INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

2015, 28
Fuat Balci
Special Issue Editor
Peer-reviewed

Temporal Averaging Across Stimuli Signaling the Same or Different Reinforcing Outcomes in the Peak Procedure

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The present study examined factors that affect temporal averaging in rats when discriminative stimuli are compounded following separate training indicating the availability of reward after different fixed intervals (FI) on a peak procedure. One group of rats, Group Differential, learned that a flashing light stimulus signaled that one type of food pellet reward could be earned for lever pressing after an FI 5 s interval and that a second type of food pellet reward could be earned after an FI 20 s interval in the presence of a tone stimulus. A second group of rats, Group Non-Differential, was similarly trained except that both types of rewards were scheduled across flash and tone trials. When given non-reinforced flash + tone compound test trials the interval containing the maximal response rate was no different than on flash alone test trials, although some responding also appeared near the long FI time. After these FI contingencies were reversed (flash signaled FI 20 s and tone signaled FI 5 s), however, further compound test trials more clearly revealed a temporal averaging pattern in both groups. The peak interval was shifted to the right of the FI 5 stimulus. Moreover, Group Differential rats acquired the reversed discrimination somewhat more rapidly than Group Non-Differential rats, and in a final selective satiation test Group Differential rats responded less in later intervals after they had been sated on the FI 20 s reward. These data suggest that temporal averaging in stimulus compound tests occurs even when the stimuli being combined signal qualitatively different rewards, but that decreasing the value of one of those rewards can shift responding away from the relevant time interval in a selective satiation test. However, when an especially salient stimulus (e.g., flashing light) signals a short FI, rats tend to process the compound stimulus more in terms of its individual elements.

There has been growing interest in recent years in studying the interactions between interval timing and associative learning processes (e.g., Arcediano & Miller, 2002; Balsam & Gallistel, 2009; Balsam, Drew, & Gallistel, 2010; Bouton & Hendrix, 2011; Buhusi & Oprisan, 2013; Delamater & Oakeshott, 2007; Delamater, Desouza, Rivkin, & Derman, 2014; Galtress & Kirkpatrick, 2009; Kirkpatrick & Church, 1998; 2000; Miller & Barnet, 1993). One of the main challenges facing this area of research is determining how to best conceptualize the encoding of time while at the same time recognizing the contributions of associatively based stimulus selection processes. For years investigators have recognized the importance of studying conditioning processes using compound conditioning tasks. Studies of this sort have been extremely influential in guiding our thinking about basic associative learning processes. The emergence of several highly influential models of Pavlovian conditioning (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Pearce, 1987, 1994, 2002; Rescorla & Wagner, 1972; Wagner, 1981; Wagner & Brandon, 1989, 2001) was directly related to interest in studying learned behaviors in situations involving the possibility of stimulus control when multiple stimuli could compete or cooperate in the learned control over behavior. Focus on interactions among stimuli has generally not been the focus of studies of interval timing (though see Balsam & Gallistel, 2009; Gallistel & Balsam, 2014).

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https://doi.org/10.46867/ijcp.2015.28.02.12

One especially interesting issue in the study of associative and interval timing processes concerns what happens when independently trained stimuli are combined in a test compound. For example, if a rat were to be given pairings of a tone conditioned stimulus and electric foot shock, then the animal develops a new conditioned fear response to the tone. If a second stimulus, for instance, a light, were to be paired with foot shock on separate conditioning trials, then a fear response would develop to that stimulus as well. On test trials with the tone + light stimulus compound we expect to observe a compounding of these two conditioned fear responses such that the overall amount of fear displayed would be greater than that observed on test trials with just the tone or just the light by themselves. This classic additive summation effect has been observed in a wide number of conditioning preparations (e.g., Delamater, Sosa, & Katz, 1999; Hendry, 1982; Kehoe & Gormezano, 1980; Lattal & Nakajima, 1998; Rescorla & Coldwell, 1995; Weiss, 1972), and under a wide variety of circumstances. Consequently, most associative theories typically assume that such summation of responding reflects an underlying associative summation process of one form or another.

However, in this situation it is quite possible that rather than seeing an additive summation effect, the two sources of stimulus control could have, in principle, averaged their separate contributions. For instance, suppose that in the presence of one stimulus a reward is presented, on average, once every 75 s, and in the presence of a second stimulus a reward is presented, on average, once every 150 s. When compounding these two stimuli what level of responding would be expected? One possibility is that the animal will respond to this compound in the same way that they would respond to a third stimulus that was trained with reward occurring, on average, every 112.5 s (the average of these two intervals). In contrast, Andrew and Harris (2011) performed such an experiment (with rats in a Pavlovian magazine approach task) and observed that subjects responded to this compound stimulus similar to a third stimulus that was paired with reward, on average, once every 50 s. In other words, the animals summed their separate reward rate estimates (1 pellet every 75 s + 1 pellet every 150 s = 3 expected pellets every 150 s) across the two elements of the stimulus compound.

It is potentially important that in this procedure, Andrew and Harris (2011) trained rats with variable duration stimuli where the rewards occurred after variable amounts of time. A very different situation is where each stimulus signals reward occurring after a fixed specific amount of time. In the classic *peak procedure* lever press responding is reinforced on a fixed interval schedule, and on non-reinforced probe trials the rats' response curve (averaged over a number of test trials) steadily increases up to some peak level before gradually decreasing thereafter. This result shows strong temporal control. Matell and his colleagues (Matell & Kurti, 2014; Swanton, Gooch, & Matell, 2009; Swanton & Matell, 2011) have recently demonstrated that when different stimuli are trained with different FI schedules in this peak procedure the rats will average their response distributions, under many conditions, rather than respond in a way that reflects a simple additive summation process. For instance, if additive summation occurred, then the responding on nonreinforced compound stimulus tests should appear bimodal with separate peaks at the trained FI values. Instead, the rats in these studies displayed a third peak distribution whose peak occurred at an interval intermediate between the two trained FI values. This result also displays strong temporal control, but it illustrates how the two stimuli when combined can control behavior in a dramatically different way than would be expected on the basis of an additive summation process.

It should be noted that Matell and Kurti (2014) provided evidence to suggest that under some circumstances additive summation occurs (i.e., most clearly illustrated by a bimodal peak distribution) and under other circumstances temporal averaging occurs. One variable that appears to be critical is the relative value of the two stimuli trained with different FIs. Specifically, Matell and Kurti (2014) manipulated the relative reinforcement probabilities of an auditory and visual stimulus and found that the visual stimulus tended to exert greater control than the auditory stimulus, for instance, it appeared to be generally more salient to the rat. However, if the reinforcement probability to the visual stimulus was reduced relative to the auditory stimulus, then averaging was a more common result (i.e., a distinct distribution of responses emerged on compound test trials with a peak that was intermediate between the other two). Similarly, the stimulus signaling the short FI interval also tends to exert greater control during compound test trials, but as the reinforcement probability associated with the short FI stimulus was reduced relative to the long FI stimulus averaging was also more likely to occur.

