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Behavioral Contrast in a Group Foraging Paradigm

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Two experiments examined multiple schedule behavioral contrast in a group foraging paradigm. Groups of five rats foraged simultaneously in a large open field apparatus with two feeding stations. Food pellets were delivered at each of the feeding stations on multiple Variable Time schedules. As predicted by both the matching law and the ideal free distribution, the relative distribution of behavior between the two feeding stations roughly matched the relative rate of food delivery at the feeding stations. These differences were reflected in both the behavior of individual animals and in the behavior of the group. Positive behavioral contrast was found in Experiment 1, evidenced by an increase in the frequency of response in one component produced by a decreased rate of food delivery in the other component. Negative behavioral contrast was found in Experiment 2, evidenced by a decreased frequency of response in one component produced by an increased rate of food delivery in the other component. Interestingly, there was virtually no correlation between the behavior of an individual animal and the number of pellets consumed by that animal. The present results support other attempts to compare the matching law to the ideal free distribution. The data also show that behavioral contrast is predicted by both models and in fact occurs in ways consistent with both models.

Contrast effects come in many varieties. Following Crespi's (1942) classic study, numerous paradigms have been employed to study contrast effects, and numerous contrast effects have been identified. We have simultaneous contrast, successive contrast, incentive contrast, consummatory contrast, local contrast, dimensional contrast, and behavioral contrast, just to name a few. Some of these contrast effects may be related on a theoretical level, while in other cases contrast phenomena may share only a name. Regardless, it is safe to say that a wide variety of contrast effects have been studied for over 50 years.

In the operant literature, multiple schedule behavioral contrast (Reynolds, 1961) is the paradigm of choice. Multiple schedule behavioral contrast is an inverse relationship between the rate of responding in one component of a multiple schedule and the rate of reinforcement provided in the other component (McSweeney & Norman, 1979). Behavioral contrast has been of particular interest because it is a classic contextual phenomenon. That is, behavioral contrast demonstrates how responses are affected not only by the reinforcers they produce but by other reinforcers available in the environment. Contextual operant models such as the matching law (Baum, 1974, Herrnstein, 1970) have generally done a good job describing contrast effects, at least on a qualitative level (but see Dougan, Farmer-Dougan, & McSweeney, 1989).

The present experiments extend the study of contrast to a new paradigm (group foraging) and a new conceptual model (the ideal free distribution—Fretwell

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& Lucas, 1970). Groups of rats foraged in a large open field environment, with food pellets provided at two different feeding stations on multiple schedules of reinforcement. The results are examined in ways typical of both the matching law and the ideal free distribution, in the hopes that contrast-like effects could be found in both paradigms.

The relationship between matching, contrast, and the ideal free distribution is relatively complex. Therefore, each will be discussed in some detail in the following sections.

The Matching Law as a Contextual Model

Research over the past 50 years has repeatedly shown that the power of a reinforcer to control behavior is a function not only of that specific reinforcer, but of other reinforcers available in the situation. In particular, the power of a specific reinforcer is relatively high when few alternative reinforcers are available and relatively low when many alternative reinforcers are available (Herrnstein, 1961, 1970). These effects are often referred to as "contextual" phenomena because the value of a reinforcer is determined in the context of other available reinforcers.

The matching law (Herrnstein, 1961) is a leading model of these contextual effects. Herrnstein (1961) originally proposed the simple matching law (Equation 1) to account for responding on concurrent schedules. According to the simple matching law

$$P_1 /(P_1+P_2) = R_1 /(R_1+R_2) \qquad \text{(Equation 1)}$$

where P_1 and P_2 represent the response rate in two concurrent schedule components. R_1 and R_2 represent the reinforcement rate in those two components. The model is contextual because the rate of P_1 if affected not only by its own reinforcer (R_1) but also by the alternative reinforcer (R_2).

Baum (1974) argued that an equivalent equation based on ratios instead of proportions better described the concurrent schedule data than did Herrnstein's simple matching law. According to Baum

$$(P_1/P_2) = b(R_1/R_2)^a \qquad \text{(Equation 2)}$$

where two free parameters, a and b, represent sensitivity to reinforcement and response bias respectively. Equations 1 and 2 are algebraically equivalent when the a and b parameters both equal one. Equation 2 is also commonly expressed in logarithmic form

$$\log (P_1/P_2) = a \log (R_1/R_2) + \log b. \qquad \text{(Equation 3)}$$

Baum's (1974) version of the equation is typically called the Generalized Matching Law. It is used more often because the free parameters give it added flexibility in accounting for systematic variance in the data.

The matching law was originally developed as a model of choice behavior using nonhuman animals in highly controlled laboratory settings. Despite these humble origins, the model has been applied to diverse populations both in and out of the laboratory. One of the most intriguing developments is the recent recognition that the matching law is functionally equivalent to a model describing the distribution of foragers between patches, the ideal free distribution.

Matching and the Ideal Free Distribution

First described by Fretwell and Lucas (1970), the ideal free distribution is a model of optimal foraging which describes the relative distribution of foraging animals between patches differing in resource density. In its simplest form, the ideal free distribution predicts that the number of animals in each of two patches (N_1 and N_2) will be related to the resource density of the two patches (A_1 and A_2) as shown in Equation 4 (see also Baum & Kraft, 1998, Gray, 1994):

$$(N_1/N_2) = (A_1/A_2) \qquad \text{(Equation 4)}$$

Equation 4 also has a logarithmic form (Baum & Kraft, 1994; Fagen, 1987; Kennedy & Gray, 1993; Kraft & Baum, 2001):

$$\log (N_1/N_2) = a \log (A_1/A_2) + \log b \qquad \text{(Equation 5)}$$

where *a* represents the degree of sensitivity of the group behavior to differences in resource distribution. The *b* parameter represents bias toward a patch unrelated to resource ditribution.

Equations 2 and 3 are remarkably similar to Equations 4 and 5, with the exception that the matching law predicts individual behavior (*P*) based on obtained reinforcement rates (*R*) and the ideal free distribution predicts group behavior (*N*) based on the allocation of resources (*A*). These differences aside, both the matching law and the ideal free distribution suggest that the relative distribution of behavior is a function of the relative distribution of reward.

Despite the formal similarity between the matching law and the ideal free distribution, relatively little research has directly compared the models. Studies that have made a direct comparison have had intriguing but mixed results. Comparisons between matching and the ideal free distribution have been made in a relatively small number of species and research paradigms, including sparrows in an indoor aviary (Gray, 1994), pigeons in an outdoor coop (Baum & Kraft, 1998; Bell & Baum, 2002), humans in a group choice task (Kraft & Baum, 2001) and humans in a discrete trials and free operant tasks (Madden, Peden, & Yamaguchi, 2002). In general, both the matching law and the ideal free distribution have provided good quantitative descriptions of the data, though these studies have typically found significant undermatching (i.e., sensitivity parameters less than 1.0), often to a greater degree than what is found with traditional studies of individual behavior (Baum, 1979). At least one study (Baum & Kraft, 1998) has suggested that the group behavior described by the ideal free distribution is not a product of matching at the individual level.

