Increasing the discriminability of schedules results in both negative and positive behavioral contrast in the running wheel

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Increasing the Discriminability of Schedules
Results in Both Negative and Positive Behavioral Contrast
in the Running Wheel

by
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Presented in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy
The University of Montana
May 1999

Approved by
Chairperson
Dean, Graduate School
Date

5-26-99

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An experiment was conducted examining behavioral contrast in rats under different levels of effort in the running wheel. It was hypothesized that the failure to elicit positive contrast in prior research was due to the rats' inability to effectively discriminate between the concurrent schedules. To overcome this discrimination problem, the schedules were shortened and the specific schedules were signaled. Two groups of six rats each chose between two concurrent schedules, a constant component (VI 1 min) vs. a changing component (VI 1 min, VI 15 sec, or VI 4 min). Distance run under each schedule was recorded. The results clearly demonstrated both positive and negative contrast effects, thus supporting the hypothesis that the failure to obtain positive contrast effects in previous studies is likely due to schedule discrimination problems. Additionally, the higher effort group ran significantly less overall compared to the lower effort group. Results are discussed in terms of bridging the gap between incentive and behavioral contrast paradigms.
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Introduction

Contrast in the learning literature is conceptualized in two major categories: incentive contrast and behavioral contrast. While both incentive and behavioral contrast theories attempt to explain conceptually similar phenomena, the methods employed, typical results obtained, and the theoretical explanations offered are quite dissimilar. In a discussion of the differences between the two major methodologies used in animal learning, Mellgren and Olson (1983) define the two methodologies as operant and maze. Incentive contrast falls into the maze methodology, being studied primarily with rats in runways, while behavioral contrast falls under operant. Among the most obvious differences between operant and maze methods, and also between incentive and behavioral contrast, are: the experimental design (single subject vs. group), the trials (continuous sessions vs. discrete trials), the nature of the response (manipulandum vs. running), the behavior under study (steady-state vs. transitional) and the apparatus (automated vs. semi-automated) (Mellgren & Olsen, 1983). Incentive contrast studies (Flaherty, 1982; Williams, 1997) are typically based on a rat/running model using discrete trials, group design, and a semi-automated preparation, while behavioral contrast studies (Williams, 1983, 1997) are almost exclusively based on a pigeon/keypeck model using free-operant continuous sessions, small-n design, and an automated preparation.

There has been very little linkage between incentive and behavioral contrast. Williams (1997) suggests this may be due to the breaking of animal learning into two camps: the associative learning camp which focuses on discrete trials procedures.
(incentive contrast), and a behavioral analysis camp which employs free operant procedures (behavioral contrast). It is also possible that the lack of linkage stems from the differences between the specific behaviors examined, specifically maze behavior/incentive vs. operant behavior/behavioral (Mellgren and Olson, 1983). In addition, Timberlake (1993) suggests that these behaviors are inherently different: key-pecking and treadle/lever pressing can be thought of as consummatory behavior, while running is a class of behavior somewhat removed from direct contact with food. Both Mellgren and Olson as well as Timberlake suggest that the type of behavior used would relate to the results found. To truly compare incentive and behavioral contrast, one must be able to run the same species of subjects performing the same behavior through both an incentive contrast paradigm and a behavioral contrast paradigm, and that has proven to be quite difficult to manage.

One procedure that shows promise of being a bridge between incentive and behavioral contrast is the running wheel. Running is a much less directly consummatory behavior than key-pecking, lever-pressing or treadle-pressing; given the conjecture that behavioral contrast may be directly linked to consummatory behavior (Hemmes, 1973), this distance from consummatory behavior may have an effect on the ease or even on the possibility of finding behavioral contrast (Timberlake, 1993). In addition, wheel-running seems to span both operant and maze procedures (Mellgren and Olsen, 1983). For example, while “traditional” behavioral contrast behaviors involve physical contact with a discrete manipulandum (a lever, key or treadle), wheel-running involves movement through space more usually associated with incentive contrast (although in the case of
wheel-running there is no actual spatial displacement). While running is used in incentive contrast in trials with a distinct beginning and end, here running is continuously available, as lever-pressing or key-pecking is in behavioral contrast. It is distinctly possible that there may be differences and difficulties in finding contrast in a behavior that seems to be a cross between the two dominant paradigms of appetitive behavior: a traditional incentive behavior/species in a behavioral contrast paradigm.

Szalda-Petree, Haddad, Zachary, Fosbender, and Martin (1999) examined behavioral contrast in rats using a running wheel response. Two wheels were used, each 36 cm in diameter (113 cm in circumference), connected by a Plexiglas chamber between the two wheels in which the food cup was placed. These wheels were individually braked, allowing for varying effort levels. The rats were divided into two groups, each assigned to a different effort level (defined as tangential force needed to turn the wheel—either 20g or 80g). The subjects were then exposed consecutively to concurrent schedules involving a baseline (VI-2 min VI-2 min) as well as setups for positive (VI-2 min VI-5 min) and negative (VI-2 min VI-15 sec) contrast. Both the high-effort and the low-effort rats showed a negative contrast effect; however, they did not show positive contrast.

In addition, effort did have an effect on the results; the subjects in the higher effort groups showed a smaller level of negative contrast. This is similar to what has been found in other studies of effort: higher effort decreases responding (Friman and Poling, 1995; Chung, 1965; Crossman and Serna, 1982; Collier, Hirsch, Levitsky, and Leshner, 1975; Haddad, Szalda-Petree, Karkowski, Foss and Berger, 1994; Brooks, 1994).
The discovery of negative contrast but no positive contrast is similar to that found by researchers investigating behavioral contrast in pigeons pressing a treadle rather than pecking a key. Initially, researchers were unable to elicit behavioral contrast in pigeons treadle-pressing (Hemmes, 1973; Westbrook, 1973). McSweeney (1978) attempted to elicit behavioral contrast using multiple schedules with pigeons pressing a treadle on schedules identical to those used for pigeons key-pecking. Negative contrast was elicited, but positive contrast was not.

Davison and Ferguson (1978) suggested that the difference in contrast between key-pecking and treadle-pressing may be due to the relatively low rate of responding; contrast is best found with a high level of responding, and the usual VI schedules for key-pecking may not allow for a fast enough rate of responding for contrast to be apparent in studies involving treadle-pressing.