Determining when responding reflects an averaging or an additive summation process would appear to be critical for our further understanding of the mechanisms underlying stimulus control. Given the theoretical importance of this temporal averaging effect, the present study examined if another variable might also play a role. Elsewhere, we, and others, have noted that when two conditioned stimuli are associated with qualitatively different reinforcing outcomes, rats will learn to subsequently distinguish between those stimuli more easily than if those stimuli are associated with the same reinforcing outcome (Delamater, 1998, 2012; Delamater, Kranjec, & Fein, 2010; Ramirez & Colwill, 2012). In the present context, if two stimuli signaling different FI values were also trained with distinct reinforcing outcomes (e.g., different flavored food pellets), would this influence whether or not rats would average their temporal estimates on compound test trials? If the differential outcome treatment effectively increases the discriminability between the two stimuli (e.g., Delamater, 2012) those two stimuli might be more likely to control responding during the compound test more independently. In contrast, when pairing two stimuli with the same reinforcing outcome, this can lead to the stimuli becoming, effectively, more *equivalent.* Thus, a temporal averaging result might be more likely to occur under these circumstances. It is noteworthy that all of the temporal averaging studies performed to date have used a single reinforcer, leaving open the possibility that averaging may partly depend upon the fact that both stimuli signal the same reward.

The present study explored this idea. Table 1 shows the experimental design. Two groups of rats were trained on a multi-interval instrumental peak procedure. All rats were initially trained to lever press for food reward on an FI 5 s schedule in the presence of a flashing light stimulus (measured from stimulus onset), and on an FI 20 s schedule in the presence of a tone stimulus (again measured from stimulus onset). Once differential peak response curves developed on non-reinforced probe trials with the flash and tone presented alone, flash + tone compound probe trials were added. Earlier work found different results (summation or averaging) depending on whether the visual stimulus signaled the short or long FI schedule (e.g., Matell & Kurti, 2014). In order to explore this further the present study used a reversal procedure. Following the original training and compound test phases, the rats were given reversal training in which the flashing light signaled the FI 20 s schedule and the tone signaled the FI 5 s

schedule. Further compound probe tests were conducted after stable differential responding emerged in this reversal phase on flash and tone probe trials. One of the two groups, Group Differential, was trained throughout with distinct stimulus-reinforcer assignments (two qualitatively different pellet types were used). In the other group, Group Non-Differential, each stimulus signaled that each of the two types of pellets used could be earned across different training trials (in both the initial acquisition and reversal phases). Finally, in order to further assess the degree to which anticipated rewards might influence averaging performance the rats were given a selective satiation test at the end of the experiment (see Table 2). In this test, the rats consumed one of the pellet types for 1 hr prior to a test session in which non-reinforced probe trials occurred with the flash + tone compound. The question of interest here was whether temporal averaging would be sensitive to the current value of an anticipated outcome. If one of the anticipated rewards has been devalued, then perhaps the compound response distribution would shift away from the interval controlled by that stimulus in the averaging test.

Method

Subjects

Subjects were 16, experimentally naïve, male (n = 8) and female (n = 8) Long-Evans rats bred at Brooklyn College, but derived from Charles River laboratories. The free feeding body weights varied between 385 and 477 g for the males and between 236 and 305 g for the females at the beginning of the experiment. The rats were housed in groups of 2-4 animals in plastic tub cages with wood chip bedding (17 x 8.5 x 8 in, l x w x h) in a colony room that was on a 14 hr light/10 hr dark cycle, and they were maintained at 85% of their free feeding body weights by daily supplemental feedings (given following the experimental session each day). Experimental sessions occurred during the light phase of their light/dark cycle, approximately 2.5 hr after light onset.

Apparatus

The apparatus consisted of a set of eight identical standard conditioning chambers (BRS Foringer RC series), each of which was housed in a Med Associates sound- and light-resistant shell. The conditioning chambers measured 30.5 cm x 24.0 cm x 25.0 cm. Two end walls

Table 1
Experimental Design

Group	Acquisition Phase	Test 1	Reversal Phase	Test 2
Differential	Flash - O1 (FI 5")	Flash - O1 (FI 5")	Flash - O1 (FI 20")	Flash - O1 (FI 20")
	Tone - O2 (FI 20")	Tone - O2 (FI 20")	Tone - O2 (FI 5")	Tone - O2 (FI 5")
	Flash (Probe)	Flash (Probe)	Flash (Probe)	Flash (Probe)
	Tone (Probe)	Tone (Probe)	Tone (Probe)	Tone (Probe)
		Flash + Tone (Probe trials)		Flash + Tone (Probe trials)
Non-Differential	Flash - O1/O2 (FI 5")	Flash - O1/O2 (FI 5")	Flash - O1/O2 (FI 20")	Flash - O1/O2 (FI 20")
	Tone - O1/O2 (FI 20")	Tone - O1/O2 (FI 20")	Tone - O1/O2 (FI 5")	Tone - O1/O2 (FI 5")
	Flash (Probe)	Flash (Probe)	Flash (Probe)	Flash (Probe)
	Tone (Probe)	Tone (Probe)	Tone (Probe)	Tone (Probe)
		Flash + Tone (Probe trials)		Flash + Tone (Probe trials)

Note. O1 and O2 were BioServ Purified Pellets and TestDiet Grain pellets, respectively. All probe trials were non-reinforced. FI 5" and FI 20" refers to fixed interval schedules (5 or 20 s).

Table 2
Selective Satiation Test Procedure

Group	Satiation Test 1		Satiation Test 2		Satiation Test 3		Satiation Test 4	
Differential	O1 (1 hr):	Flash (Probe) Tone (Probe) Flash + Tone (Probe trials)	O2 (1 hr):	Flash (Probe) Tone (Probe) Flash + Tone (Probe trials)	O1 (1 hr): or O2 (1 hr):	Flash (Probe) Tone (Probe) Flash + Tone (Probe trials)	O2 (1 hr): or O1 (1 hr):	Flash (Probe) Tone (Probe) Flash + Tone (Probe trials)
Non-Differential	O2 (1 hr):	Flash (Probe) Tone (Probe) Flash + Tone (Probe trials)	O1 (1 hr):	Flash (Probe) Tone (Probe) Flash + Tone (Probe trials)	O1 (1 hr): or O2 (1 hr):	Flash (Probe) Tone (Probe) Flash + Tone (Probe trials)	O2 (1 hr): or O1 (1 hr):	Flash (Probe) Tone (Probe) Flash + Tone (Probe trials)

Note. O1 and O2 were BioServ Purified Pellets and TestDiet Grain pellets, respectively. One of the outcomes was available for 1 hr before each test session. All tests consisted of non-reinforced probe trials.

were constructed of aluminum, and the sidewalls and ceiling were made from clear Plexiglas. The floor consisted of 0.60 cm diameter stainless steel rods spaced 2.0 cm apart. In the center of one end wall 1.2 cm above the grid floor was a recessed food magazine measuring 3.0 x 3.6 x 2.0 cm (length x width x depth). The reinforcers were 45-mg pellets supplied by TestDiet (MLab rodent grain pellets) and BioServ (Purified rodent pellets), and were dropped onto the magazine floor when scheduled. Pilot studies in our lab have revealed that the rats could easily discriminate between these two pellet types, and that selective satiation effects with instrumental responses can easily be obtained when using these reward types. Both of these diets contain similar amounts of calories (3.3 and 3.6 kcal/g, respectively) and similar carbohydrate, protein, and fat profiles, but the BioServ pellets have most of its carbohydrate content coming from sucrose

and dextrose, whereas the TestDiet pellet carbohydrate content primarily is derived from starch. Thus, one of these pellet types is sweet and the other is not. On the inner walls of the recessed magazine were an infrared detector and emitter (Med Associates ENV-303HDA) enabling the automatic recording of head movements inside the magazine. These were located 0.9 cm above the magazine floor and 0.8 cm recessed from the front wall. Located 3.0 cm to the right and left of the magazine and 8.0 cm above the floor were different response levers (4 cm in width). These levers protruded into the chamber at all times, but a sheet metal covering prevented access to the right lever at all times. Access to the left lever was prevented by another sheet metal covering during magazine training, but was available at all other times. Two 28 volt, 2.8 W light bulbs were mounted on the top of the end wall opposite the wall with the food magazine. These bulbs were covered by a translucent plastic sheet angled between the ceiling and top portion of the rear wall that served to protect the bulbs while still projecting light throughout the chamber. When activated, these light bulbs flashed with equal on-off pulse durations at a frequency of 2/s. A Med Associates sonalert module (ENV-223AM) was centrally mounted on the outer side of the ceiling of the conditioning chamber, and was used to present a tone stimulus (2900 Hz, 6 dB above a background level of 74 dB, C weighting, Radio Shack Sound Level Meter [Cat #33-2050]). The chamber was dark except when the visual stimulus was presented. A fan attached to the outer shell provided cross-ventilation within the shell as well as background noise. All experimental events were controlled and recorded automatically by a Pentium-based PC and Med Associates interfacing equipment located in the same room.

