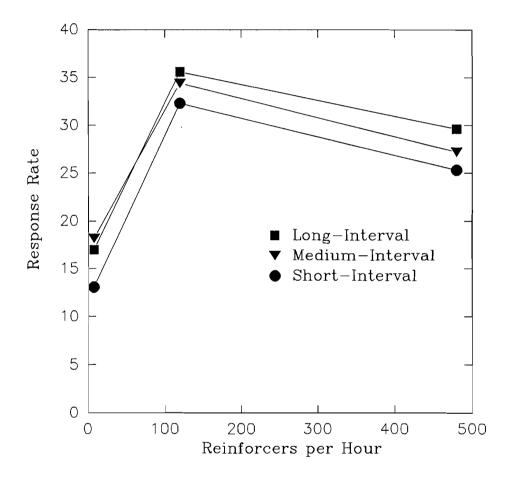
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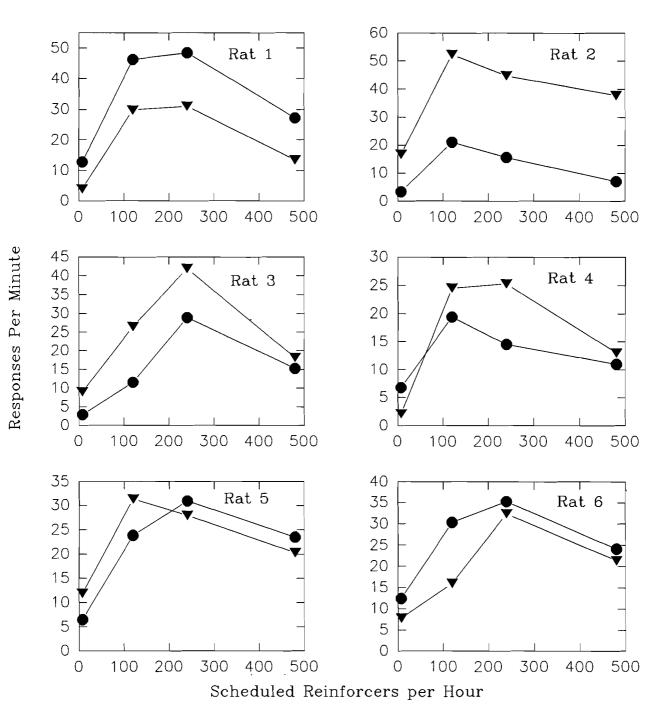


■ Long-Interval

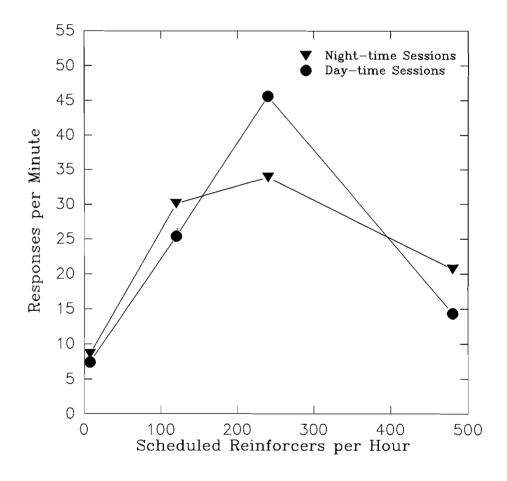
Response Rate

- ▼ Medium-Interval
- Short-Interval





- ▼ Night-time Sessions
- Day-time Sessions



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