McSweeney (1982) compared positive and negative contrast in multiple schedules for key pecking with negative contrast in treadle-pressing. In key-pecking, the size of both positive and negative contrast varied inversely with the duration of availability for each key; thus the shorter the time a key was available for pecking, the larger the contrast effects were. For treadle-pressing, however, the longer the component the larger the negative contrast; this may help explain the relatively easy eliciting of both positive and negative behavioral contrast in concurrent schedules, where the keys were available at all times (McSweeney, 1975). When the VI used with the multiple schedules was altered to maximize discriminability by shortening the baseline VI and using extinction as the alternative, both positive and negative contrast was found in pigeons treadle-pressing.
(McSweeney, 1983). Increasing the component duration for pigeons treadle-pressing was later found to be as important for positive contrast as it was for negative contrast (McSweeney, Dougan, Higa and Farmer, 1986). In addition, they reported that both positive and negative contrast in key-pecking increased with increased baseline rate of reinforcement.

Eliciting behavioral contrast in rats was also difficult, although adopting some of the procedures used with pigeons treadle-pressing aided in finding results. For example, Gutman (1977) found positive contrast in rats lever-pressing under multiple schedules when the VI schedules were paired with extinction. Nallan and McCoy (1979) found similar results.

Norman and McSweeney (1978) investigated contrast in lever-pressing in rats using concurrent schedules. During manipulations of the schedules, the researchers found that the rats showed both positive and negative contrast. McSweeney, Melville and Higa (1988) also studied rats lever-pressing and found that positive contrast was more easily elicited in concurrent schedules than in multiple schedules, similarly to the results found with pigeons treadle-pressing (McSweeney, 1982; McSweeney, Dougan, Higa and Farmer, 1986).

Dougan, Farmer-Dougan, and McSweeney (1989) directly compared behavioral contrast with pigeons key-pecking and rats lever-pressing. The two species were tested on identical multiple schedules. All of the subjects showed positive contrast for VI-15 sec contrasted with extinction, but as the VI length increased, the rats were less likely than the pigeons to show contrast. Analysis indicated that the pigeons were better at
discriminating the different schedules than the rats, with the rats thus requiring a more extreme difference between the two schedules in order to show positive contrast. It appears likely that the initial difficulties in eliciting contrast in rats may be due to the rats having trouble discriminating between the alternative schedules. Other researchers found that the physical layout of the apparatus can affect contrast, with multiple schedules using two levers that alternate eliciting larger contrast effects than procedures using only one lever (Dougan, McSweeney and Farmer, 1985).

The present experiment was designed to address the absence of a positive contrast effect in Szalda-Petree et al (1999) as a possible discrimination problem. While it appears that the rats were able to discriminate between the VI-15 sec and the VI-2 min (baseline) schedules, it is possible that the difference between the VI-2 min and the VI-5 min was not discriminable. Most of the prior behavioral contrast studies investigating positive contrast pair a particular VI schedule with extinction, thus stressing the difference between the schedules (Reynolds, 1961; Westbrook, 1973; Hemmes, 1973; Gutman, 1977; Nallan and McCoy, 1979; McSweeney, 1978; McSweeney, 1982; McSweeney, 1983; McSweeney et al, 1986; McSweeney et al, 1988; Dougan et al, 1989). Wheel-running is much more complex and strenuous than bar-pressing, key pecking, or treadle-pressing, as well as less closely linked to consummatory behavior. When contrast was generalized from pigeons key-pecking to other species and behaviors, shortening the VI schedule and thus increasing discriminability was often necessary to obtain a positive contrast effect (McSweeney, 1983). Given that rats appear less able to discriminate between similar schedules of reinforcement than pigeons (Dougan et al, 1989), shortening
the VI schedules to create maximum discrimination may aid in obtaining positive contrast.

In addition, visual cues in the form of lights were used to distinguish between the constant baseline VI schedule and the fluctuating (shorter or longer) VI schedules. Much of the research involving multiple schedules and contrast employs signaling which schedule is present at any given time, using lights with pigeons (McSweeney, 1975; McSweeney, 1978; Nevin, Mandell and Whittaker, 1978, McSweeney, 1982; Hemmes, 1973) and sounds and/or lights with rats (Gutman, 1977; Nallan and McCoy, 1979; Bernheim and Williams, 1967). It is hypothesized that signaling the schedule and shortening the intervals will increase the discriminability of the schedules and thus result in both positive and negative behavioral contrast effects.

Method

Subjects:

Twelve naive, male Sprague-Dawley rats, approximately 80-90 days in age at the beginning of the experiment, served as subjects. Upon arrival at the laboratory the rats were provided with ad-lib water and food for seven days. They were maintained on 85% of their predeprivation individual body weight for the duration of the experiment on a diet of Purina Rat chow. Water was continuously available in the home cage.

Apparatus:

Two Wahman running wheels were modified to allow computer monitoring of wheel movement through a computer mouse attached to the wheel axle via a system of
reduction pulleys (Petree, Haddad and Berger, 1992; Szalda-Petree, Karkowski, Brooks, and Haddad, 1994). Response effort was manipulated by applying pressure, via an adjustable tensioning bar, on a 7.62 cm aluminum disc approximately 1.3 cm thick that was attached to the wheel axle protruding from the nonmovable side of the wheel (Haddad et al, 1994).

A Lexan choice box (23 cm X 23 cm X 30 cm) was placed between the two wheels and linked to each wheel via a 12 cm-long tunnel 8 cm in diameter. Reinforcers were delivered to the food cup located along the end wall of the choice box, equidistant from both wheel entrances. Each pair of wheels and their accompanying choice box was housed in a large (.6 m X .6 m X 1.2 m) sound-attenuated cabinet with a blower to provide ventilation and masking noise. In addition, small light bulbs 1 cm in diameter, used to signal the schedule for the wheel, were centered in the choice box 3.5 cm directly above the tunnels. All mechanical operations (signal lights, feeders, wheel movement detectors) were controlled via a PC computer/Alpha bus relay system.