Procedure

The rats were initially magazine trained with the two types of pellet rewards. On each of two days, one magazine training session with one outcome was followed immediately by a second session with the other outcome. The order in which magazine training sessions occurred with the two outcomes was counterbalanced across days. In each session, 20 pellets of one kind were delivered according to a variable time 60-s schedule. The two pellet types were delivered to the same food magazine through a Y tube connected to different feeders located near the outside of the food magazine.

Instrumental training. All rats were then trained with continuous reinforcement schedules first to press the lever for one outcome (TestDiet pellets) and then for the other outcome (BioServ pellets). This training was terminated after each outcome was earned 50 times in a single session.

Instrumental peak interval acquisition (phase 1). Over the next 28 days, the rats were trained to earn food on different fixed interval (FI) schedules in the presence of two different discriminative stimuli (flashing light and tone). To facilitate the rats adjusting to the discriminative training schedule, the length of the inter-trial interval was increased from 40 s in the first two days of peak training, to 80 s in the next two days, and then to 120 s thereafter. The stimuli were presented for 60 s on all training trials, but the flashing light stimulus signaled that only the first lever press response occurring 5 s after stimulus onset would be reinforced (FI 5 s). The tone stimulus signaled that only the first lever press response occurring 20 s after stimulus onset would be reinforced (FI 20 s). There were 16 trials of each stimulus randomly interspersed in each session, and four of these 16 for each stimulus were non-reinforced probe trials.

In addition, the rats were segregated into two groups. Group Differential rats were trained with different reinforcing outcomes in the presence of each discriminative stimulus (flashing light–Bioserv pellet, tone–TestDiet pellet). Group Non-Differential rats were trained with each discriminative stimulus signaling reward by each of the two outcomes (randomly determined across trials).

Temporal averaging test 1. Temporal averaging tests occurred over the next eight sessions. These sessions were similar to training sessions, except that there were four additional non-reinforced probe tests in each session in which the flashing light and tone stimuli were presented in a simultaneous compound. Thus, there were four probe tests with flash alone, tone alone, and flash+tone, in addition to 12 reinforced trials with flash alone and tone alone for a total of 36 trials per session.

The next four sessions were conducted under extinction conditions. In each session, there were eight non-reinforced probe trials with the flashing light stimulus, the tone stimulus, and the flash + tone compound stimulus. These data will not be reported as responding overall just generally declined across these trial types, but the patterns did not differ from that seen in the earlier eight test sessions.

Instrumental peak interval reversal (phase 2). This training phase was similar to the first peak

training phase, except that the FI reinforcement contingencies were reversed. Specifically, the flashing light stimulus now signaled reward on the FI 20 s schedule and the tone stimulus signaled reward on the FI 5 s schedule. However, the specific stimulus-outcome assignments were not changed across the two groups of rats. Thus, flash was still paired with the BioServ pellet and tone with the TestDiet pellet in Group Differential, whereas each stimulus signaled that each pellet type could be earned (randomly determined across trials) in the presence of flash and tone in Group Non-Differential rats.

Temporal averaging test 2. These eight test sessions were conducted as in temporal averaging test 1 (except that the reversed FI contingencies remained in effect on all rewarded trials).

Selective satiation tests. Over the next four sessions, the rats were given a set of selective satiation tests (see Table 2). These tests consisted of non-reinforced probe trials only. There were eight probe trials with flash alone, tone alone, and flash + tone (and no reinforced trials) in each test session. For one hour immediately prior to each test session the rats had unlimited access to one of the reinforcing outcomes in separate wire mesh feeding cages. Due to a running error Group Differential rats were sated on the TestDiet pellet in test 1 and the BioServ pellet on test 2, whereas Group Non-Differential rats were sated on these pellet types in the opposite way. During tests 3 and 4, half of each group were sated on BioServ and half TestDiet pellets in each session, with the order counterbalanced across these two tests.

Statistical Analysis. The rate of lever pressing was assessed in each 1 s time bin throughout each 60 s stimulus presentation to give an overall impression of the animals' behavior. More detailed analyses were performed on the peak intervals (i.e., the interval in which the maximal response rate occurred) in the presence of the tone, flash, and tone + flash stimulus compound during test trials. Moreover, in order to assess the width of the resulting peak response distributions, responding in the presence of each stimulus was converted to cumulative probability distributions over time and the intervals containing the 25^{th}, 50^{th}, and 75^{th} percentile of overall responding was recorded for each rat. In order to estimate the width of the response distribution, the interval containing the 25^{th} percentile response was subtracted from the interval containing the 75^{th} percentile response. Finally, in order to determine if the width of these distributions scaled with their means in the presence of the different stimuli the resulting width measure was divided by the interval corresponding to the 50^{th} percentile response. Henceforth, we refer to this as a normalized width measure.

The data were analyzed using analysis of variance (ANOVA) techniques recommended by Rodger (1974, 1975). Briefly, these methods entail reconceptualizing factorial designs (e.g., with I and J factors) in terms of a one-way design (e.g., with I x J levels). For a 2 x 4 split plot form of experiment, for example, the analysis consists of conducting repeated measures analyses for each of two groups, as well as conducting a between group main effect test. If any of these tests achieve significance, then interesting interactions among the conditions and groups are uncovered through post-hoc analysis. This method was chosen over others because the method avoids any ambiguity regarding statistical decisions concerning all of the data to be evaluated and because it is among the most powerful presently available ANOVA techniques at detecting true effects (see also Rodger & Roberts, 2013).

More specifically, the method entails constructing a mutually orthogonal linearly independent set of contrasts (with $\nu 1$ contrasts), post-hoc, for statistical evaluation of all rejected *F* tests. Rejected contrasts are assigned a non-zero value expressed in σ units, $\delta = g\ \sigma\ \sqrt{\Sigma c^2}$ (c refers to the contrast coefficients), whereas non-rejected contrasts are assigned a value of $\delta = 0$. These values are weighted by a factor, g (conceptually similar to Cohen's *d*), that is scaled by the observed size of effect, $g = \sqrt{(\nu_1\ F_h/N)}$ (where F_h is the obtained contrast *F computed by Rodger's contrast formula (1974)*). These statistical decisions for contrasts within a set can then be used to deduce a quantitative description of the relative positions among the population means through Rodger's implication formula:

$$\mu_j - \mu_. = {}_1\delta_h\ ({}_hC_j\ {}_jC_h^T)^{-1}\ {}_hC_j \qquad (1)$$

Each contrast set (${}_hC_j$) with its own set of statistical decisions (i.e., ${}_1\delta_h$ values) gives rise to one quantitatively unique set of implied population means (expressing, in σ units, the difference between each implied population mean from the overall grand mean, $\mu_j - \mu_.$), and reflects a quantitatively precise and clear statement as to the nature of the differences in the data set. These values will be reported here.