Additional research comparing the matching law to the ideal free distribution is clearly needed. Particularly useful would be research involving different species and different research paradigms. One strategy for such additional research would be to examine a phenomenon typically studied in the operant lab under conditions more commonly associated with the ideal free distribution (or vice versa). Multiple schedule behavioral contrast (Reynolds, 1961) is potentially one such phenomenon.

Multiple Schedule Behavioral Contrast

First described by Reynolds (1961), multiple schedule behavioral contrast is an inverse relationship between the rate of responding in one component of a multiple schedule and the rate of reinforcement provided by the other component (see McSweeney & Norman, 1979). Behavioral contrast is typically studied using a three-schedule series. In the *Baseline* phase, each component of the multiple schedule provides the same rate of reinforcement. During the *Contrast* phase, the reinforcement rate in one component of the schedule is changed, but remains constant in the other component. Finally, there is a *Baseline Recovery* phase, with reinforcement rates identical to the original baseline. Positive behavioral contrast occurs when the reinforcement rate is decreased in one component during the contrast phase. A positive behavioral contrast effect is defined as an increase in response in the constant component during the contrast phase, relative to the rate of response in that component in the surrounding baseline phases. Negative behavioral contrast occurs when the reinforcement rate is increased in one component during the contrast phase. A negative behavioral contrast effect is defined as a decrease in the rate of responding in the constant component during the contrast phase, relative to the rate of response in that component in the surrounding baseline phases.

Because behavioral contrast is a contextual phenomenon, it is logical that the matching law has been suggested as an explanation. However, the matching law as originally proposed (Equations 1, 2, and 3) predicts changes in relative response rates and behavioral contrast is indicated by changes in absolute response rates. A version of the matching law proposed by Herrnstein (1970) does predict changes in absolute rates and is therefore appropriate for describing behavioral contrast. According to Herrnstein's (1970) absolute rate equation for multiple schedules, the absolute rate of responding is described by Equation 6:

$$P_1 = (k\,R_1) / (R_1 + m\,R_2 + Ro) \qquad \text{(Equation 6)}$$

There are three free parameters. The k parameter represents the maximum rate of responding, obtained when R_1 is the only source of reinforcement. The m parameter, which varies between 0 and 1, represents the degree of interaction between the multiple schedule components. Finally, the Ro parameter represents unknown and unscheduled sources of reinforcement.

In the language of Herrnstein's equation, behavioral contrast would be represented by an inverse relationship between P_1 (the response rate in one component) and R_2 (the reinforcement rate in the other component). An examination of Equation 6 shows that Herrnstein's equation predicts just such an inverse relationship for all cases in which the m parameter is greater than 0. This is because R_2 is in the denominator of the equation, meaning that any change in R_2 should result in an opposite change in P_1 (all else held equal). Thus, the matching law provides at least a qualitative description of contrast, though evidence suggests it may not always provide a good quantitative description (Dougan et al., 1989).

Behavioral contrast is traditionally studied under conditions typical of operant research. That is, the behavior of an individual organism is recorded in a free operant paradigm while that organism responds alone in a Skinner box. Despite these traditions, behavioral contrast *could* also be studied with multiple organisms simultaneously responding in a large apparatus. That is to say, the contrast paradigm could be expanded to resemble the conditions under which the ideal free distribution is typically studied.

An examination of the equations for the ideal free distribution (Equations 4 and 5) suggests that a contrast-like phenomenon might be found in a group-foraging paradigm. Both Equation 3 and Equation 4 predict an inverse relationship between the number of individuals responding in a patch and the rate of reinforcement in other patches. In fact, following the logic of Herrnstein (1970) it would be possible to construct a parallel equation to describe contrast effects in a group foraging task:

$$N_1 = (k\,A_1)/(A_1 + m\,A_2 + Ao) \qquad \text{(Equation 7)}$$

where the *m* parameter might represent the degree of interaction or proximity between patches, the *k* parameter would represent the total number of foraging organisms, and the *Ao* parameter would represent resources found outside the two patches under consideration. Equation 7 predicts a contrast-like effect in a group foraging paradigm because the number of organisms in a patch (N_1) is inversely proportional to the resources found in the other patch (A_2).

The present experiments, therefore, examine behavioral contrast under group foraging conditions. Groups of rats were placed in a large open field with two feeding stations. The rate of food delivery at the two feeding stations was varied in a way that might produce positive behavioral contrast (Experiment 1) and negative behavioral contrast (Experiment 2).

Experiment 1

Experiment 1 arranged conditions that might produce positive behavioral contrast. The rate of food presented at one feeding station was decreased while the rate of food provided at the other station remained constant. A positive behavioral contrast effect would be indicated by an increase in the frequency of response at the constant feeding station produced by the decreased rate of food delivery at the other station.

Method

Subjects. Five male, experimentally naive Sprague-Dawley rats, approximately 3 months old (250-300 g) served as subjects. The rats were individually housed on a 12:12 h light:dark cycle with free access to water. Animals were maintained at a minimum of 90% ad libitum body weight throughout the duration of the experiment. All five rats had been exposed to the apparatus prior to the study, but did not have any formal experimental history. Prior to each session, each rat was marked with nontoxic colored tempera paint so that the subject could be identified from a distance. The color used for a particular animal remained the same from day to day, so all animals are subsequently identified by their colors.

Apparatus. A large rectangular open field (2.5 m by 1.25 m with 30 cm walls) was used for all testing. The floor was constructed of plywood covered with vinyl floor material. The walls were constructed of a coated fiberboard shelving material. Two feeders (BRS/LVE) were mounted inside the box at opposite corners (SE and NW). Two stainless steel “foraging” pans (21 cm x 25 cm with a 2 cm side) were located immediately below and in front of each feeder. The pans were positioned such that food pellets dropped from the feeder and fell directly into the foraging pans. A small 5 W bulb was located immediately above each of the feeders. All experimental events were controlled via a Windows PC running Med Associates Med-State software connected to a Med Associates interface.

Procedure. The back of each rat was marked with a non-toxic tempera paint immediately prior to each session. Each rat received a different color marking (blue, red, green, purple or black) allowing easy identification of individual rats from a distance. The paint was allowed to dry briefly (less than one minute) after which the rats were transferred into the foraging chamber. The experimenter or an assistant individually placed each rat into the center of the chamber, with the order of placement randomized. When all five rats were in the chamber, the control program was initiated and the 30-m session began.