Procedure:

Subjects were initially magazine trained in each of the two running wheels on two consecutive days during which 40 reinforcers (45 mg Noyes pellets) were delivered on a VT 20 sec schedule. Upon completion of the magazine training, subjects received single wheel run training for two consecutive days during which subjects were reinforced on a FR schedule that was gradually increased from 5 to 55 cm. Subjects then received 5 minutes of magazine training in the central choice box with 20 reinforcers delivered to the food cup in the box and access to the wheels blocked. All subjects were then allowed
access to the central chamber and one wheel at a time, with reinforcers delivered to the
food cup in the central choice chamber on a VR schedule ranging from 5 cm to 300 cm.
After two days of this shaping, subjects received access to both wheels for two
consecutive days during which subjects were reinforced on a FR 55 cm schedule.

The experiment consisted of a concurrent schedules five phase behavioral contrast
procedure: Baseline (VI 1 min : VI 1 min), Negative contrast (VI 1 min : VI 15 sec),
Baseline (VI 1 min : VI 1 min), Positive contrast (VI 1 min : VI 4 min), and Baseline (VI
1 min : VI 1 min). A discriminative light cue was illuminated during the positive and
negative phases (e.g., lights located above the tunnel leading to the wheel with the altered
schedule component) to maximize discrimination. Subjects received 1 pellet of
reinforcement upon completing a 55 cm run following the termination of the variable
interval. During the negative and positive contrast phases, schedules were
pseudorandomized such that a single wheel was not associated with a given schedule for
more than two consecutive sessions to control for wheel preferences. The subjects were
randomly placed into two groups: low effort (requiring 20g or more of tangential force to
turn the wheel) and high effort (with 80g or more tangential force required). Each daily
session lasted 45 minutes per subject, with schedules alternating between sessions. Each
phase continued until stable responding, defined as no upward or downward movement
trend in running distances over three consecutive days, were obtained.
Results

For each phase, running distances were averaged across the last three stable days yielding a mean run distance for each subject at each phase. A comparison of the different baselines showed no difference within an effort group among the three baseline phases ($F(2,20) = 1.77, p > .05$), so the baselines were collapsed for the remaining analysis. Contrast was evaluated in two separate 2 (phase) x 2 (response effort) mixed factorial ANOVAs conducted on mean run distance for the positive and negative phases compared to the average of the three baseline phases. The positive contrast ANOVA revealed a significant effort main effect ($F(1,10) = 5.62, p < .05$), a significant phase main effect ($F(1,10) = 15.53, p < .05$), and no effort x phase interaction ($F(1,10) = 1.12, p > .05$). The negative contrast analysis revealed a significant effort main effect ($F(1,10) = 6.15, p < .05$), a significant phase main effect ($F(1,10) = 38.41, p < .05$), and no significant effort x phase interaction ($F(1,10) = .42, p > .05$). Thus, the analysis shows that subjects ran significantly less during the negative phase compared to the baseline phase, demonstrating a negative contrast effect, and significantly more during the positive phase compared to the baseline phase, demonstrating a positive contrast effect. Additionally, the 20 g group ran significantly farther than the 80 g group in all phases.
Table 1. Mean Distance Run (in meters) for each Phase and Effort Level*

<table>
<thead>
<tr>
<th>Effort Level (g)</th>
<th>Phase</th>
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<tbody>
<tr>
<td></td>
<td>Baseline (VI 1 : VI 1)</td>
<td>Negative (VI 1 : VI .25)</td>
<td>Positive (VI 1 : VI 4)</td>
</tr>
<tr>
<td>20 (n=6)</td>
<td>229.64 (6.89)</td>
<td>145.08 (10.44)</td>
<td>278.86 (17.66)</td>
</tr>
<tr>
<td>80 (n=6)</td>
<td>186.26 (6.92)</td>
<td>117.65 (9.47)</td>
<td>214.63 (17.70)</td>
</tr>
</tbody>
</table>

* standard error in parenthesis

Discussion

The results indicate that both negative and positive behavioral contrast were obtained using a concurrent schedules behavioral contrast preparation examining wheel running in rats. Although negative contrast has previously been demonstrated (Szalda-Petree et al, 1999), this is the first time that positive behavioral contrast has been found in the running wheel. These results are similar to those found with other preparations involving concurrent schedules with pigeons pecking (Davison and Ferguson, 1978), pigeons treadle-pressing (McSweeney, 1975) and rats lever-pressing (Norman and McSweeney, 1978; McSweeney et al, 1988), thus suggesting that the same mechanism of behavioral contrast underlies them all, despite differences in subjects and methodologies. In addition, effort also had an effect on running, with rats with the higher level of effort running shorter distances than the rats with the lower level of effort.

It appears quite likely that the addition of signal lights as well as the shortening of the VI schedules aided the behavioral contrast. Prior researchers had suggested that rats
might have problems with discriminating schedules of lengths longer than 1 minute or so (Dougan et al, 1989); shortening the schedules and adding signaling lights can both aid in discrimination. Studies involving both pigeons treadle-pressing and rats lever-pressing in behavioral contrast studies have utilized both signals and shortened intervals with success (McSweeney, Dougan, Higa and Farmer (1986) for enriching the schedule; McSweeney (1975); McSweeney (1978), Gutman (1977), Nallan and McCoy (1979), Bernheim and Williams (1967) for signaling).

The results in terms of effort are also consistent with prior evidence indicating that increased effort causes a decrease in responding (Friman and Poling, 1995; Chung, 1965; Crossman and Serna, 1982; Collier, Hirsch, Levitsky, and Leshner, 1975; Haddad, Szalda-Petree, Karkowski, Foss and Berger, 1994; Brooks, 1994; Szalda-Petree et al, 1999). It appears that effort serves as a modulator in this task. It suppressed running in all of the phases run, and did not interact with the schedules directly; while Szalda-Petree et al (1999) found an interaction between level of effort and the amount of negative contrast, none was found here. It is possible that the lack of interaction was due to the relatively small number of subjects used. If effort tends to modulate effects rather than directly influences them, it may take more subjects to show any modulatory effects present.