Furthermore, once these implied means are computed, then an estimate of the overall effect size, i.e., the amount of variation among the implied population means, can be calculated as:

$$\Delta = N \Sigma(\mu_j - \mu.)^2/\sigma^2 \quad (2)$$

This computed value, Δ, is an estimate of the non-centrality parameter that defines the non-central *F* distribution when the null hypothesis is false. Perlman and Rasmussen (1975) discovered a uniformly minimum variance unbiased estimator of this non-centrality parameter and the implied means calculated by equation (1) above were rescaled to conform to Perlman and Rasmussen's (1975) estimate of this non-centrality parameter. In addition to reporting *F* scores and the implied means produced by this statistical analysis, this measure of effect size, Δ, will also be reported for all rejected *F* tests.

This approach conceives of type I error in terms of an expected rate of rejecting true null contrasts, where Rodger's table of critical *F* values (Rodger, 1974) are the basis of these statistical decisions. It is, therefore, a decision-based definition of type I error, and, in the present study this rate was set to equal 0.05. Using these techniques, the present sample sizes (n = 8) were chosen to ensure that moderately large sized effects (Rodger's g = 1) would be detected with a power level of at least 0.85.

All of the statistical techniques used here can be performed with a publically available software package, "Simple, Powerful Statistics" (see also Roberts, 2011), downloadable from the following website: https://sites.google.com/site/spsprogram/home.

Results

Temporal Averaging Tests

The main results came from the temporal averaging test sessions conducted following the original acquisition and reversal phases (test 1 and test 2, respectively). The data were collapsed across the 8 test sessions after each training phase and are illustrated in Figure 1. Lever responding is shown separately for each group in 1 s bins during the 20 s pre-stimulus periods as well as during the 60 s tests with flash, tone, and the flash + tone compound. It is clear that strong temporal control emerged across both training phases, and that the reversed contingencies were effectively learned. Very little responding occurred in the pre-stimulus periods, and responding rapidly increased and then decreased during the FI 5 stimulus but more slowly increased and decreased during the FI 20 stimulus. Responding generally peaked at approximately the 5 s and 20 s points during stimulus alone test trials, but the FI 20 peak occurred somewhat earlier following the reversal phase. These patterns were observed in both groups. Responding on flash + tone compound trials varied across the two phases. Responding on these compound trials closely resembled responding on flash alone trials after the initial acquisition phase, in which the flashing light signaled the FI 5 schedule. This was true for both Group Differential and Non-Differential rats. However, a pattern of responding on compound trials that more clearly resembled temporal averaging emerged in the tests conducted after the reversal phase, in which the flashing light signaled the FI 20 schedule. In these tests, a third distribution was seen on compound trials in both groups with a peak that was intermediate between those seen on flash and tone alone trials.

These data were quantitatively evaluated in several ways. First, an analysis was performed on peak responding. The intervals containing the maximal response rate were determined for each animal in the presence of flash, tone, and flash + tone, and this was done for each group of rats. The mean peak interval data (+/- *SEM*) are displayed in Figure 2. For the tests conducted following the initial acquisition phase, maximal responding was seen in intervals close to the FI 5 and FI 20 s values in the presence of the flash and tone, respectively. Further, maximal responding in the presence of the flash+tone compound was nearly identical to that seen to the flash (FI 5 s) stimulus alone. However, in the tests conducted following the reversal phase maximal responding during the FI 20 s stimulus (flash) now fairly substantially underestimated the FI 20 s value, but, more importantly, responding in the presence of the flash+tone stimulus compound was maximal at a value intermediate between flash and tone alone. Indeed, these values were close to the arithmetic means based on each rats' flash and tone alone values (cf., 10.2 +/- 1.4 vs. 8.9 +/- 1.1 [obtained value +/- *SEM* vs. arithmetic mean value +/- *SEM*] for Group Differential, and 8.8 +/- 1.8 vs. 9.7 +/- 1.2 for Group Non-Differential).

An ANOVA performed on each group for the acquisition tests (using a pooled error term, $MSE = 16.847$) revealed highly reliable differences across the three test trial types, $F(2, 28) = 32.34$, $\Delta = 58.1$, $p < 10^{-7}$, for Group Differential, and $F(2, 28) = 27.17$, $\Delta = 48.5$, $p < 10^{-6}$, for Group Non-Differential. Overall responding did not differ between the groups (i.e., the main effect of Group was not significant). Further post-hoc tests revealed that peak responding occurred during the same intervals in the presence of the flash and flash + tone stimuli and this interval was much lower than in the

presence of the tone. The specific values of the implied means (in σ units) are indicated in the figures above each data point, and reflect the obtained statistical differences. A similar analysis performed on the reversal phase test data (pooled *MSE* = 9.382) also revealed reliable differences across the three test trial types in each group, $F(2, 28) = 12.06$, $\Delta = 20.4$, $p < 0.0005$, for Group Differential, and $F(2, 28) = 24.58$, $\Delta = 43.7$, $p < 10^{-6}$, for Group Non-Differential. However, in this case post-hoc tests revealed that flash + tone compound peak responding occurred in both groups at an interval intermediate between that produced by tone (FI 5) and flash (FI 20) alone.

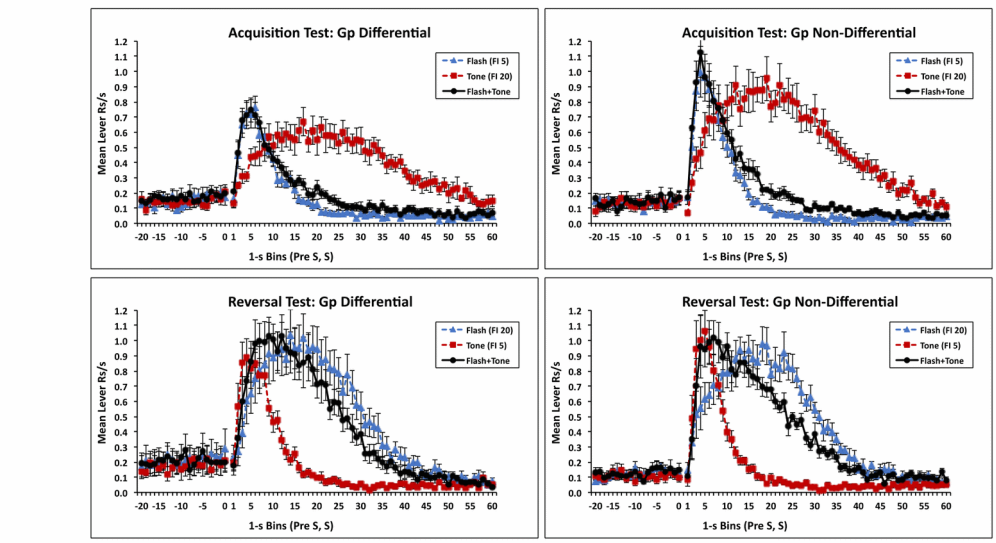

Figure 1. Mean (+/- *SEM*) rates of lever responding on non-reinforced probe tests with Flash, Tone, and Flash + Tone compound trials following acquisition and reversal training in groups for whom the flash and tone stimuli signaled qualitatively distinct rewards either differentially or non-differentially throughout training. Responding is shown in 1 s time bins both during the 20 s immediately before the stimuli (Pre S) as well as in each of 60 s during the stimuli (S).