During each session, the rats were exposed to multiple Variable Time Variable Time (*mult* VT VT) schedules with each of the schedule components associated with one of the two feeding stations (SE or NW). Components alternated once per minute, such that only one component (the “active” component) delivered pellets at a time. The active component was signaled by the cue light immediately above the feeder. The component active at the start of the session was determined randomly. When a component was active, reinforcement (a single 45 mg Noyes food pellet) was delivered on the VT schedule, independent of the behavior of any of the animals. Although the reinforcers were delivered independent of behavior, competition between subjects made it essentially necessary for a rat to be close to the feeding station at the time of delivery if the rat was to have any chance to consume the food pellet.

The experiment was conducted in three phases. In the *baseline* phase, both SE and NW feeding stations delivered pellets on a VT 15 s schedule when they were active. During the contrast phase, the SE feeding station continued to produce food on a VT 15 s schedule, but the rate of food delivery for the NW component was reduced to VT 900 s. During the *baseline recovery* phase, conditions present during baseline were restored. That is, both components produced food on a VT 15 s schedule. The actual rates of pellet consumption were far lower than these scheduled values because the total number of pellets was divided between five subjects. Note that the rate of pellet delivery at the SE feeding station remained constant across the three experimental conditions. Behavior at the SE station is thus critical for the assessment of positive behavioral contrast because the response frequency at the SE station should increase during the contrast phase relative to the surrounding baseline phases. Each phase was in effect for 20 days, with data collected over the final 5 days of each phase. The schedule values were chosen because similar rates of food delivery have been found to produce contrast in rats in Skinner boxes (Dougan, et al, 1989).

Two observers collected data during each foraging session. Observer 1 recorded which rat consumed each food pellet delivered. On occasion, pellets were not consumed because the rats did not find them. This generally occurred when pellets were delivered at a time when no rats were present in the feeder area, or when pellets bounced out of the immediate vicinity of the feeder. On rare occasions it was impossible for the observer to determine which rat had consumed a pellet, in which case consumption was not recorded for that pellet. As a result of these factors the recorded consumption rate was typically less that the scheduled rate of pellet delivery. The second observer used a point-in-time sampling procedure, noting the location of each individual rat. Rats were recorded as being in the SE feeder area, in the NW feeder area, or outside the feeder area. When outside the feeder area, the rats were recorded as moving or still. The time sampling observations were made once every 30 s.

Results and Discussion

Figure 1 presents the data in a way typical of traditional operant research. That is, response frequencies of individual animals are plotted across the conditions of the experiment. Data in Figure 1 include the mean number of intervals each rat was in the SE (constant) and NW feeder area during baseline, contrast, and baseline recovery phases. Rats were rarely found to be in the area between feeding stations (typically less than 15% of the time), so those data have been excluded from Figure 1.

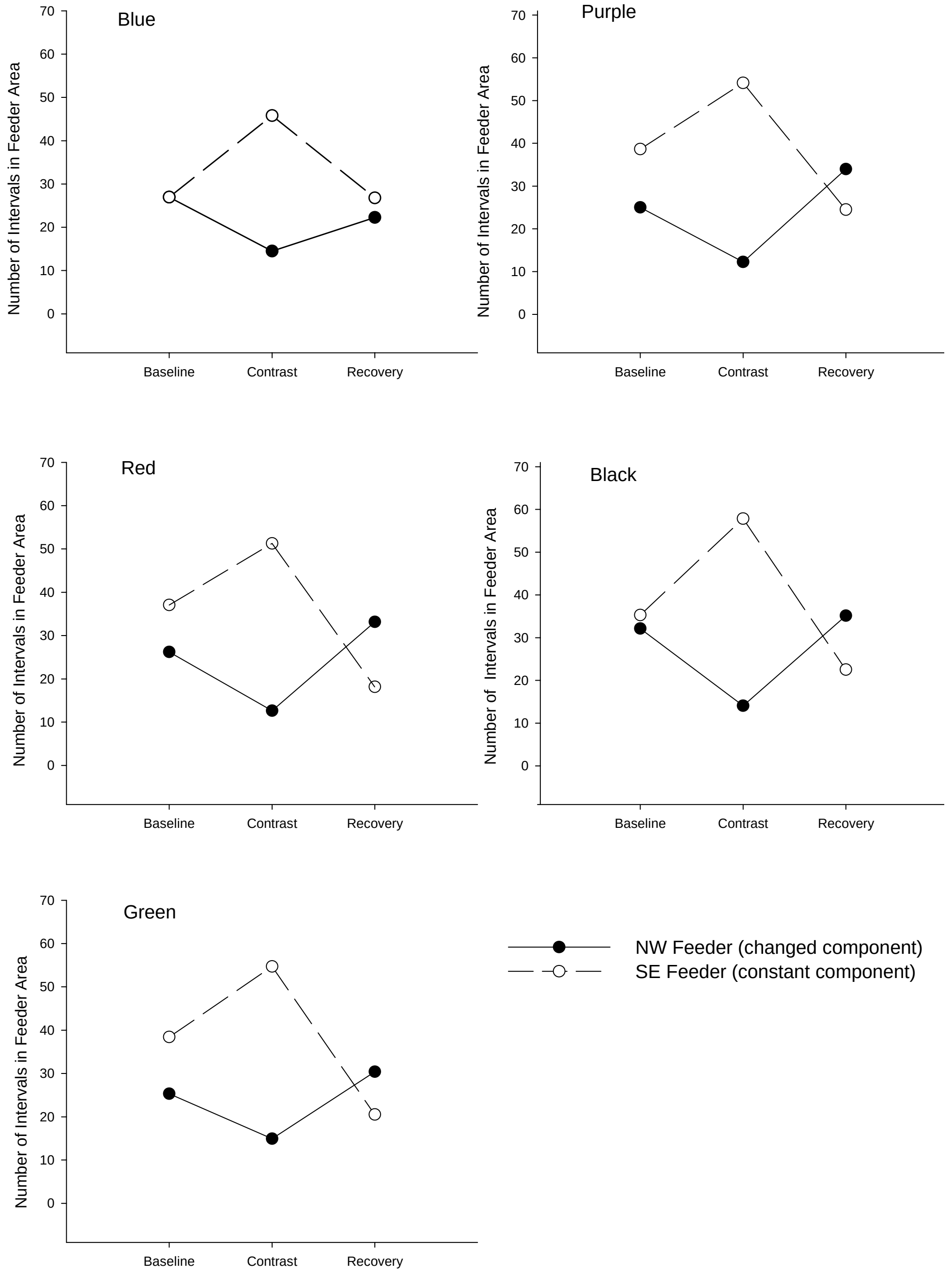

Figure 1. The total number of intervals per session during which each rat was in the NW (changed) and SE (constant) feeding stations, for all three conditions of Experiment 1 (Baseline, Contrast, and Baseline Recovery).