Behavioral contrast using concurrent schedules is usually thought to occur via the matching law (McSweeney, 1975; Norman and McSweeney, 1978), where the rate of responding is directly proportional to the rate of reinforcement in that component. The current research does not follow the matching law. While the matching law suggests that
the rats would run in the VI 1 min wheel only 20% of the total distance when it is paired with the VI 15 sec wheel, they actually ran 34% of the total distance in that wheel; for positive contrast, where again matching would suggest 20% in the VI 4 min wheel, the rats ran 44% in that wheel.

It is quite possible that the lack of matching is due to bias. Baum (1974) notes that bias can prevent data from conforming to the matching law. Nearly all of the rats showed some form of side bias, ranging from very mild to extreme. This bias may be altering the results from those expected from the matching law. However, this bias varies between animals, both in terms of degree of bias and which side is favored, and thus is somewhat random and may be dealt with in later experiments. It should also be reiterated that this bias did not prevent positive or negative contrast from occurring.

Research in contrast using multiple schedules avoids some of the problems of concurrent schedules, most obviously the element of direct competition between choices that is present using concurrent schedules (Williams, 1983). Multiple schedules may also avoid some of the problems of side bias if they only use one key/treadle/lever for both schedules; however, much research in multiple schedules has involved using two keys/treadles/levers, and some researchers have even noted that using two manipulanda aids in discrimination (McSweeney, 1978; McSweeney, 1983).

Theories of behavioral contrast with multiple schedules involve more than just the matching law. Major theories of behavioral contrast include the additivity theory, which suggests that contrast occurs in pigeon key-pecking due to the addition of pecks classically conditioned to the key to the normal baseline rate of pecking (Williams, 1983);
hence contrast is due to consummatory responses directed toward the key. Not surprisingly, while this theory is supported by much of the keypecking-by-pigeons literature (Williams, 1983), it is not fully supported by contrast involving other actions or species such as rats pressing bars (Gutman, 1977) or pigeons treadle-pressing (McSweeney et al., 1986). Nor would it be logical, given the separation of consummatory and travel behavior present, for additivity theory to explain contrast in rats wheel-running.

A second theory of multiple schedules involves competition, though of a different type than that found in concurrent schedules: this competition is between the behavior of interest and interim behaviors (Hinson and Staddon, 1978). In multiple schedules, more of the interim behaviors (grooming, resting, exploring) would be allocated to the less desirable/reinforcement-rich schedule, with more keypecking/lever pressing/treadle pressing/running occurring during the richer schedule. As no measures were taken of behavior in the wheels, tunnels and choice boxes other than running, it is impossible to tell whether this reallocation of behavior caused the contrast.

A third theory of contrast in multiple schedules involves suppression (McSweeney, 1987): there is an excitatory and an inhibitory effect present during behaviors, with the excitatory component acting in direct proportion to the rate of reinforcement and the inhibitory effect occurring in response to delay of reinforcement. Specifically, in multiple schedules the second schedule affects responding to the first schedule; if the second schedule becomes richer and thus reduces delay to reinforcement in that schedule, suppression is increased for the first schedule and there is negative contrast; if the second schedule is made less rich so that there is a longer delay to
reinforcement for this second schedule, suppression is reduced for the first schedule and positive contrast occurs. Given the emphasis on prior and following schedules, this theory seems to refer specifically to multiple schedules. While the current study did show both excitation and inhibition, it appears that the suppression theory has not been applied to concurrent schedules; given this theory's reliance on multiple schedules, it is possible that matching may still be a better explanation for the current results.

The current data do not support Davison and Ferguson's (1978) contention that contrast can only be found with high levels of responding. The effort in this experiment as well as in Szalda-Petree et al (1999) served to suppress responding in the higher effort levels for all conditions, yet contrast was still found. It appears that a high rate of responding is less important than discriminability of the schedules. However, it is also possible that even at the higher levels of effort there is a high enough level of responding to create contrast. Future researchers may wish to examine the possibility of such a threshold with running behavior.

It is increasingly obvious that behavioral contrast is a much more robust phenomenon than was initially assumed, when pigeons key-pecking was considered to be the only subjects/behavior in which such contrast could be found (Hemmes, 1973). It is also apparent that behavioral contrast and incentive contrast may not be as different as researchers have assumed. Williams (1997) describes simultaneous incentive contrast, in which two alternating stimuli are correlated with different levels of reinforcement, and specifically anticipatory consummatory contrast (comparing the target solution being consumed with the solution that always follows it), as similar to multiple-schedule
behavioral contrast. However, the wheel-running research presented here provides another comparison between behavioral and incentive contrast, by using traditional incentive contrast subjects and behavior (rats running) with a traditional behavioral contrast paradigm (concurrent schedules of continuous behavior), and still achieving behavioral contrast.

With the success of finding positive and negative contrast in a behavioral contrast paradigm using subjects and behaviors traditionally used in incentive contrast, it appears that a bridge has begun to be created between not only behavioral and incentive contrast but between operant and maze behaviors as well, closing a gap that has existed for many years. Mellgren and Olson (1983) suggest that this consolidation would allow for a view of an organism that is more generalizable across behaviors, not just focusing on one type of behavior or another. It would be quite interesting to take this research one step farther by pairing traditional behavioral contrast subjects/behavior (pigeons key-pecking is the obvious choice) with an incentive contrast paradigm to see if this bridge runs both ways.

Future research involving rats running in behavioral contrast may involve running more subjects to determine whether the amount of contrast interacts with level of effort. Szalda-Petree et al (1999) discovered that effort and amount of negative contrast do interact: with more effort the amount of negative contrast is lessened. It is possible that this interaction may also occur with positive contrast; Szalda-Petree et al found no such interaction in negative contrast with 12 subjects, but did find it with 24 subjects. Perhaps by running more subjects and providing more data this finding will be also discovered in positive contrast.
References


Appendix 1: Literature Review

Contrast, or a change in responding due to a change in rate or ratio of reinforcement, is an unusual phenomenon for two reasons. First, the process of contrast itself rather upsets some of the assumptions of reinforcement theory, and second, this one term manages to span both operant research as well as research involving discrete responses.