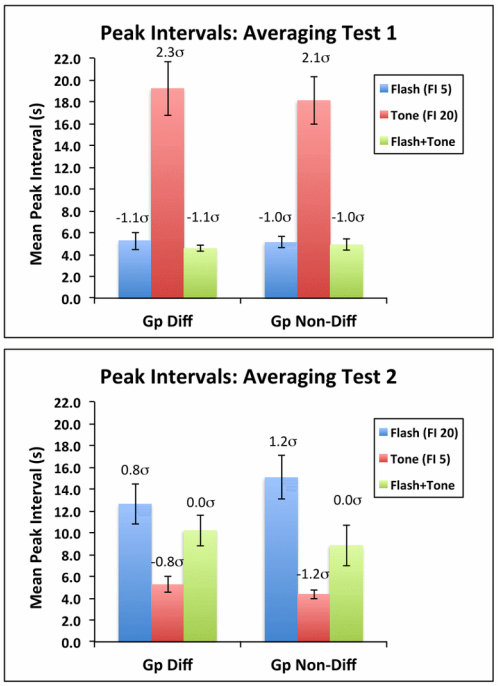

Figure 2. Mean (+/- *SEM*) peak interval responding is shown on nonreinforced Flash, Tone, and Flash + Tone probe trials following acquisition (test 1) and reversal (test 2) training for both groups differential (Gp Diff) and non-differential (Gp Non-Diff). The interval (FI 5 or FI 20) signaled by each stimulus in each phase is indicated in parentheses. The statistically implied population means are indicated in σ units above each data point.

A measure of the width of the distributions depicted in Figure 1 was estimated by computing the interval in which the 25th and 75th percentile response occurred, based on the cumulative probability distribution of responses within each trial type. The cumulative responses occurring across 1 s bins were expressed as proportions of total responses within the stimulus, and then these resulting distributions were used to determine the 25th and 75th percentile responses. Thus, this measure of the width of the distribution is not based on any curve fitting assumptions required by other approaches (e.g., Matell & Kurti, 2014) and is, therefore, purely descriptive. Figure 3 displays these mean cumulative probability distributions and Figure 4 displays the mean width estimates based on these curves for each group during the acquisition and reversal phase tests. In Figure 3, it is clear that the mean cumulative probability response distributions rise at different rates in the presence of the FI 5 and FI 20 stimuli. This reflects the fact that animals responded more earlier on in the interval on FI 5 than FI 20 trials. This was true for both training groups and in both phases of testing. It is also true that in all conditions the flash + tone distributions were intermediate between the other two distributions, though they generally tended to be closer to the flash distribution in both training phases.

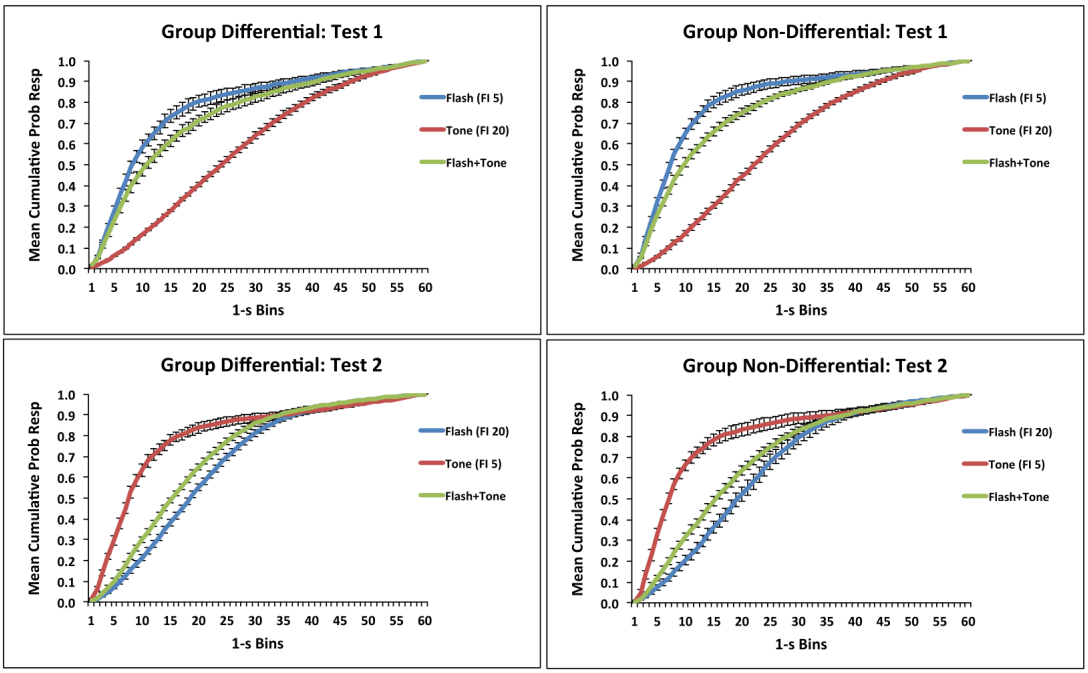

Figure 3. Mean (+/- *SEM*) cumulative response probability distributions across 1 s time bins are shown for both groups (Differential, Non-Differential) on each of the three non-reinforced probe tests (Flash, Tone, Flash+Tone) following acquisition (test 1) and reversal training (test 2).

Whereas the mean width of the distributions (see Figure 4) was greater in the FI 20 s than the FI 5 s stimulus in both phases, the width of the flash + tone compound distribution was intermediate between the other two stimuli in the acquisition test but was no different from the width of the FI 20 s stimulus in the reversal phase test. These data were analyzed with repeated measures ANOVAs performed on each group in the acquisition and reversal phase tests (*MSE* = 10.214 for acquisition and *MSE* = 7.259 for reversal). Significant differences were seen across the three stimuli in Group Differential, $F(2, 28) = 14.23$, $\Delta = 24.4$, $p < 0.0001$, and $F(2, 28) = 12.15$, $\Delta = 20.6$, $p < 0.0005$, and Non-Differential, $F(2, 28) = 22.39$, $\Delta = 39.6$, $p < 10^{-6}$, and $F(2, 28) = 11.02$, $\Delta = 18.5$, $p < 0.0005$, in the acquisition and reversal tests, respectively. Further post-hoc tests revealed that the width of the flash + tone distribution was intermediate between the flash and tone alone distributions in the acquisition test for both groups, but was, like on flash alone (FI 20) trials, wider

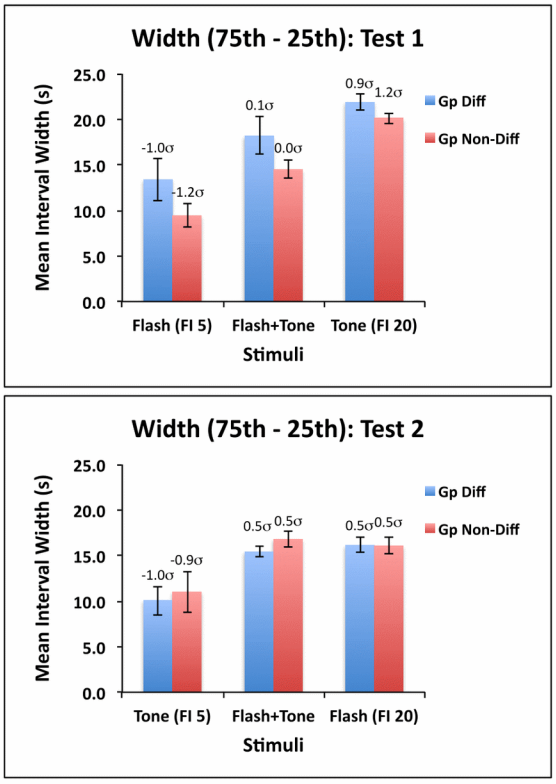

Figure 4. Mean (+/- *SEM*) interval widths derived from the cumulative response probability distributions for both groups (Gp Diff, Gp Non-Diff) on each of the test trials (Tone, Flash, Tone+Flash) in the tests conducted following acquisition (test 1) and reversal (test 2) training. The statistically implied population means are indicated in σ units above each data point.

than the tone (FI 5) distribution in the reversal test in both groups. This is consistent with the distribution being shifted to the left of the FI 20 stimulus on compound trials during the reversal phase.