Figure 1 shows that rats were found substantially more often in the SE feeder area than at the NW feeder area during the contrast phase. Furthermore, the absolute number of intervals at the SE feeder was substantially higher for all subjects during the contrast phase compared to the surrounding baseline phases. The absolute numbers of intervals at the NW feeder was substantially lower for all rats during the contrast phase compared to the baseline and recovery phase.

Statistical analysis confirmed the visual analysis of data in Figure 1. A Friedman Analysis of Variance by Ranks showed a significant difference across the three conditions for the number of intervals spent in the SW feeder area, $X(2) = 9.579$, $p = 0.008$. Wilcoxin Sign tests revealed significant differences between both the baseline and recovery *mult* VT 15 s VT 15 s schedules and the contrast condition (VT 15 s VT 900 s), $z = -2.02$, $p = 0.04$ for both. The two baseline schedule conditions did not significantly differ from one another.

The data presented in Figure 1 resemble a typical instance of positive behavioral contrast. Positive behavioral contrast is defined as an increase in the frequency of responding in one component of a multiple schedule caused by a decrease in the rate of food delivery in the other component of the schedule. The data in Figure 1 show an increased probability of being at a particular feeding station (the SE station) when the rate of food presentation at the other station (the NW station) was decreased.

Figure 2 presents the data in a way more typical of the ideal free distribution. That is, the proportion of organisms found in a patch is plotted over experimental conditions. The proportion of rats found at the NW and SE feeding stations at each recording interval is plotted for the baseline, contrast, and baseline recovery conditions. Note that the percentages do not add to 100 because it was possible for the rats to be in locations other than the feeding stations. As seen in Figure 2, rats were slightly more likely to be at the SE feeder than the NW feeder in each of the conditions. More interesting, though, is the marked increase in the number of rats in the SE feeder during the contrast condition relative to surrounding baseline conditions. This represents a contrast-like effect: The numbers of rats at a particular feeding station was inversely related to the rate of food delivery at the other feeding station. Note the similarity between Figures 1 and 2. Both figures suggest positive contrast-like effects even though the data are presented in very different ways.

Interestingly, the contrast-like effects shown in Figures 1 and 2 were unrelated to the actual consumption of the food pellets. Figure 3 plots the mean number of pellets consumed by each animal at each feeding station during baseline, contrast, and baseline recovery phases. As seen in Figure 3, the mean number of pellets consumed remained relatively constant across conditions at the SE station, but decreased dramatically during the contrast condition relative to baseline at the NW station. This is not surprising because it is consistent with the scheduled rate of food delivery. What is more surprising is the wide variation in the number of pellets consumed by individual animals, and the apparent lack of correlation between the rate of pellet consumption by individual animals and the contrast-like data presented in Figure 1. All rats showed relatively consistent patterns of contrast (Figure 1) white the same rats consumed vastly different numbers of pellets (Figure 3). A Pearson r correlation coefficient confirmed that there was only a slight, nonsignificant correlation between the number of pellets consumed at the SE (constant) station and the amount of time a rat spent in that area (*r* = 0.13). To complicate matters, there is some suggestion in the data that rats consuming more pellets also showed a slightly higher magnitude of contrast, although this is not clear enough to draw firm conclusions. Overall, the data suggest that the contrast-like effects presented in Figure 1 may be related to factors other than pellet consumption. For example, social variables and competition effects may have contributed to the effect. Future studies should examine this in greater detail.

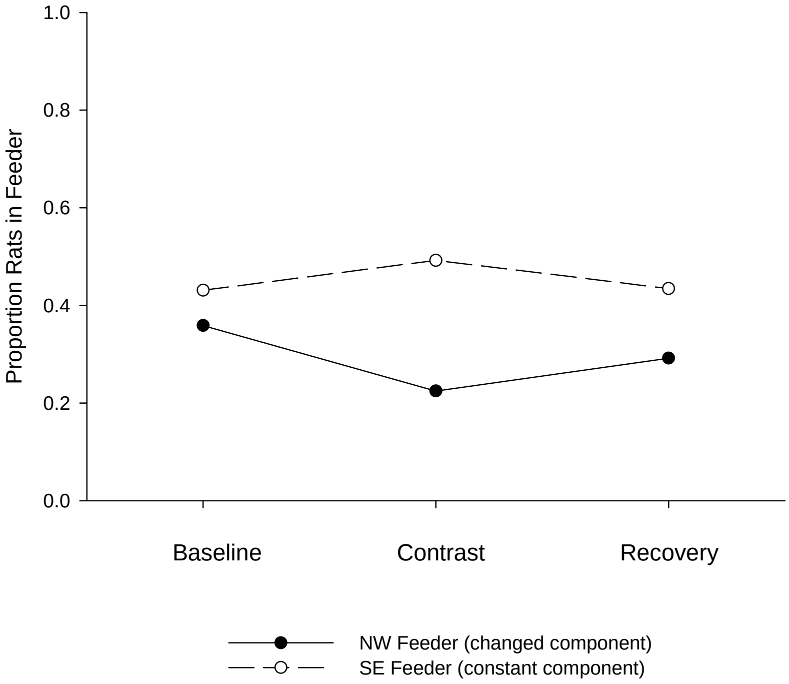

Figure 2. The mean proportion of total animals found at the NW (changed) and SE (constant) feeding stations areas for all three conditions of Experiment 1 (Baseline, Contrast, and Baseline Recovery).

In summary, Experiment 1 found positive contrast-like effects. The effects were present when the data were analyzed in a manner similar to that found in traditional contrast studies (Figure 1) and in a manner similar to that found in studies of the ideal free distribution (Figure 2). Experiment 2 examines conditions that might be expected to produce a negative contrast effect.

Experiment 2

Experiment 2 arranged conditions that might produce negative behavioral contrast. The rate of food presented at one feeding station was increased while the rate of food provided at the other station remained constant. A negative behavioral contrast effect would be indicated by a decrease in the frequency of response at the constant feeding station produced by the increased rate of food delivery at the other station.