Most of the research involving magnitude of reinforcement indicates that the larger the reinforcement, the more quickly a particular behavior is performed (Pubols, 1960; Bonem and Crossman, 1988). However, with contrast it is not the absolute amount or rate of reinforcement that controls the speed of a behavior, but rather the relative amount/rate of reinforcement. For example, rats which learn to run in an alley for a particular amount of reinforcer will not only run faster when switched to a larger amount of reinforcer, but they will also run faster than rats trained on the larger amount of reinforcer from the beginning (Bower, 1961). Contrast research involving rate of reinforcement finds similar results; animals which respond equally to two multiple or concurrent schedules of reinforcement will respond more often to an unchanged rate of reinforcement when the alternative rate is reduced, and will respond less often to the constant rate if the alternative rate is increased (Norman and McSweeney, 1978).

In terms of global types of research, Mellgren and Olson (1983) divide the methods traditionally used in appetitive behavior (including contrast) into two types, the operant and the maze. An operant usually involves what is colloquially called a "Skinner
box", which is a chamber with keys or levers available for the animal to respond on. A maze, on the other hand, involves movement through space and can involve a simple runway or more sophisticated (and more conventionally "mazelike") configurations. Mellgren and Olson lay out a number of points of comparison contrasting the different procedures. For example, operant procedures involve continuous trials in one location while maze procedures involve discrete trials involving spatial location, in operant procedures the subject is required to directly manipulate some object (a key or lever) in order to be reinforced while in maze procedures movement through space is the reinforced response, etc.

Contrast itself comes in two different types: incentive contrast, where in a discrete trials procedure an altered reward causes changes in behavior (Flaherty, 1982); and behavioral contrast, where differences between two multiple or concurrent schedules cause changes in the rate of responding of an operant activity (Williams, 1983). The two types of contrast fit neatly into Mellgren and Olson's two categories: incentive contrast is traditionally studied as a "maze" type behavior, while behavioral contrast is an "operant" behavior.

**Incentive Contrast**

Incentive contrast has been studied primarily with rats in a runway. Rats are trained to run for a particular amount of food. When the amount of food with which they are reinforced is increased from the baseline amount, the rats run faster; when the amount is decreased, the rats run slower (Flaherty, 1982). The first effect was called the "elation
effect” by Crespi (1942), who was the first to demonstrate contrast in rats, with the second effect called the “depression effect”.

Flaherty (1982) attempted to standardize the terminology used to describe incentive contrast studies since Crespi’s initial findings. What Crespi called the elation effect is now called positive contrast, with the depression effect called negative contrast. In addition, different classifications of incentive contrast have been developed. Crespi’s initial procedure produced what is now called successive contrast, where amount of reward is increased or decreased from what was used for training. The other type of incentive contrast is called simultaneous contrast, where the running speed from animals trained with two different levels of reinforcement is compared to that of animals which have received only one level of reinforcement. For example, Bower (1961) trained rats in two different runways, one black and one white, with each runway associated with a different level of reinforcement. Rats that were run in both alleys and thus received both reinforcement levels tended to run slower for the smaller reward than rats which had only run in the “small” alley and had never received the larger reinforcer. This was called simultaneous negative contrast, with simultaneous positive contrast indicated by rats exposed to both levels of reinforcement running faster for the larger reward than rats only exposed to the larger reward condition.

Behavioral Contrast

Behavioral contrast was initially studied with pigeons key-pecking for reinforcement (Reynolds, 1961) and most behavioral contrast research has involved the
same species performing that particular activity (Dougan, Farmer-Dougan and McSweeney, 1989). However, behavioral contrast (positive, negative or both) has been found with at least three other conditions/species: treadle-pressing by pigeons, lever-pressing by rats, and wheel-running by rats.

The procedures used to create contrast differ somewhat depending on the species and behavior. Timberlake’s (1993) behavioral systems approach to reinforcement may help explain the differences in procedures and, perhaps, in results. Timberlake argues that an animal’s behavior is governed by systems which allow the animal to respond well to different aspects of its environment. For example, Timberlake (1993, page 118) breaks down a rat’s predatory feeding behaviors into hierarchical groupings called systems (such as predatory), subsystems (general search, focal search, handle/consume), modules for each of the subsystems (the module “general search” includes the subsystems travel, socialize, investigate, chase) and actions for each of the modules (for travel, actions include locomote and scan). Using this type of system to categorize behavior found in behavioral contrast studies, one could easily place key-pecking, treadle-pressing, and lever-pressing into the “handle/consume” module, with key-pecking being closer to the actual consummatory behavior of the animal than the other two behaviors. Pigeons peck to pick up food and manipulate the ground with their feet to make food more accessible, while rats usually pick up the food they eat with their forepaws. Wheel-running, on the other hand, would be in the “general search” module, far from the specific food handling and consumption of the other behaviors. Therefore, each of the different operants used in behavioral contrast will be discussed separately.
**Key-Pecking**

Behavioral contrast was first demonstrated by Reynolds (1961), using pigeons in a keypecking paradigm. Pigeons were exposed to 30 cycles of six minutes duration per day. During half of the cycle, a red or orange light illuminating the key indicated a VI-3 min schedule of reinforcement, which was never changed. The second half of the cycle was indicated either by a green or blue illumination, indicating schedules which varied from a VI-3 min to an extinction phase to a “reinforced non-response” phase, or if the key was not lit a “time-out” phase. Pigeons increased pecking during the constant VI-3 min schedule when the alternative component of the schedule offered less reinforcement.

Most subsequent researchers in behavioral contrast followed similar procedures, with pigeons key-pecking. This is a very robust behavior (pigeons autoshape key pecking easily (e.g. Hemmes, 1973, Hamilton and Silberberg, 1978)) and it allows for the acquisition of both positive and negative contrast easily (Williams, 1983; Williams, 1997).

**Pigeon treadle-pressing**

Finding behavioral contrast in subjects and actions other than pigeons key-pecking was difficult; in fact, some researchers such as Hemmes (1973) had claimed that due to the nature of key-pecking, contrast would not be found in other species or other behaviors. For a long time, negative results from experiments involving rats or pigeons bar-pressing or treadle-pressing supported this theory (Williams, 1983).