Finally, in order to determine if the width of these distributions scaled with the means, the normalized widths were calculated for each subject's distributions on tone, flash, and flash + tone test trials. This measure took the distribution width (as defined above) divided by the interval in which the 50th percentile response occurred (based on the cumulative probability distributions in Figure 3). These data are depicted in Figure 5 for both groups in the acquisition and reversal phases. The normalized widths were very similar in both groups for flash and flash + tone trials during acquisition and reversal testing. However, the mean normalized width on tone trials was lower in acquisition (when it signaled the FI 20) and higher in reversal (when it signaled the FI 5) than the other two trial types.

ANOVAs performed on these data confirmed most of these impressions. Group Differential rats displayed significant differences across the trial types in acquisition, $F(2, 28) = 15.94$, $MSE = 0.074$, $\Delta = 27.6$, $p < 0.00005$, but not during reversal testing.

Group Non-Differential rats displayed significant differences across the three trial types in both acquisition, $F(2, 28) = 8.62$, $MSE = 0.074$, $\Delta = 14.0$, $p < 0.005$, and reversal

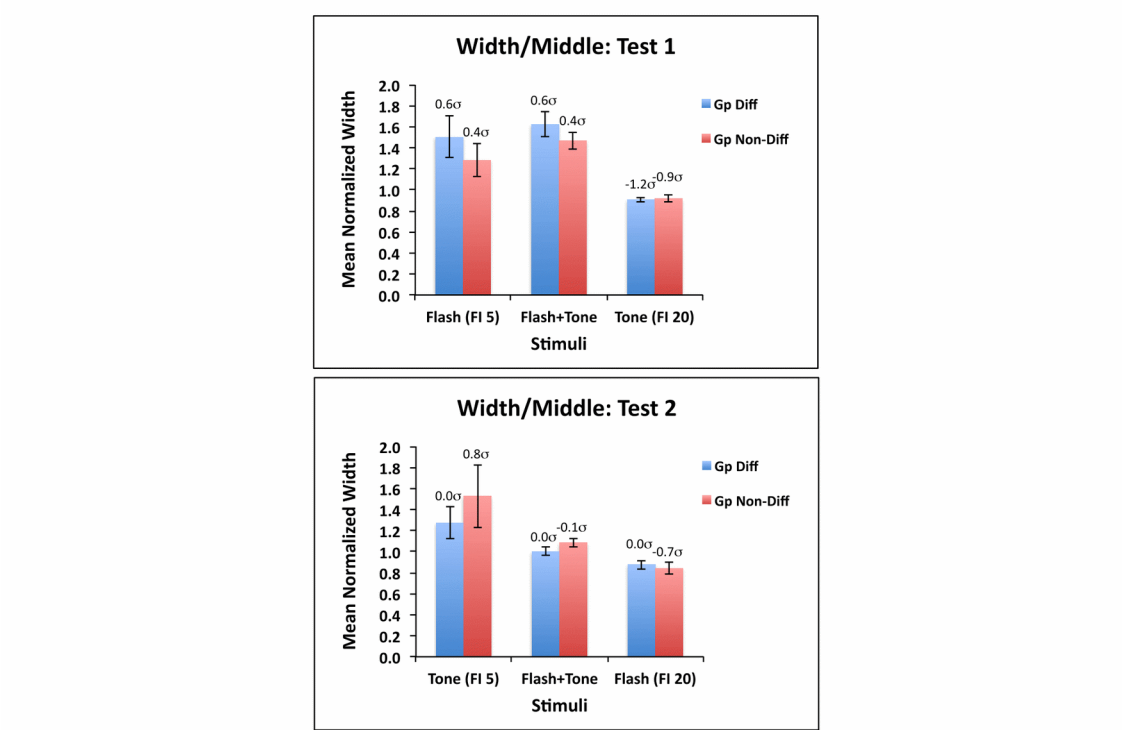

Figure 5. Mean (+/- *SEM*) normalized width values (width/middle) obtained from the cumulative response probability distributions for each of the test trials (Tone, Flash, Flash+Tone) in each group (Gp Diff, Gp Non-Diff) on tests conducted after acquisition (test 1) and reversal (test 2) training. The statistically implied population means are indicated in σ units above each data point.

testing, $F(2, 28) = 7.25$, $MSE = 0.133$, $\Delta = 11.5$, $p < 0.005$. Post-hoc tests revealed that the mean normalized width on tone trials was lower than on the other two trial types, which did not differ, in acquisition for both groups. In reversal testing Group Non-Differential displayed a mean normalized width on flash+tone trials that was intermediate between the other two trial types. Indeed, only 4 of the 16 animals failed to show a slight increase in this measure of the normalized width on flash + tone trials compared to flash alone trials during the reversal phase. This is consistent with the finding that the overall width of the distributions did not differ on these trials, but that the 50th percentile response did.

Reversal Phase Training Data: Group Differential versus Group Non-Differential

An additional analysis was performed on the reversal phase data in order to assess the effectiveness of the differential outcome manipulation. Inspection of the results suggested that Group Differential rats acquired the reversal somewhat more rapidly than Group Non-Differential rats, as would be expected if training with differential outcomes results in an acquired distinctiveness effect between the two stimuli. The data was averaged over 8, 4-session blocks of reversal training. Inspection of the response rate distributions for both stimuli suggested that Group Differential rats

first convincingly began to reverse their response patterns in the presence of the tone and flash stimuli in block 3. Group Non-Differential rats were somewhat poorer in this block of reversal training. These data can be seen in the upper panels of Figure 6. In this block it can be seen that Group Differential rats showed a clear difference in responding during the early and later portions of the probe trials in the presence of the tone (FI 5) and flash (FI 20) stimuli. The early stimulus discrimination was lacking in Group Non-Differential rats.