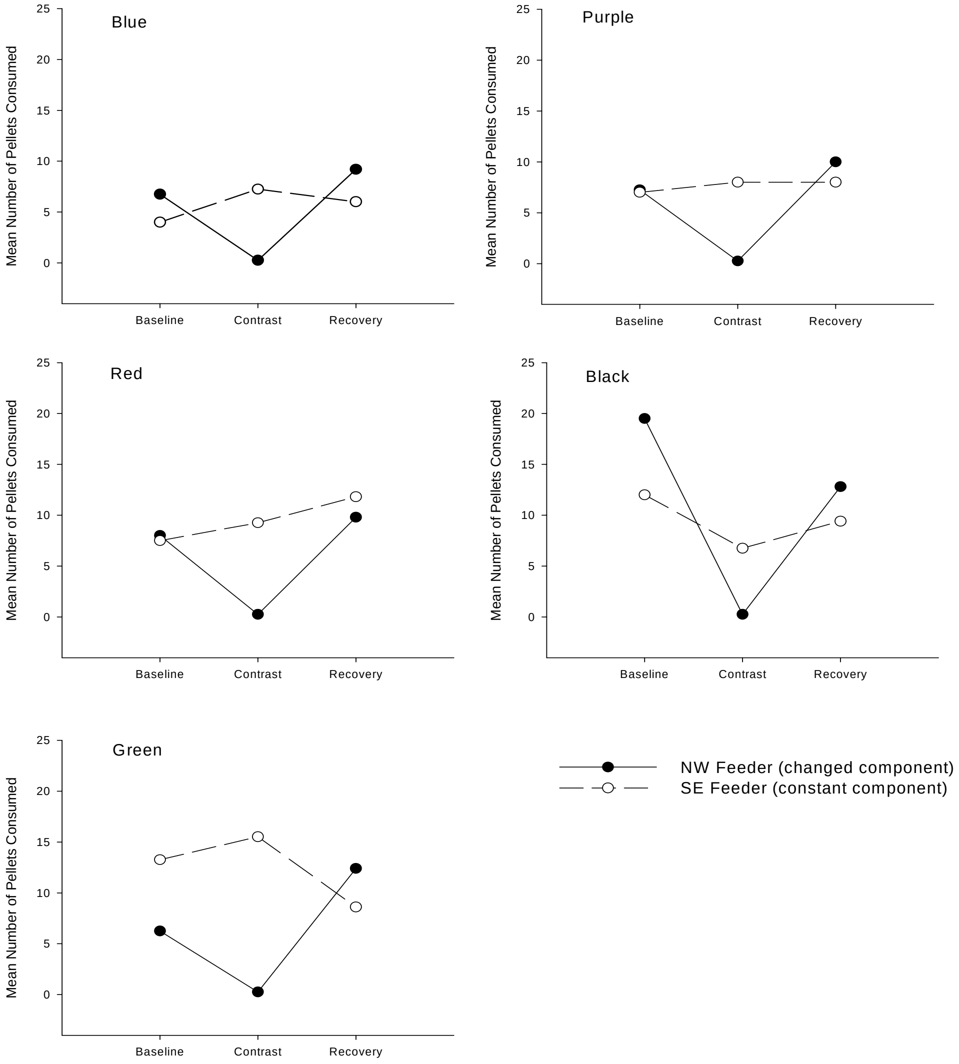

Figure 3. Number of food pellets consumed by each rat in the NW (changed) and SE (constant) feeder areas for all three conditions of Experiment 1 (Baseline, Contrast, and Baseline Recovery).

Method

Subjects. The subjects were five experimentally naïve, male Sprague-Dawley rats, approximately 3 months old (250-300 g) at the start of the experiment. Housing and care conditions were identical to those described in Experiment 1.

***Apparatus and Procedure*.** The apparatus was the same as in Experiment 1. The procedure was also the same as in Experiment 1, with the following exception: In the *baseline* phase, both SE and NW feeding stations delivered pellets on a VT 60 s schedule when they were active. During the contrast phase, the SE feeding station continued to produce food on a VT 60 s schedule, but the rate of food delivery for the NW component was increased to VT 15 s. During the *baseline recovery* phase, conditions present during baseline were restored: Both components again produced food on a VT 60 s schedule. As in Experiment 1, the rate of food delivery at the SE station remained constant across all conditions. Once again, behavior at the SE station is critical for the assessment of negative behavioral contrast because the response frequency at the SE station should decrease during the contrast phase relative to the surrounding baseline phases.

Results and Discussion

Figure 4 plots the data in a way similar to traditional operant studies. The figure shows the mean number of intervals each rat the spent at the SE and NW feeding stations. As seen in Figure 4, rats were found substantially more often in the NW feeder area than at the SE feeder area during the contrast phase. Furthermore, the number of intervals at the SE feeder was lower for all subjects during the contrast phase compared to the surrounding baseline phases. The absolute numbers of intervals at the NW feeder was substantially higher for all rats during the contrast phase compared to the baseline recovery phase.

The data presented in Figure 4 resemble a typical instance of negative behavioral contrast. Negative behavioral contrast is defined as a decrease in the frequency of responding in one component of a multiple schedule caused by an increase in the rate of food delivery in the other component of the schedule. The data in Figure 4 show a decreased probability of being at a particular feeding station (the SE station) when the rate of food presentation at the other station (the NW station) was increased. Note that these results are somewhat less robust than the positive contrast data in Experiment 1. All of the individual animals in the present experiment showed a contrast-like effect, but in some cases the change between baseline and contrast conditions was relatively small.

As in Experiment 1, statistical analyses confirmed the visual analysis of the data in Figure 4. A Friedman Analysis of Variance by Ranks showed a significant difference across the three schedules for percentage of times spent in the constant feeder area, $X(5) = 7.90$, $p = 0.019$. Wilcoxin Sign tests revealed significant differences between the initial baseline schedule (VI 60 s VI 60 s) and the contrast condition (VI 60 s VI 15 s), $z = -2.023$, $p = 0.04$. There was no significant difference between the second baseline schedule and the contrast condition, suggesting that responding did not return to baseline levels in Experiment 2. This may be due to the relatively small changes in behavior found for some of the animals.

Figure 5 presents the data in a way typical of the ideal free distribution. The average proportion of rats found in each feeding station is plotted across baseline, contrast, and recovery conditions. As seen in Figure 5, the proportion of rats in the SE feeder was lower during the contrast condition compared to the surrounding baseline and recovery conditions. This is equivalent to a negative contrast effect because the proportion of animals at one feeder decreased as a function of an increased rate of food delivery at the other feeder.