However, when the procedures used with key-pecking were modified somewhat,
researchers began to find positive results. McSweeney (1975) produced positive and negative contrast in concurrent schedules in pigeon treadle-pressing, after other attempts to measure behavioral contrast in non-pecking multiple-schedule paradigms had failed (e.g. Hemmes, 1973; Westbrook, 1973). McSweeney trained pigeons to step on two treadles provided in a testing enclosure, with an exertion of approximately .7N necessary to depress the treadle to prevent responses from pecking. The pigeons were then exposed to concurrent signaled schedules on the treadles, with the left treadle always illuminated with white light and always a VI-2 min schedule and the right treadle illuminated with a blue light indicating schedules ranging from VI-30 sec to VI-4 min. Both negative contrast, when responding to the constant VI-2 schedule decreased when the alternately-available schedule of reinforcement was shorter, and positive contrast, where responding to the constant schedule increased when the alternately-available schedule was longer, were found for all of the schedules.

Behavioral contrast using pigeons pressing treadles in multiple schedules, where only one schedule was available at a time, was more difficult to find. Davison and Ferguson (1978), in a study of contrast involving both key-pecking and treadle-pressing, suggested that contrast may be more difficult to find in treadle-pressing due to the relatively low rate of responding; contrast is best found with a high level of responding, and using the usual VI schedules for key-pecking in studies involving treadle-pressing apparently does not allow for a fast enough rate of responding for contrast to be apparent.

Negative contrast in multiple-schedule treadle-pressing was first reported by McSweeney (1978). She trained pigeons to step on two treadles provided in a testing
enclosure, with an exertion of approximately .25N necessary to depress the treadle. The pigeons were then exposed to multiple signaled schedules on the treadles, with the right treadle illuminated with white light indicating a VI-2 min schedule, alternating every 2 minutes with the left treadle illuminated with a red light indicating a variable schedule ranging from extinction to VI-30 sec, VI-1 min, VI-2 min, and VI-4 min. Responses on the non-lit treadle were not reinforced or counted. The pigeons consistently responded less to the constant (VI-2 min) component when the varying schedule changed to a higher rate (VI-15 sec), thus showing negative contrast. However, they did not respond more to the constant component when the alternate schedule changed to a lower rate (VI-4 min), so no positive contrast occurred.

McSweeney (1982) compared positive and negative contrast in multiple schedules for key pecking with negative contrast in treadle-pressing. In key-pecking, the size of both positive and negative contrast varied inversely with the duration of availability for each key, signaled by red or white lights on the key (with red light signaling VI-2 min and the white light signifying either VI-2 min or extinction); thus the shorter the time a key was available for pecking, the larger the contrast effects were. For treadle-pressing, however, the longer the component the larger the negative contrast.

McSweeney (1983) did later find positive contrast in multiple schedules for treadle-pressing pigeons, by reducing the length of the constant VI and increasing the length of the alternative schedule. As before, a light above a particular treadle indicated which schedule was in effect: a white light for the right treadle indicated a VI-15 sec, and a red light for the left treadle indicated either a VI-15 sec or an extinction schedule.
Schedules were alternated every 60 seconds, with the right (constant VI-15 sec) always coming first in a session. The pigeons responded more to the VI-15 sec schedule when it was contrasted with extinction rather than with another VI-15 sec, thus showing positive contrast. McSweeney suggested that this result was due to shortening the VI schedule, presumably making it easier to discriminate between the two schedules.

McSweeney, Dougan, Higa and Farmer (1986) investigated component duration for positive contrast in treadle-pressing, and found positive contrast also increased with component duration. In addition, they reported that both positive and negative contrast in key-pecking increased with increased baseline rate of reinforcement.

**Lever-pressing in rats**

Finding behavioral contrast in rats was also difficult. One of the initial findings of positive contrast in lever-pressing rats was reported by Gutman (1977). Rats were trained on a multiple VI-30 sec VI-30 sec schedule, then were exposed to a multiple VI-30 sec extinction schedule, where the different schedules were indicated by white noise or by a light. The subjects showed positive contrast, responding more to the VI-30 sec than the extinction schedules when the two were presented in sequence.

Nallan and McCoy (1979) trained rats in a positive-contrast paradigm, where they lever-pressed under two different schedules which were indicated by either a noise or a light signal. The schedules were a multiple VI-30 sec extinction, with components presented for 1 minute separated by a 5-sec. blackout, with sessions lasting 30 minutes. Nine of the ten rats showed large positive contrast effects, with the rats responding more
to the VI-30 sec component than to the extinction component.

Norman and McSweeney (1978) investigated contrast in lever-pressing in rats using concurrent schedules. Rats were given access to two levers, which were on a concurrent VI-1 min VI-1 min schedule. During manipulations of the schedules, the researchers found that the rats showed both positive and negative contrast, using intervals of VI-1 min as baseline contrasted with VI-15 sec, VI-30 sec, and VI-2 min.

McSweeney, Melville and Higa (1988) researched positive contrast in rats lever-pressing, using both concurrent and multiple schedules and varying the reinforcement offered. Rats were shaped to press the right lever for water reinforcements (with alcohol to 10% by volume added later in the study) and to press the left lever for food reinforcers. In concurrent schedules, positive contrast occurred for both reinforcers when VI-30 sec schedules were paired with extinction. However, in multiple schedules, positive contrast did not always occur; the rats showed positive contrast when put on a multiple VI-30 sec-food extinction-alcohol schedule, but not for VI-30 sec-alcohol extinction-food, VI-15 sec-alcohol extinction-food, or VR-30 sec-alcohol extinction-food schedules. The results suggest that multiple-schedule contrast may not always be found when using different types of reinforcers; in addition, it appears to be easier to find positive contrast on concurrent schedules rather than multiple ones.

Dougan et al (1989) directly compared behavioral contrast involving two different species and behaviors: pigeons key-pecking and rats lever-pressing. The two species responded on identical multiple schedules, with variable intervals of length 15 sec, 30 sec, 60 sec and 120 sec alternating at 90 second intervals with extinction. All of the
subjects showed positive contrast for VI-15 sec contrasted with extinction, but as the VI length increased, the rats were less likely than the pigeons to show contrast. Analysis indicated that the pigeons were better at discriminating the different schedules than the rats were, with the rats thus requiring a more extreme difference between the two schedules in order to show contrast. It appears likely that the lack of positive contrast may be due to the rats having trouble discriminating between the schedules.