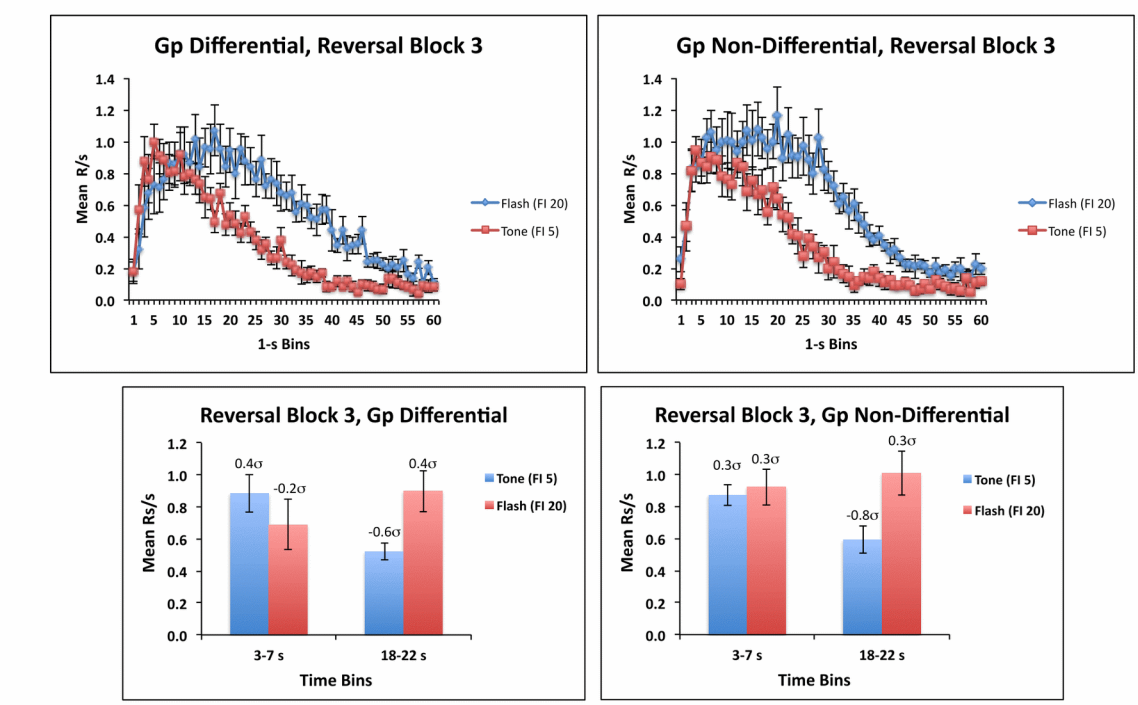

Figure 6. Mean (+/- *SEM*) response rates over 1 s time bins within the stimuli on nonreinforced Flash and Tone probe trials during reversal block 3 for Groups Differential and Non-Differential (upper panel). The lower panel shows mean (+/- *SEM*) response rates on Tone and Flash trials in the 5 s periods surrounding the FI 5 and FI 20 training time bins during reversal block 3 for the two groups (Gp Differential, Gp Non-Differential). The statistically implied population means are indicated in σ units above each data point in the lower panel.

These data were analyzed in the following manner. Responding in the 5 s periods surrounding the FI values (i.e., 3-7 s and 18-22 s) were averaged together and compared during the tone and flash probe trials in block 3. These data are depicted in the lower panels of Figure 6 for both groups. The figure shows that Group Differential rats responded more during the early period on tone (FI 5) trials than on flash (FI 20) trials, but more on flash trials than on tone trials later in the stimulus. Group Non-Differential rats only showed discrimination around the 20 s point on tone and flash trials. One-way repeated measures ANOVAs were applied to each group based on a common error term, $MSE = 0.034$. Both Group Differential, $F(3, 42) = 7.66$, $\Delta = 18.9$, $p < 0.0005$, and Group Non-Differential, $F(3, 42) = 7.66$, $\Delta = 18.9$, $p < 0.0005$, displayed differences across these four conditions. However, post-hoc contrasts revealed that only Group Differential responded more during the tone than the flash in the early portion of the stimuli, whereas, both groups responded more to the flash than tone during the latter portion of the stimuli. These results show that the animals processed the distinct

rewards and that training with differential outcomes facilitates learning the reversal (see also Delamater, 1998).

Satiation Test Results

One final analysis was performed, and this was on the data from the satiation tests. It is possible that responding during the compound stimulus might have been biased one way or the other depending on whether the rats were sated on the early or late reward. To examine this, the satiation test data were averaged over the 4 satiation test sessions, and responding during flash + tone compound trials was examined as a function of whether the rats were sated on the TestDiet grain pellet (the FI 5 reward) or on the BioServ pellet (the FI 20 reward). Since these tests were not fully counterbalanced for the order in which the rats were sated on the two reward types (or for the identity of the rewards themselves), this meant that Group Differential rats were first sated on the early grain pellet (FI 5). Since these tests were all conducted under extinction conditions, it meant that responding was higher in the first test session. In order to examine the effects of satiation, therefore, the response rates occurring in each 1-s interval were expressed as a proportion of maximum responding in order to minimize confounds introduced by different overall levels of responding across the tests. These data are depicted in Figure 7.

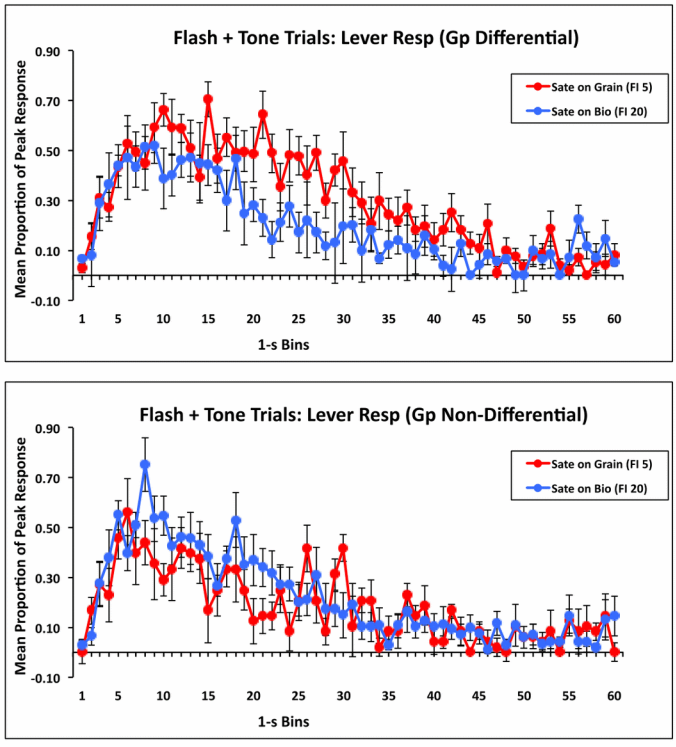

Figure 7. Mean (+/- *SEM*) responding expressed as a proportion of maximum responding on Flash + Tone compound trials for the two groups (Gp Differential, Gp Non-Differential) in selective satiation tests in which the rats were first sated on the TestDiet grain pellet or the BioServ pellet. The grain pellet signaled FI 5 reward availability and the BioServ pellet

Although this data should be regarded with caution, they show that Group Differential rats responded less during the latter portions of the stimuli, especially from about 20 to 33 s when they had been sated on the FI 20 reward (the BioServ pellet). Group Non-Differential rats, predictably, did not respond differently as a function of which pellet type they had been sated. However, it is noteworthy, that responding during the early portion of the stimulus compound did not differ in these two conditions and this suggests that the selective satiation treatment in Group Differential rats exerted a specific effect on the temporal distribution of responding rather than just generally reducing overall response levels. The data were analyzed by pooling over responding during the intervals from 20-33 s. The mean response rates during this period were lower for Group Differential rats when they were sated on the FI 20 reward than when sated on the FI 5 reward (*Ms* = 0.19 +/- 0.03 responses per second vs. 0.42 +/- 0.05). However, Group Non-Differential rats displayed no difference (*Ms* = 0.23 +/- 0.05 vs. 0.21 +/- 0.04). An ANOVA performed on these data revealed a significant difference between the two satiation conditions in Group Differential, $F(1, 14) = 17.37$, $MSE = 0.012$, $\Delta = 13.9$, $p < 0.001$, but not in Group Non-Differential.