Figure 6 shows the number of food pellets consumed at the SE and NW feeders for individual rats. As shown in Figure 6, the number of food pellets consumed by the animals varied widely across the five rats, and across the three conditions. The contrast-like effects displayed in Figure 4 are relatively consistent across animals despite wide variation in the number of pellets consumed (Figure 6). Further, some rats showed the contrast-like effects despite individually consuming very few pellets. As in Experiment 1, there was virtually no statistical correlation between the amount of time an animal spent in a feeder and the number of pellets consumed from that feeder (Pearson $r = 0.08$, NS). This again suggests that factors other than food consumption are driving the present results. Such factors will need to be examined in future studies.

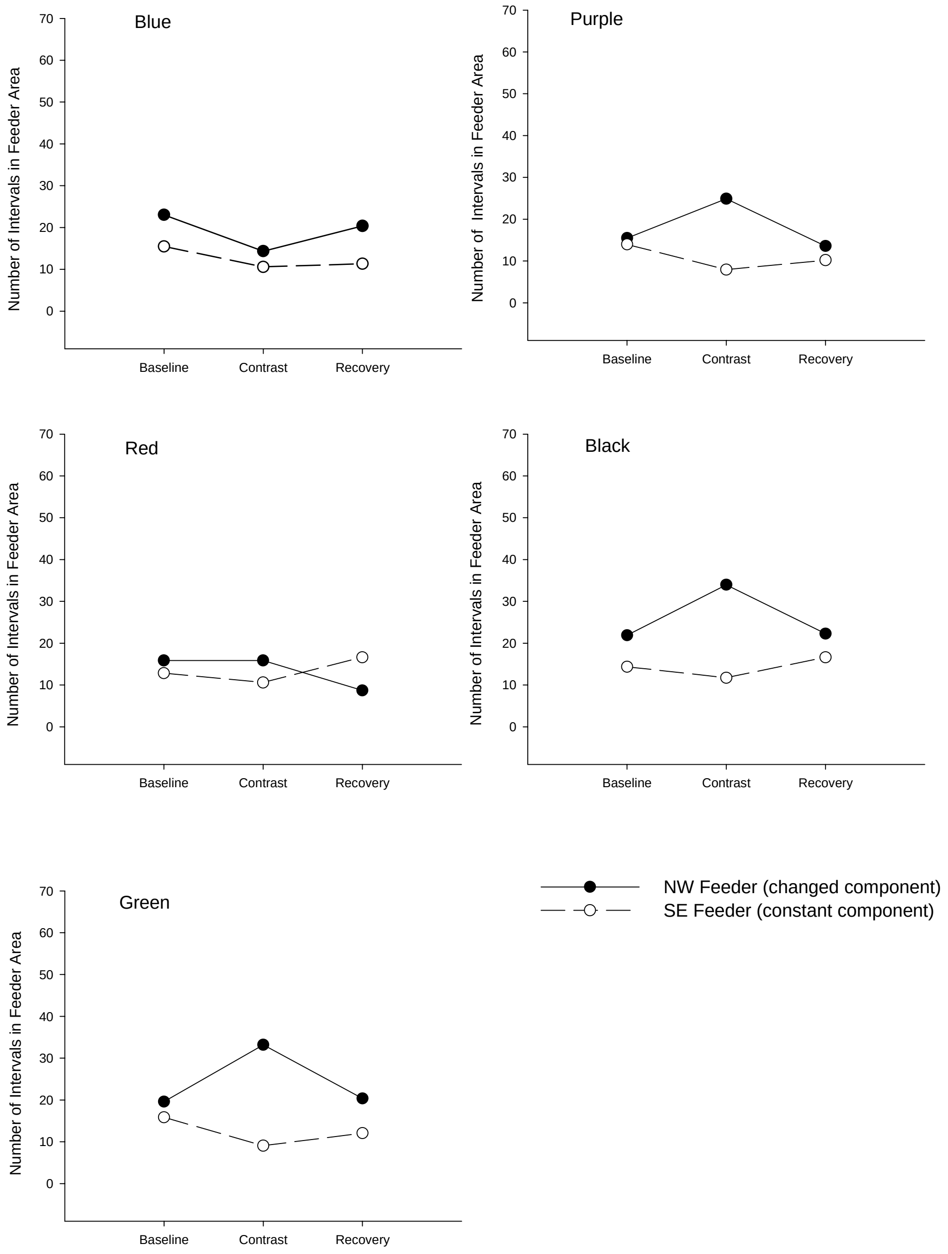

Figure 4. The total number of intervals per session during which each rat was in the NW (changed) and SE (constant) feeding stations, for all three conditions of Experiment 2 (Baseline, Contrast, and Baseline Recovery).

In summary, Experiment 2 found a negative contrast-like effect. This occurred both when the data were examined in a manner typical of operant studies (Figure 4) and in a way typical of studies of the ideal free distribution (Figure 5).

The negative contrast effects observed here are somewhat weaker than the positive contrast effects found in Experiment 1.

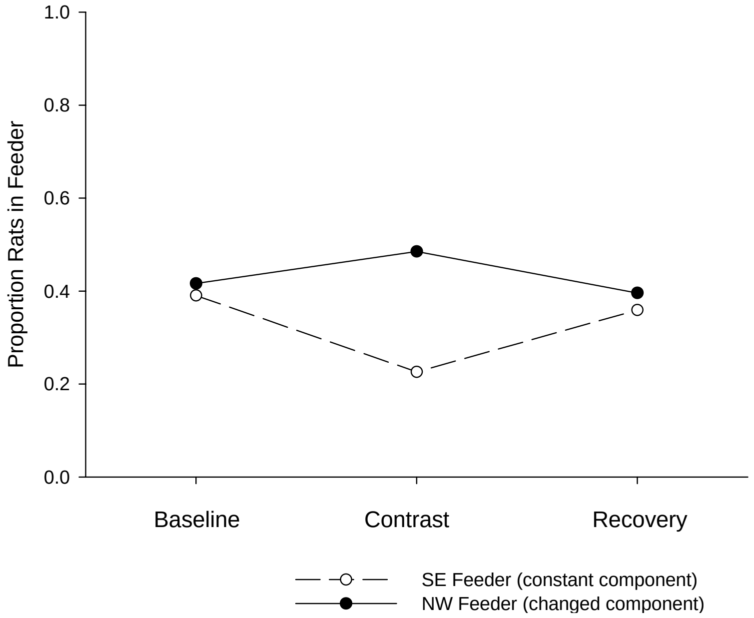

Figure 5. The mean proportion of total animals found at the NW (changed) and SE (constant) feeding stations areas for all three conditions of Experiment 2 (Baseline, Contrast, and Baseline Recovery).

General Discussion

The present investigation experiments examined positive behavioral contrast (Experiment 1) and negative behavioral contrast (Experiment 2) under a group foraging paradigm similar to that typically used in studies of the ideal free distribution. As predicted, contrast-like effects were found in both experiments.