Dougan, McSweeney and Farmer (1985) investigated multiple schedules in rats bar-pressing. However, instead of the rats responding to one lever, two levers were used, one for each schedule. This tended to increase contrast and thus discrimination of schedules, though the rats showed less contrast when the constant component alternated with extinction was increased from VI-15 sec to VI-60 sec.

Wheel-Running in Rats

Finding contrast in wheel-running is of interest for two reasons. First, as noted above, running is a much less directly consummatory behavior than key-pecking or lever-pressing or even treadle-pressing. Second, wheel-running seems to span both operant and maze procedures. For example, while “traditional” behavioral contrast behaviors involve physical contact with some sort of object to cause the response, wheel-running involves movement (although this movement does not result in any actual change in space) more usually associated with incentive contrast. While running is used in incentive contrast in discrete trials, here running is continuously available. It is distinctly possible that there may be differences and difficulties in finding contrast in a behavior that seems to be a
cross between the two dominant paradigms of appetitive behavior.

The first evidence of the use of wheel-running to test contrast is by Bernheim and Williams (1967). Four rats were run in a low-inertia running wheel which was 6 ft (183 cm) in circumference. The running wheel ran a generator, which allowed for a voltage-sensitive device setting criterion speed, with a perforated disk and a photocell registering distance. The wheel turned in only one direction, with the food cup placed on one wall of the wheel so that the rats could only reach it when the wheels were braked. Normal running speed for the rats was 20 inches/sec. The rats were reinforced on VT schedules; as long as the rat was running to criterion (which was set at 1 inch/second), a clock was running and the schedule was active. The schedules were VT-60 sec VT-10 sec, with the length of the different schedule components being 1, 3 or 5 minutes presented in a counterbalanced schedule. The different schedules were signaled by either a different sound signal for each, or by a sound signal for one and a visual signal for the other. Time and distance run was recorded every 30 seconds. When the schedule changed from VT-10 sec to VT-60 sec, the animals showed a type of negative contrast by running slower (although this finding was not robust, especially following short component presentations of the VT-10, and it tended to deteriorate as the experiment progressed). When the schedule changed from VT-60 to VT-10, two of the four animals ran faster in the shorter schedule, which was considered positive contrast. Interestingly, these two animals also showed the most robust negative contrast, and they were also the only subjects to have auditory stimuli alone associated with the different schedules, rather than one signal being auditory and the other being visual.
Zachary (1998) also investigated contrast in a running wheel, though the wheel and the procedure differed from the above study. Two wheels were used, each 36 cm in diameter (113 cm in circumference), connected by a Plexiglas chamber between the two wheels in which the food cup was placed. These wheels were individually braked, allowing for varying effort levels. The wheel was monitored by a computer through the use of a modified computer mouse. Rats were trained to run in either wheel for reinforcement on a FR-56 cm schedule, until reliable running was obtained for the subjects. Next the rats were divided into two groups, each assigned to a different effort level (defined as tangential force needed to turn the wheel—either 20 g or 80 g). The rats were then exposed consecutively to several concurrent schedules: a VI-2 min VI-2 min, VI-2 min VI-15 sec, VI-2 min VI-2 min, VI-2 min VI-5 min, VI-2 min VI-2 min. Schedules were assigned pseudorandomly to wheels, and were changed between daily 45-minute sessions. Both the high-effort and the low-effort rats showed a negative contrast effect, responding more to the VI-15 sec than to the VI-2 min schedule. However, after the rats were returned to baseline running, they did not show a positive contrast effect when the schedules were changed to VI-2 min VI-5 min.

It is possible that the presence of concurrent schedules rather than multiple schedules may be involved in the lack of positive contrast. However, this seems unlikely. McSweeney (1975) showed both positive and negative contrast relatively easily when investigating behavioral contrast in treadle-pressing pigeons. McSweeney et al (1988) also noted that contrast appears to be more easily found in rats lever-pressing with concurrent schedules rather than multiple ones. Nevin, Mandell and Whittaker (1978)

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investigated concurrent schedules of reinforcement in key-pecking in pigeons, and found both positive and negative contrast.

It is also possible that the lack of results found in wheel-running as well as the differences in results between the three “established” types of behavior used in contrast studies could be a result of the behaviors involved. The three behaviors most commonly found in behavioral contrast research all involve some sort of consummatory behavior. The nature of running, being of an entirely different category of behavior only distantly related to consummatory behavior (Timberlake, 1993), may influence contrast studies utilizing this behavior; treadle-pressing in pigeons and lever-pressing in rats both require some modifications of the procedure used in key-pecking, and it may be possible that finding behavioral contrast in the running wheel will require modifications also.

It is also possible that the lack of positive contrast may be due to the rats being unable to consistently differentiate between the VI-2 min and the VI-5 min schedule. The length of the VI schedules have been found to be important in pigeons treadle-pressing (McSweeney, 1983). Steinhauer (1996) noted that in pigeons in a key-pecking behavioral contrast study, contrast occurred only when the pigeons were able to discriminate between the different schedules. Dougan et al (1989) reported that rats were less able to distinguish between different VI schedules than pigeons were. Given the more strenuous and less consummatory nature of running, shortening the VI schedules may allow for the development of positive contrast in wheel-running in rats.
Effort

In areas of investigation other than contrast, increasing effort in a task tends to decrease the amount of activity or number of responses, among other effects (Friman and Poling, 1995). For example, Alling and Poling (1995) studied effort in rats pressing a lever, and reported that increasing the amount of effort necessary to depress the lever decreased the rate of responding and increased the intervals between responses. Mintz, Samuels, and Barber (1976) investigated increased effort on bar-pressing, measuring not only responding that reached threshold and resulted in reinforcement but also responding that was not effortful enough to reach criterion. Increased effort resulted in no difference in the total amount of responding, but did result in a decrease in responses that reached threshold and were reinforced.

Chung (1965) placed pigeons on a key-pecking concurrent VI-1 min VI-3 min schedule, and then varied the amount of force necessary to depress either key, with forces varying from 25g to 300g. The pigeons always chose the VI-1 min key more often than the VI-3 min key, but as effort increased the pigeons pecked at a much lower rate.