Discussion

There were several key findings in the present study. First, we replicated the temporal averaging effect reported by Matell and colleagues (Matell & Kurti, 2014; Swanton, Gooch, & Matell, 2009; Swanton & Matell, 2011) when an auditory stimulus signals a short FI and a visual stimulus signals a long FI. The response distribution on probe trials with the flash + tone compound stimulus was shifted to a point that was intermediate between the flash and tone alone distributions. This point approximated the arithmetic average of the two distributions, although the three distributions did not appear to be scalar as our measure of the normalized widths did not appear to be constant across the three trial types. During the reversal phase the width of the flash + tone distribution in both groups did not differ from that seen on flash alone trials, but their peak times did differ on these trials. A different pattern emerged in the tests conducted following the initial acquisition phase. Like Matell and Kurti (2014; also Swanton & Matell, 2011) we observed that the flash + tone distribution closely resembled responding on flash alone test trials. The same peak interval occurred on these trial types. However, the width of the distribution on flash + tone trials was larger than on flash alone trials even here. This was largely due to the fact that responding was slightly elevated on compound trials at around the time when tone responding was at its peak. Thus, it appears as though in the acquisition tests responding was largely governed by flash, but responding was also affected by tone to a lesser degree. When the flash signaled the short FI and the tone the long FI, responding appeared to be governed by an additive summation process (albeit a differentially weighted one). This conclusion agrees with Matell and Kurti's (2014) conclusion that the visual stimulus is more salient and under such conditions both stimuli will individually contribute to stimulus control. However, when the tone signaled the short FI and the flash the long FI, then the relative salience, or relative *value*, of the two stimuli will be more similar. Under these conditions, the two stimuli are more likely to become integrated with behavior controlled by an averaged temporal expectation.

In addition, we observed that training with a differential outcome procedure had little impact on this temporal averaging effect. Both groups displayed similar results in stimulus compound tests conducted after acquisition and reversal phases. This was in spite of the fact that Group Differential rats acquired the reversed discrimination somewhat more rapidly than Group Non-Differential rats. This difference was most evident during the third reversal block where Group Differential rats responded differentially during both early and late portions of the stimuli on probe trials with the tone and flash stimuli, whereas Group Non-Differential rats had greater difficulty with the discrimination at early portions of the interval. Apparently, rats will temporally average stimuli signaling different times to reinforcement whether those stimuli signal the same reward or qualitatively different rewards, providing that the relative salience of the stimuli is not itself very different. One qualification on this conclusion is that the compound response distributions during the reversal test (Figure 1) show a pattern that more clearly resembles an averaging pattern, at least qualitatively, in Group Differential than in Group Non-Differential. However, this very subtle apparent difference was not manifest in any of the quantitative analyses we provide. Thus, at present we must conclude that an averaging pattern can be seen when training occurs with differential or non-differential outcomes. This finding was not in agreement with our intuition that averaging might be less likely to occur among stimuli that are more differentiated.

Another noteworthy aspect of the current findings was that learning about the specific outcomes did affect temporal control during flash + tone compound trials after selective satiation on one of the anticipated outcomes. Although we must express caution in interpreting these data due to the lack of a complete counterbalancing protocol, it is of some interest that responding during compound trials was selectively reduced in Group Differential rats during the late FI interval after they had been sated on the late FI reward. Because Group Non-Differential rats could not selectively associate different reward types with short or long FI values, this group can be regarded as a control for any non-specific effects of being sated on one of the outcomes. Since this group did not respond differently when sated on the two pellet types, it is more likely that the effect we observed in Group Differential rats was caused by a true selective satiation effect. This means that when rats tend to average two intervals signaled by distinct stimuli, the specific weighting given to the two stimuli can vary depending upon the relative values of the anticipated outcomes. This view is largely in agreement with Matell and Kurti's (2014) view that the relative values of the two stimuli govern whether the elements of the stimulus compound are to be averaged or processed independently. However, our results further suggest that the value of the anticipated outcomes also can importantly affect this process, though more research is clearly needed to substantiate this claim.

The present results can be seen in the context of a more general research strategy that attempts to understand how associative and timing processes might interact to influence learned behaviors (Delamater et al., 2014). We demonstrate here that temporal averaging processes can largely occur independently of a classic associative manipulation, although reversal learning may be somewhat enhanced if different stimuli signal qualitatively different reward types. Exactly how these associative and temporal processes might interact is a matter for future research, but apparently it is important just what reward type is being anticipated as well as when that reward might be expected to occur in learning to discriminate between two different stimuli. However, when all else is equal, temporal averaging may be as likely to occur between stimuli signaling distinct or non-distinct outcomes. On the other hand, if the value of one of the outcomes has been diminished prior to the test, then this could play a role in determining how individual stimuli might be processed during a compound trial.

While it is clear that stimuli can be processed in different ways during tests with compound stimuli, a problem for future research will be to more clearly identify the conditions whereby one processing strategy or another might control performance. As noted in the introduction, when using a procedure that does not lend itself to a specific temporal expectation Andrew and Harris (2011) observed that rats processed two stimuli in compound by summing across the reinforcement rates associated with each stimulus. Yet, in the present studies and in those reported by Matell and his colleagues rats sometimes appear to process the two stimuli of a compound by averaging across two anticipated times of reward arrival. Just why additive summation should occur when specific temporal intervals cannot be anticipated, but averaging should occur when they can, is also a matter for future research. Apparently, the processes underlying the anticipation of a specific temporal interval and of a particular rate of reward are rather distinct processes. Further work will be needed to assess the generality of this claim.

One final point should be made about the theoretical importance of the temporal averaging phenomenon itself. Current associative theories of timing explicitly assume that learned temporal control arises from an inherently associative process whereby time is regarded as an internal stimulus. Specifically, when a stimulus is paired with reward after, say, 10 s, it is often assumed that the stimulus initiates a temporal cascade of temporally discriminable processes. According to this view (e.g., Buhusi & Schmajuk, 1999; Killeen & Fetterman, 1988; Ludvig, Sutton, & Kehoe, 2012; Machado, 1997; Pavlov, 1927; Staddon & Higa, 1999; Vogel, Brandon, & Wagner, 2003) the final temporal process (peaking at around 10 s in this example) that co-occurs with reward becomes most strongly associated with reward and will control behavior as a result. This view has been applied to a wide range of phenomena and can perhaps go a long way towards explaining the results of many key experiments. However, the temporal averaging effect would appear to be in conflict with this approach to timing. Importantly, if two stimuli come to signal different reward times one would expect that compounding those two stimuli to result in control by a summation process. It is difficult to see how such a theory could explain temporal averaging. Perhaps this is the strongest evidence against such a theory.

In summary, we have determined that training on a peak procedure results in temporal control in stimulus compound tests that resembles an additive summation process when a flash stimulus signals a short FI and a tone stimulus signals a long FI, but that temporal averaging appears to occur when these assignments are reversed. Furthermore, we showed that these effects occur whether or not the two stimuli signal two reinforcing outcomes differentially or non-differentially. Nevertheless, we also provide some evidence that the rats processed these different outcomes by showing that reversal learning occurred more rapidly in animals for whom the stimuli signaled these two reinforcers differentially, and we also provide some preliminary evidence to suggest that selective satiation on the late outcome prior to a stimulus compound test appears to bias subjects response distribution toward the earlier interval. These findings replicate prior work on the temporal averaging phenomenon, and extend those findings by showing that the effect occurs more generally when training with multiple reinforcer types. The results speak to the importance of identifying the rules by which stimulus compounds come to influence learned behaviors.

Acknowledgments

The authors would like to thank Sam Edeson for assisting with data collection, and Peter Balsam and Matt Matell for helpful discussions concerning the quantitative and conceptual analyses of the data. Please direct any email correspondence to andrewd@brooklyn.cuny.edu.

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Financial conflict of interest: The research reported here was supported by a National Institute on Drug Abuse and the National Institute for General Medical Sciences (SC1DA 034995) grant awarded to ARD.
Conflict of interest: No stated conflicts.

Submitted: *August 31rd, 2015*
Resubmitted: *October 16th, 2015*
Accepted: *December 1st, 2015*