In Experiment 1, both the amount of time spent at the SE feeder (Figure 1) and the proportion of rats found at that feeder (Figure 2) increased when rate of food delivery at the NW feeder decreased. This occurred despite the fact that the rate of food delivery at the SE feeder remained constant. The effect was found in the behavior of each of the individual animals, and was also confirmed with a statistical analysis. This effect resembles positive behavioral contrast because the frequency of behavior directed to one source of food increased as a function of a decrease in the rate of food available elsewhere.

In Experiment 2, both the amount of time spent at the SE feeder (Figure 4) and the proportion of rats found at that feeder (Figure 5) decreased when the rate of food at the NW feeder increased. This effect resembles negative behavioral contrast because the frequency of behavior directed to one source of reinforcement decreased as a function of an increase in the rate of food available elsewhere. It is important to note that the results of Experiment 2 are somewhat less robust than the results of Experiment 1. In Experiment 2, the contrast effects were found in the data of each of the individual animals. However, statistical significance was not found between the contrast condition and the baseline recovery condition, possibly because of the relatively small size of the behavioral changes combined with some variability between subjects.

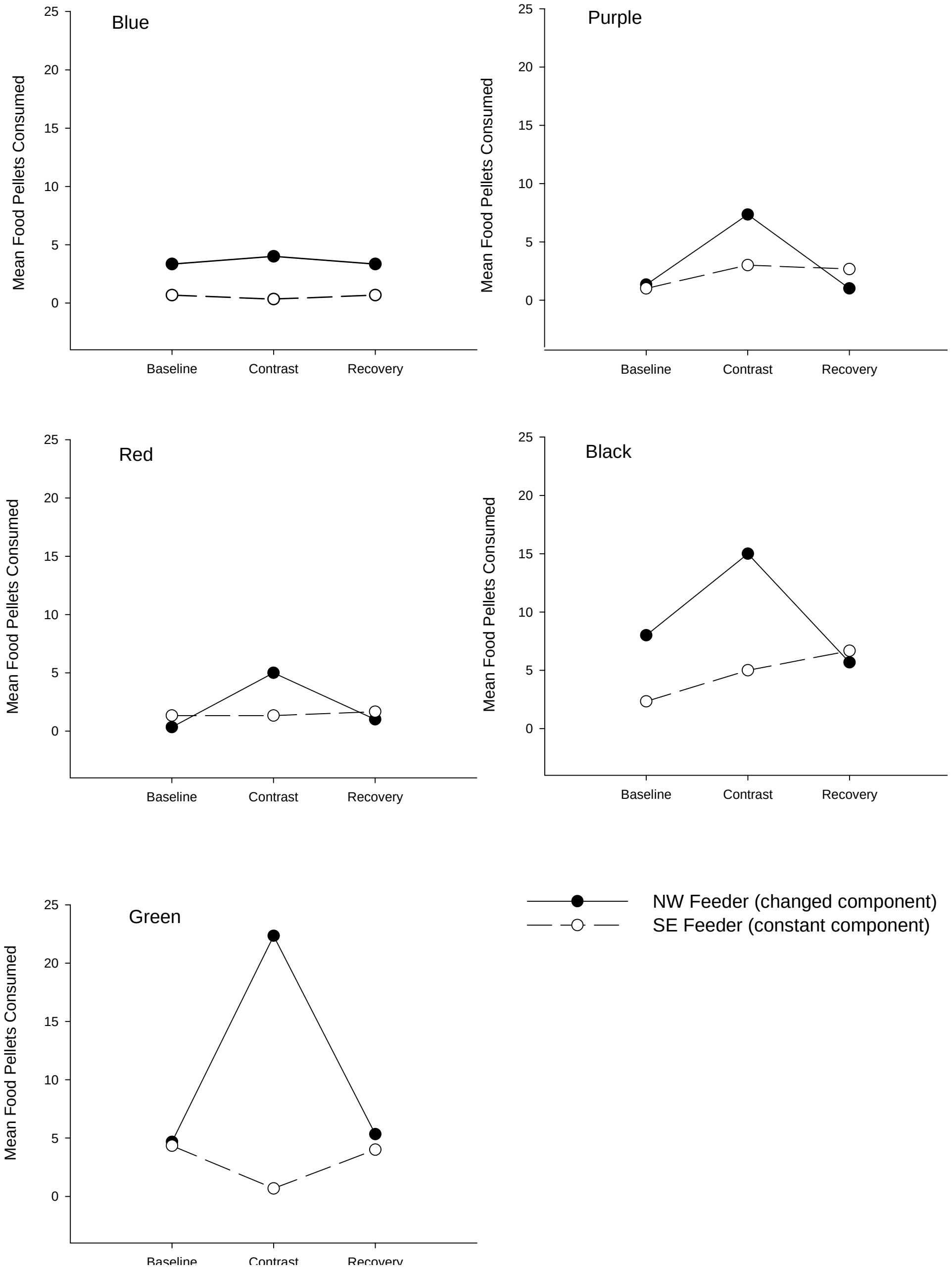

Figure 6. Number of food pellets consumed by each rat in the NW and SE feeder areas for all three conditions of Experiment 2 (Baseline, Contrast, and Baseline Recovery).

The present data are qualitatively consistent with the models of contrast based on the matching law (Equation 6). As discussed in the introduction, the matching law predicts that the rate of a response will be inversely proportional to the rate of reinforcement provided by alternative sources. The contrast-like effects shown in Figures 1 and 4 represent just such an inverse relationship. It is important to note that the present data do not allow a quantitative evaluation of the matching law. Quantitative analysis would require a much larger range of schedules to be used.

The present data are also qualitatively consistent with a model based on the ideal free distribution (Equation 7). As developed in the introduction, the ideal free distribution predicts that the distribution of animals in a patch should be inversely related to the density of resources. The data presented in Figures 2 and 5 show just such an effect. The rats were relatively evenly distributed between patches when the resource distribution was roughly equal (baseline and baseline recovery conditions). When resource allocations shifted during the contrast phase, the allocation of rats between patches shifted in the same way. As with the matching law, the present data do not allow a quantitative evaluation of the ideal free distribution.