Crossman and Serna (1982) also varied the amount of effort needed to depress a key, but instead of altering the tension on the key, as Chung did, they altered the distance the key needed to travel to engage the mechanism. Two different ratio lengths were used; with a FR-2 schedule the pigeons increased the length of the preratio pause as well as the interresponse time, while with a FR-20 schedule the pigeons merely increased the preratio pause.

Research in running wheels has found similar results. Collier, Hirsch, Levitsky,
and Leshner (1975) investigated running in a braked running wheel and found that increased effort (defined as amount of torque applied to a wheel) resulted in a decrease in the distance run. Haddad, Szalda-Petree, Karkowski, Foss and Berger (1994) also increased the amount of force required for rats to turn a running wheel, and determined that increased effort lowered running speeds. Brooks (1994) examined running speed in rats in a running wheel; increasing tangential effort necessary to turn the wheel influenced running speeds, with higher effort leading to lower speeds.

Effort in incentive contrast studies usually comes in the form of lengthening the distance and adding curves to the runway the rat traverses (e.g. Seybert and Mellgren, 1972). This tends to increase the amount of positive contrast, possibly due to the elimination of ceiling effects as given the extra effort/distance, rats tend to run slower.

Effort in behavioral contrast studies involves manipulating the effort needed to perform the operant behavior. In many contrast studies, however, effort appears to be important only to ensure, for example, that pigeons actually press on a treadle rather than peck it (McSweeney, 1975; McSweeney, 1978).

Hunter and Davison (1982) investigated force in behavioral contrast studies in pigeons key-pecking. Five pigeons were run through a total of 43 different conditions where concurrent VI schedules and force requirements were altered. While both positive and negative contrast was found when the schedules of reinforcement were altered, force did not seem to be as large a factor. For example, for sessions where the VI schedule was the same for both keys, the pigeons did not show any preference for a low-effort key over a high-effort key, or vice versa.
Zachary (1998) found that increased effort affected the distances rats ran in a running wheel. For example, during the baseline VI-2 min, when the effort level to turn the wheel was set at 20 g, rats ran an average of 285 meters during the interval; when the effort level was set at 80 g, rats ran only 169 meters during the same period. In all cases, rats under higher effort ran significantly less, though effort appeared to have no effect on the type or degree of contrast effects.

It is possible that effort itself may be a form of contrast. Keehn (1981) tested rats on concurrent VI-30 sec VI-30 sec schedules, varying the weight of one bar at a time while keeping the reinforcement schedules constant. The force required to depress the bar varied from 10g to 60g. As the weight of one bar increased, the rats tended to respond less often on that particular bar, while still responding on it often enough to keep reinforcement rate relatively steady. Only when the force required reached 60g did the reinforcement rate drop off for that bar.

Chung (1965) placed pigeons on a VI-1 min schedule, but instead of altering the schedule on successive components, the effort needed to depress the single key was changed. When the effort was changed from low to high, pigeons would initially respond less often for a brief period before returning to a relatively-stable level. When effort was altered from high to low, the pigeons would briefly respond more quickly before again leveling out. While Chung called this “suppression” and “enhancement”, it is certainly similar to contrast. However, in a related experiment when Chung (1965) placed pigeons on a concurrent VI-1 min VI-1 min schedule, no difference in the rate of responding was found when the force necessary to depress one of the keys varied while the force for the
other remained the same.

Robert Eisenberger has been investigating what he terms “self-control” or “transfer of persistence” in rats. For example, Eisenberger, Carlson, Guile and Shapiro (1979) trained rats to bar-press, with varying amounts of effort necessary to depress the lever. After the rats were responding well, they were placed in a runway and required to run for reinforcement. Those rats that were required to exert more effort on the lever tended to run faster in the runway. Conversely, when rats were trained to run first followed by bar-pressing, those rats which were required to perform more shuttle runs for reinforcement tended to bar-press faster when switched to that behavior. The results were interpreted as the rats either learning to exert more effort on tasks or to find effort less frustrating.

Subsequent research by Eisenberger has found similar results. For example, Eisenberger, Terberg, and Carlson (1979) expanded the above research somewhat by adding a control level, in which rats were not required to run in the runway to be reinforced. The rats which need to run five traverses of the runway bar-pressed the fastest, followed next by those rats required to run through the runway once, with the rats not required to run at all bar-pressing the slowest.

Eisenberger, Weier, Masterson, and Theis (1989) trained rats in bar-pressing on a VI schedule, then switched the rats to a runway. Different rats were required to run different amounts for reinforcement, some one time through the runway, others five times. When the rats were returned to lever-pressing, those rats required to run the longer distance bar-pressed faster when returned to the initial lever-pressing schedules.
However, the above results are confounded by at least two factors. First, when effort is defined as more repetitions of a particular behavior, the time needed to perform the additional repetitions may affect the behavior. Rats may be pressing the levers faster to minimize time to reinforcement.

More germane to this discussion is the suggestion that these rats are responding in this way due to a form of contrast. As the researchers made no effort in these tasks to control for level of effort in the “self-control” behaviors, it is possible that the increased bar-pressing or running may be due to a “effort contrast”; the animals may be performing at a higher rate merely because it is relatively easier for them to do so in that different behavior, not because they have learned “self-control”.

The following experiment expands on Zachary’s (1998) research, which investigated behavioral contrast in rats wheel-running. Negative contrast was evident under different levels of effort, although no positive contrast was found.

While it appears that the rats were able to discriminate between the VI-15 sec and the VI-2 min schedules, it is possible that the difference between the VI-2 min and the VI-5 min was not discriminable. Wheel-running is much more complex and strenuous than bar-pressing, key pecking, or treadle-pressing, as well as being less closely linked to consummatory behavior. When contrast was generalized from pigeons key-pecking to other species and behaviors, decreasing the VI schedules and thus increasing discriminability often aided results (McSweeney, 1983). Given that rats appear less able to discriminate easily between similar schedules of reinforcement than pigeons are
(Dougan et al. 1989), shortening the VI schedules to help differentiate between them may aid in finding positive contrast.
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