The present data also support recent attempts to draw a parallel between matching and the ideal free distribution (Baum & Kraft, 1994; Gray, 1994; Kraft & Baum, 2001; Madden, et al 2002). The same data set produced results qualitatively consistent with the matching law (Figures 1 and 4) and with the ideal free distribution (Figures 2 and 5). This means that the same conditions producing a contrast-like effect in the behavior of individuals also produces a contrast-like effect in the distribution of animals between patches. These findings are consistent with the ideal that a single theoretical process may underlie both the matching law and the ideal free distribution, although such conclusions must be tentative in the absence of quantitative analysis. In addition, other data (Baum & Kraft, 1998) suggest that the ideal free distribution may be an emergent phenomenon unrelated to the behavior of individual animals. The present data would not, in fact, be particularly interesting if contrast at the group level arose directly from matching at the individual level. A more interesting result, supported to some extent by the present data and by Baum and Kraft (1998), is that contrast at the group level is not directly caused by matching at the individual level. Additional research on this question is clearly warranted.

One of the most interesting aspects of the present data is the lack of correlation between pellet ingestion and distribution of behavior. As noted in Figures 3 and 6, there was virtually no relationship between the rate at which individual animals consumed food pellets and the behavior of those individual animals. In typical studies of behavioral contrast it is assumed that behavior is governed by consumption of the reinforcer. The present results call that assumption into question. The results suggest that other factors—such as social and competitive behavior patterns—may contribute to the results. It is also possible that secondary reinforcers such as the sound of the food magazine and the sight of the food pellet might contribute to the results. Additional experiments should examine this possibility.

The lack of correlation between contrast and pellet consumption also has considerable theoretical implication. For example, some theories of behavioral contrast argue that the phenomenon is governed by the consumption of reinforcers. McSweeney and Weatherly (1999) have argued that behavioral contrast is caused by habituation to the reinforcer. In studies using food reinforcers, such habituation should occur when subjects consume the pellet but should not occur (or should occur to a lesser extent) when pellets are not consumed. The present finding that contrast-like effects can occur in the absence of consumption may suggest that factors in addition to habituation can contribute to contrast, or that a number of variables may contribute to contrast effects (see Dougan et al., 1989). The theoretical implications are further complicated by the possibility (discussed earlier) that contrast was less robust in the animals consuming fewer pellets. The lack of correlation also supports previous suggestions (Baum & Kraft, 1998) that the distribution of groups of animals is unrelated to matching at the individual. Substantial additional research is necessary to investigate these theoretical issues.

It is also interesting to note that the magnitude of contrast-like effects—particularly the positive effects in Experiment 1—are far larger than what is traditionally found in studies of behavioral contrast. In Experiment 1, rats were present in the SE feeder almost twice as often during the contrast phase than in the surrounding baseline phases. The contrast-like effect was found in the behavior of each of the individual animals. By comparison, positive behavioral contrast has traditionally been difficult to produce in rats, and when it is found it tends to be a much smaller effect than what was found here (Dougan et al., 1985). The large magnitude of the effects may suggest that the present paradigm simply produces more robust effects. The large magnitude might also result from methodological differences between the present experiments and the typical behavioral contrast design. These differences are discussed below.

Throughout the present paper the results have been called “contrast-like” effects. This is because both the experimental design and data collection procedures differ from traditional studies of behavioral contrast in important ways, and the variations from traditional procedures might be considered confounding factors. Some of these differences (the size of the foraging area, the use of groups of animals) were critical to the intent of the study—examination of contrast effects in a group foraging paradigm. Such differences, though potentially very important, should not be considered confounds because they represent an intentional expansion of the behavioral contrast literature into a new dimension. Other differences, including the types of schedule used and the way data were collected, were necessitated by the design but were not *conceptually* critical to the experiment. The degree to which these factors contributed to the results warrants additional study.

One such factor is the type of reinforcement schedule used. Traditional studies of behavioral contrast have utilized multiple schedules in which a specific operant response is required to produce the reinforcer. For example, many traditional studies use multiple Variable Interval Variable Interval (*mult* VI VI schedules) in which a specific operant response (typically a bar press or a keypeck) is required to produce reinforcement. The present studies used *mult* VT VT schedules, in which no explicit operant response was required to produce reinforcement. Reinforcers were delivered independently of behavior, and could in fact be delivered when no rats were in the feeding area.

In theory, the distinction between VI and VT schedules may make little difference (e.g., Baum & Rachlin, 1969). In addition, casual observation of the rats suggested that they were engaging in a “competitive” response in the area of the feeder, often climbing over each other in an apparent attempt to be near the pellet tube when food was delivered. Indeed, it was virtually necessary for a rat to be in the feeding area and actively “competing” for position if it was to consume a food pellet. Therefore, the present experiments may have replaced the explicit operant response with an implicit “competition” response. Unfortunately, data on the frequency of the “competitive” responses were not collected, nor were systematic videotapes made. Future studies should directly examine these competitive responses to determine if contrast effects are apparent in the rate of those responses.

The way multiple schedules were arranged also differed from most traditional studies of behavioral contrast. Most studies of behavioral contrast utilize pigeons as subjects, and use a single pecking key as a response manipulandum. In such traditional preparations, the discriminative stimulus (usually presented directly on the response key) alternates to signal which component of the schedule is active. A significant byproduct of such a procedure is that the subject cannot make an incorrect response by responding to an inactive schedule component. In the present procedure, the two multiple schedule components were presented in different locations, thus making it possible for the subjects to respond in an inactive component. Unfortunately, no record was kept of how often animals were found in an inactive component of the multiple schedule, though casual observation did suggest that the animals changed positions when schedules changed. It is also not clear how important this difference is. Although the present schedule arrangement does deviate from the most common procedure for arranging multiple schedule components, a parallel does exist in the contrast literature when rats respond on two different response levers. Few experiments have compared the traditional one-manipulandum procedure to the less common two-manipulandum procedure, although there is some suggestion that a two-manipulandum procedure produces more robust contrast in rats (Estle, Beaumont, & Dougan, 2000). Future research is necessary to examine the differences between one- and two-manipulandum procedures, both in the typical Skinner box setting and in the present foraging paradigm.

The method of data collection in the present study also differed from what is typically employed in studies of behavioral contrast. Traditional studies typically measure the rate of a single free operant response, with responses accumulated over the entire session. The present experiment used time allocation as the primary dependent measure, and used a time-sampling procedure to estimate allocation. The time-sampling procedure was necessitated because of the difficulty of simultaneously monitoring the behavior of five rats. There are obviously differences between free operant and time-sampling procedures, and it is unclear what effect those procedural differences might have had on the present outcomes. Future experiments should develop methods to constantly monitor the position of all the rats, so as to make the data collection procedure more comparable to traditional studies.

In conclusion, the present experiments examined behavioral contrast in a group foraging design more typical of experiments studying the ideal free distribution. Both positive and negative contrast-like effects were found. Several aspects of the data are particularly intriguing, including the lack of correlation between the behavior of individual animals and the consumption of food pellets by those animals. The present results support other studies which have compared the matching law to the ideal free distribution, and also suggest several lines for future investigation.

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